UNEP

REGIONAL SEAS

J. C. Pernetta and H. I. Manner (eds.):

The ecosystems of small islands in the Southwest Pacific (The sixth expedition of the SS "Callisto")

UNEP Regional Seas Reports and Studies No. 151

SPREP Reports and Studies No. 63

Prepared in cooperation with

SPREP

UNEP 1994

EDITORS' FOREWORD

J.C. PERNETTA[1] AND H.I. MANNER[2]

In mid 1987 the Association of South Pacific Environmental Institutions was asked to consider whether or not the account of the results of the Sixth voyage of the Callisto to various Islands of the South West Pacific was suitable for publication through the United Nations Environment Programme as a contribution to the knowledge of the area covered by the South Pacific Regional Environment Programme.

A preliminary examination of the manuscript indicated that the materials were indeed suitable and valuable but that considerable editorial and scientific review were required prior to the manuscript reaching publishable standard. The Association of South Pacific Environmental Institutions agreed in late 1987 to undertake the task of reviewing, editing and in some areas rewriting the materials for publication and the work was initiated at UNEP's request in 1988.

Each chapter was reviewed for scientific content as originally translated, by a specialist in the field. Each was then subsequently edited either by the reviewer or by the editors or in some instances by both. Both editors considered and reviewed every chapter at each stage of editing. Much of the terminology contained in the original manuscript was archaic and not used in the modern ecological and geographic literature published in English. The editors have therefore attempted where possible to use more modern equivalents, although in some instances the absence of a direct equivalent has led to the original term being retained.

The following people made substantive contributions to the editing and reviewing of various sections: From the University of the South Pacific, Dr P. Nunn, geomorphology; Professor J. Morrison, soils; from the University of Guam, Professor L. Raulerson, botanical biogeography; and Dr I. Schreiner, leaf beetles. Professor F. Kilmer of the University of Guam and Professor P. Hughes of the University of Papua New Guinea provided advice and assistance in a number of areas. One of us (JCP) took overall responsibility for reviewing the animal sections and one (HIM) responsibility for the botanical/geographical sections. Any errors arising from the editing process remain however the responsibility of the overall editors. We are also grateful to Dean David Gillespie, Mss. Rosa Muna, Carmen Santos, and Thelma Sarmiento of the University of Guam's Graduate School and Research for their support, and to Dr. Lu Eldredge of the Pacific Science Association for help with the references. In Moscow, I (HIM) am very appreciative of the warm hospitality of Drs. Vadim Skulkin and Timofei Zatsepin, Alexey Sankovsky and Nadezda Drozdova, and Professor Yuri Puzachenko.

The document is an important contribution to the literature of the South Pacific region and represents a significant breakthrough in scientific communication. Numerous expeditions have been undertaken to the Pacific by both Russian and other research vessels and frequently the results are published in languages which cannot be widely read in the region itself. This report, originally written in Russian is now available in English and as such is more accessible to the people living and working in the region. A number of the approaches and views expressed in this document provide interesting and novel insights into the nature and functioning of the environments of the region and may serve as a stimulus to further work on the islands of the world's largest ocean.

John C. Pernetta & Harley I. Manner
Guam, August 1991

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AUTHORS' PREFACE

V. Y. SOKOLOV, Y. N. BADENKOV, AND Y. G. PUZACHENKO

BACKGROUND TO THE ORGANIZATION AND IMPLEMENTATION OF THE SIXTH EXPEDITION OF THE SS "CALLISTO"

A working meeting of the All Union Co-ordinating Group of Project 7 "Island ecosystems and their rational use", a project in the UNESCO "Man and Biosphere" (MAB) Program was held in Vladivostok in May 1978. Following discussion and amplification of the many program documents the meeting identified a number of scientific problems, in particular the need for research on islands in the equatorial/tropical regions of the world.

The agreed need for such research was based on the following points:

1. A basic understanding of the organization, interaction and functioning of biotic and abiotic systems is impossible without a thorough knowledge of equatorial-tropical examples. Any model or hypothesis based solely on research on temperate islands would be incomplete if it failed to incorporate and also explain data from tropical systems.

2. An understanding of the problems of island ecosystems is of great importance as a basis for developing ideas concerning the effects of time and space upon the structure and functioning of the biotic and abiotic components of the environment. The concept of an "island" can be expanded and applied to restricted areas or communities ("habitat" islands) *sensu* MacArthur & Wilson (1967), having different characteristics from those of the surrounding environment(s). Such areas or territories exist on continental land masses, frequently being the direct result of anthropogenic activity. Rational use and sustainable development of such areas involve close examination and control of economic as well as environmental problems. Within the tropics one finds a variety of islands, illustrating different environmental conditions which thus provide promising experimental systems for research.

3. Many islands in the Pacific have been well studied, however the data have been collected by scientists from different disciplines and schools of thought. It is therefore often difficult to interpret such data without personal experience of the environment in question, and on the islands concerned. The Soviet school of geography and ecology uses approaches which differ from those of scientists elsewhere; approaches developed on the basis of large and complex expeditions to remote and extensive territories which resulted in the development of new ideas concerning the relationships between environmental components. It was anticipated that the participation of Soviet geographers in an expedition of this kind would throw new light on the functioning of island ecosystems.

4. Finally, similar research work carried out by geographers participating in the sixth expedition of the SS "Dmitriy Mendeleyev" in 1971 had resulted in the identification of some promising avenues for further research.

Recognizing these points the Pacific Institute of Geography of the Far-East Scientific Center of the USSR Academy of Sciences laid plans between November 1976 and March 1977 for a specialized island expedition undertaken within the framework of Project 7 of the National Man and Biosphere Program. The leading Soviet scientific research institutions involved in ecological and geographic studies of ecosystems, environments and their components took part in the planning and implementation of this expedition.

A large number of experts were invited to assist in designing the preliminary program, the scientific workplan and the itinerary of the expedition. Numerous alternative hypotheses concerning the structure and functioning of island ecosystems were considered and discussed, and different approaches were ultimately integrated to provide an optimal program. The research was to center on the structure and functioning of particular island systems at different scales of investigation.

Based on available current theories and general concepts, it was postulated that the structural and functional interaction of the systems to be studied would be determined by the following factors:

1. Island size.
2. Island age.
3. Geological structure.
4. Evolutionary history.
5. Remoteness from the colonizing source.
6. Patterns of rainfall and relative humidity regimes.
7. Temperature regime.
8. Anthropogenic effects.

Considering all possible combinations of the factors listed above and using a latin square approach, it was determined that the expedition would have had to investigate a minimum of 28 islands, a task which was impossible to accomplish during one expedition. In addition it is well known that not all possible combinations of the above factors actually occur in nature; therefore in compiling the expedition itinerary the following additional points were taken into account:

1. The relative importance of each of the factors listed above.
2. The selection of islands to cover as much of the matrix of possible conditions as was practicable.

In this way small islands with an area of less than 50 square kilometers were identified as the main objective for investigation. This selection was made because it was actually possible within a three to five day visit to identify the basic patterns of the island's ecosystems and because such small islands have been little studied previously. Some basic parameters for the islands visited are presented in Table 1, and a map of the cruise route is presented in Figure 1.

Taking into account the difficulties of arranging visits to these islands the original intention was to have several replicates of each "type" of island. During the expedition it was possible to investigate a group of islands which largely corresponded to those categories identified in the preliminary plan. Large islands were studied by means of available literature and through personal investigations by expedition members during their excursions to these islands.

The small islands selected were of two basic types; volcanic and atolls. One island composed of metamorphic rocks was also investigated. Geologically all of the islands belong to the oceanic and transitional zones of the Pacific, and the majority are at the same distance from potential sources of colonizers. In general all of the islands were similar in terms of their rainfall patterns though they differed in their temperature regime and geological age. The expedition examined the islands' structural characteristics, while the functional interrelationships between the various elements were studied as secondary objectives. It proved possible to investigate three aspects of each island: its landscape; the geological facies; and the biological community. This approach provided on the one hand, a relatively complete description of the island in question and on the other, a good correlation between the materials under study.

Table 1. Location and morphometry of the islands visited by the Callisto.

Island	Proximity To Nearest Landmass (km)	Area (km²)	Size L x W (km)	Height (m)	Slope Steepness ° Inclination
Bagaman	205 to New Guinea	8	5 x 2.5	219	0 - 10; 30 - 50
Pio	22 to San Cristobal	2.5	2.6 x 1.4	34	0 - 2; 15 - 32
Norfolk	780 to New Zealand	34.1	9.5 x 5.7	318	2 - 10; 15 - 25
Raoul	1000 to New Zealand	29.2	10.5 x 6.7	516	30 - 50; 50 - 90
Niuafo'ou	425 to Samoa	18	8.5 x 8	260	2 - 7; 15 - 30; 50
Suwarrow	832 to Samoa	0.4	15.5 x 17.5	4	
Pukapuka	645 to Samoa	3.8	9 x 4.5	5.5	

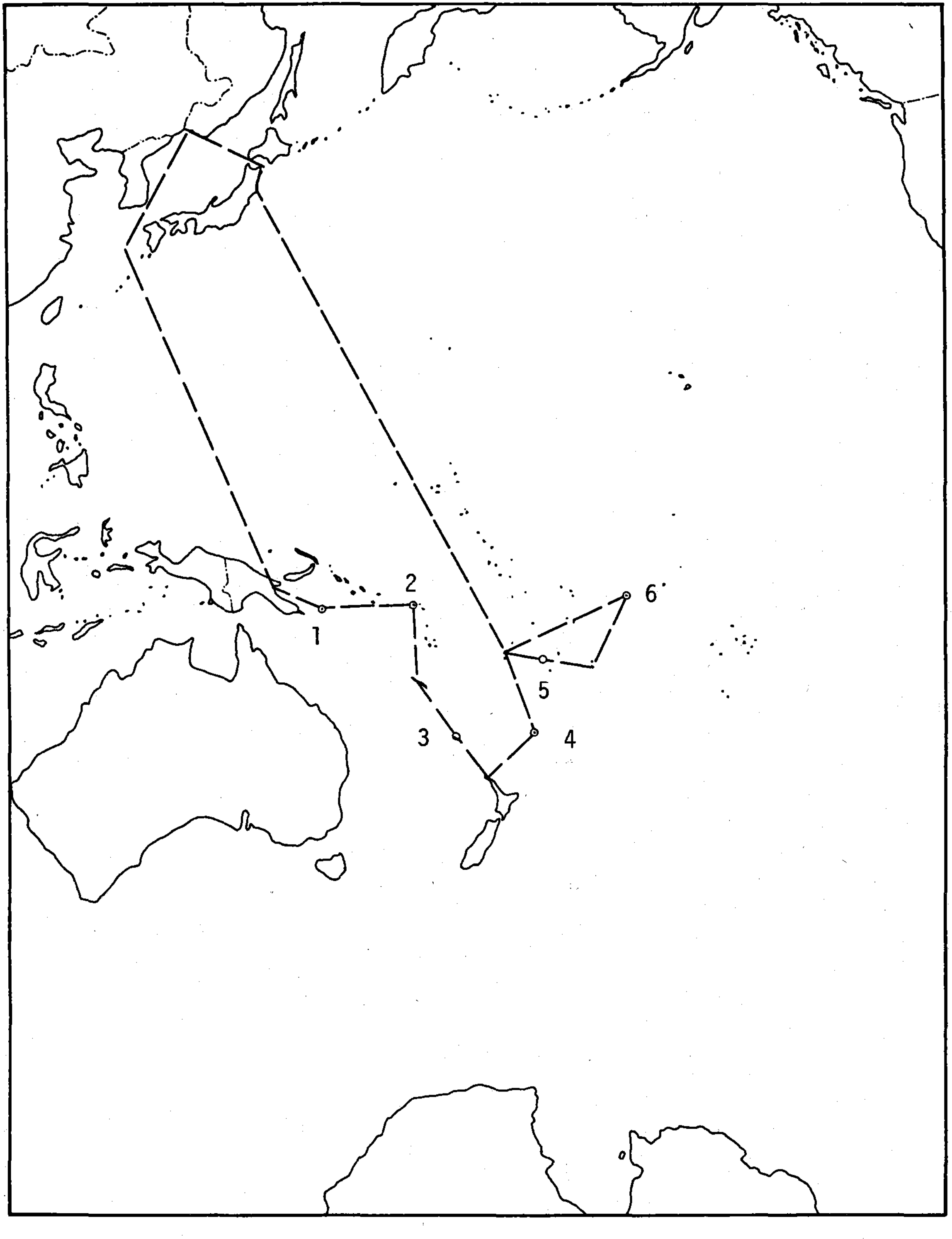

Figure 1. Route of the sixth voyage of the SS Callisto. Islands visited are indicated as follows: 1, Bagaman Island, Louisiade Archipelago; 2, Pio, Solomon Islands; 3, Norfolk Island; 4, Raoul Island, Kermadec Archipelago; Niuafo'ou Island, Tonga; 6, Pukapuka Island, Cooks Islands; Suwarrow Atoll, Cook Islands.

ACKNOWLEDGEMENTS

Y. G. PUZACHENKO

The event which resulted in this monograph, the first voyage of the scientific research ship "Callisto", was unique. This voyage was devoted to the task of studying the ecology of the small islands in the Pacific Ocean. This attempt was initiated by A. P. Kapica, the head of the Soviet Far East Scientific Center. Until that time, the Russian scientific ships worked only in the open seas, and changing this tradition was difficult to overcome.

There were many obstacles which we had to overcome, making this monograph, indeed, a minor miracle. To begin, the presence of Soviet ships in the Pacific has never been taken lightly. The majority of the Pacific island governments consider them as spy ships, making their ports of call an adventure. Our technical equipment was not very new or reliable. In fact, our most complex instruments were radar and a depth sounder which, however, didn't work during most of the expedition, particulary when the ship was close to landfall.

Few of us had any idea of the islands of the Pacific. All the islands that we eventually visited were selected using inappropriately scaled maps with obsolete and often erroneous navigational information, while we were still in Russia. Despite the poor information, but perhaps overshadowed by our romantic imaginations of these islands, we selected the islands of our expedition, several months before our voyage. To our surprise, our choices proved to be very appropriate.

The 1970s was the period of detente and the establishment of a new world order. Russian visitors to the Pacific islands were unique and attracted a lot of local attention. We would like to note that in most cases, we were accepted with great warmth and were given everything that we needed to accomplish our work. We therefore, thank the administrations of the islands we visited, the local scientific organizations and all the people who helped us. We will treasure the memories about these people for the rest of our lives. Without their unselfish assistance, we could not have solved the smallest of our problems. Of course, there were some variations to the rule. On Papua New Guinea (Vauvau Station), we were met by the representatives of the Australian intelligence service. Fortunately, alcohol worked well to ease tensions and allay their suspicions. Perhaps, for fear of their lives, the women of Niuafo'ou island preferred that their husbands stayed on land. A day after our arrival there, our main duty was to reduce the number of parties and festivals both on and off the ship.

We acknowledge with thanks, the crew of the "Callisto", who helped us, not only during the landings, but with our scientific work as well. The male sailors cleared the transect pathways of vegetation, while the female sailors wrote our notes of the islands' vegetation. For all of the expedition members, these were without doubt, the happiest days of our lives.

With this voyage, scientific expeditions into the Pacific became a tradition. The 12th and last voyage of the "Callisto" was made in 1978 to the islands of Tonga and Western Samoa. These were followed by special expeditions to the Seychelle and Vietnamese islands. While many of the research materials have been published in Russian, few have been published in English. Because of its significance, we believed that it was necessary to make this monograph available to the English reader. Fortunately, UNEP supported this idea and this monograph is the result.

There were still many other problems. The first problem concerned the translation. Unfortunately, each language is very specific and many widely used scientific words have slightly (or completely) different meanings in different languages. Although our interpreters were specialists in the different areas of science, they were sometimes confused by the peculiarities of scientific terminology. The situation was complicated by the "island" character of Soviet geography; some of our specific scientific terms have no equivalence abroad. We thank our interpreters for their efforts, acheived under trying circumstances, and our English speaking editors who did a great job to make this monograph available to the wider scientific reader.

However, the process of translation and editing has been pretty long, with the text traveling a lot across the Pacific. Finally, the text found its last "father" - Professor Harley I. Manner of the University of Guam. Professor Manner agreed to undertake the most difficult part of the work and finalize the monograph. During this final state, we realized that Guam is fairly distant from Moscow, and the airline and other connections between these two places are far from perfect. The organization of two meetings between the Russian and English editors has taken two years to accomplish as desires did not coincide with the opportunities.

Finally, we hope that our work can present new information and ideas about the ecology of the small islands of the Pacific Ocean. These islands are important models for the question of biodiversity preservation. We hope that our work will attract other scientists and applied specialists to working in these often neglected islands.

For the authors of this monograph, I thank everyone who took any part in it. I send my best wishes to all of them.

Professor Y. G. Puzachenko
Moscow, July 28, 1991

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* Deceased

CHAPTER I. MATERIAL AND METHODS OF RESEARCH

Y. G. PUZACHENKO

INTRODUCTION

The main objective of the expedition was to compare as large a series of islands of different climatic conditions, ages and geological origins as possible. This necessitated short visits to each selected island. The structure and components of the ecosystem under study were the focus of attention, while their functioning was considered to be of secondary importance.

This approach determined the use of appropriate research methods, which permitted collection of the maximum possible information on the structure of each area within the relatively brief time spent on its investigation. Obviously the most practical approaches in terms of time expended are the purely descriptive methods of geography; however, such methods are usually subjective, because their quality and completeness largely depend on the viewpoint and position of the researcher involved. Quantitative methods, which are necessary for (making) correlations, are frequently very time consuming.

In all cases the preferred methods were those which permitted objective characterization of the component under study within the shortest possible time. In this respect for example, a wide-angle lens was used to photograph the projection of crowns, and to take views of coasts; automatic systems to record the solar radiation, soil pH and other physical parameters were used. For most of the components a "hierarchy of methods" was used, including general qualitative descriptions; semi-quantitative estimations; and quantitative methods. While employing a detailed quantitative technique, all characteristics obtained through less detailed approaches were recorded. Such an approach yielded sufficient material for comparison and at the same time provided a broad picture of the spatial variations in geology, physical and biotic components.

Special attention was paid to selecting those parameters which could be typologically correlated, in order to provide accurate quantitative comparisons. For example, all the islands were described in terms of their inter-tidal and geological facies; and relief in terms of slope variations were detailed for two or three locations of similar exposure.

In this way, the combination of methods and techniques employed to examine each component, as described below, yielded very diverse but comparable information although the time allocated for our investigations was rather short.

GEOMORPHOLOGICAL STUDIES

The conditions under which the geomorphological work was undertaken were dictated by the ecosystem investigations which required detailed information about the general geological and geomorphological parameters of the islands. In view of this, the areas under examination were primarily described by means of geomorphological sketch maps. To prepare these maps, all islands were crossed by as many geomorphological traverses as possible. The traverse routes were selected after study of the available maps, aerial photographs and literature, and were chosen to reveal various types of relief; to identify the main relief-forming factors, the age of the landscape and the geological structure of the islands. In the field the geomorphology of the area involved was recorded, as was the composition of the basement rocks, which were sampled. Rock outcrops were examined and the angles of slopes and the directions of valleys and watersheds were recorded by means of surveying compasses and elevation meters. Particular attention was paid to loose coastal deposits, in order to reveal the pattern of relative vertical tectonic movements of the shore line of the islands. Microbar levelling (see below) was used to study the spatial structure of complex profiles. In addition to these studies, small scale underwater geomorphological observations were also carried out. A summary of the geological characteristics of the islands is presented in Table 2.

Table 2. Main geological features of the islands.

Island	Structural Position	Structure	Rocks	Age (Yr)	Tectonic Movement	Relief
Bagaman	Continental(?)	Fold	Metamophosed schists	0-10 million	Sinking	Erosional Medium dissected
Pio	Continental(?)	Reef platform	Coral limestone	50-60 thousand	Rising	Biogenic Undulating (rolling)
Norfolk	Oceanic ?	Volcano	Basalts	2-3 million	Stable ?	Erosional Weakly dissected
Raoul	Transitional Zone	Volcano	Pumice Sands, Ash Breccia	2 thousand	Stable ?	Erosional Strongly Dissected
Niuafo'ou	Oceanic	Volcano	Theoleiitic basalts, Ash	100	Stable ?	Volcanic cone
Suwarrow	Oceanic	Atoll	Coral sand Limestone	2-4 thousand	Sinking	Biogenic-rolling
Pukapuka	Oceanic	Atoll	Coral limestone	2-4 thousand	Stable ?	Biogenic-rolling

During this work, samples were collected to identify the absolute age of the relief by means of isotope geochronology. In total, 26 samples were collected from almost all the islands studied.

As a result of these investigations, geological and geomorphological descriptions of the islands, and geomorphological maps, were compiled.

SOIL CHEMISTRY

In the main, soil research was based on descriptions of reference sections and on sampling cores from typical horizons. Reference sections were usually 1.5 to 2.0 m deep, depending on the actual structure of the particular soil profile. These sections were made in flat areas where the effects of slope perturbations were small. The location of sections was chosen on the basis of field reconnaissance undertaken together with experts on other components of the ecosystem, and with regard to the available literature on the history of each island and its structure. When found on the transects, natural outcrops were examined and described and additional soil core samples were taken. Additional representative soil sections were taken in order to describe the spatial heterogeneity of the soil, and the variation in soils developed over the slopes.

In general, soil descriptions were based on conventional methods; the thickness of each horizon, was measured; the color of the soils described according to Munsell's Atlas; and structure, texture, mechanical composition were recorded, as was the presence of inclusions. In the field, individual soil sections were examined for their macro- and meso-morphological features using field microscopy and the "organizational" analysis of soil cover. Similar investigations of some samples were carried out in the ship's laboratory.

When soil samples were taken from points along the vegetation transects, a simplified scheme for their description was employed, including results of *in situ* tests of the pH value and hardness of soil. Certain individual sections, which were selected as typical of the area, were sampled for later laboratory analyses and comparison. The volume of the samples permitted a wide range of soil tests and analyses typical for modern soil science, to be carried out.

The combination of the field methods used in our research made it possible to formulate and, to a great extent, verify current views on the processes of soil formation in the tropics in general and on the islands within the tropical belt, in particular.

Investigations of water chemistry on the islands, were rather difficult to undertake. In the first place, because permanent water courses proved to be extremely rare, and secondly during our work on the islands there were no rains at all, it was impossible to sample water from temporary water bodies. Nevertheless, whenever and wherever possible, samples of surface water for subsequent analyses in the ship laboratory were taken. Analysis was undertaken to determine such parameters as pH, HCO_3^-, Cl^-, O_2, Ca^{++}, Mg^{++} concentration. In addition, surface and abyssal water in lakes, volcanic calderas and wells on the atolls were sampled.

FLORISTIC ANALYSIS

To obtain the best possible idea of the total flora of each island, samples of each taxon were collected for later identification. For flowering plants, fruits and flowers were collected where possible; grasses were collected complete with their underground organs. Herbarium sheets for each species were carefully prepared; where a species was large two herbarium sheets were compiled and samples were preserved in alcohol in the field. Whenever possible, local experts helped to identify the plants and in this way, field determinations were made of the bulk of plants collected on Norfolk Island; the tree species from the Kermadec Islands; and all plants down to the generic level on Viti Levu, Fiji.

Some species collected in the soil profile test areas are still undetermined. In such cases the sampled plant was assigned the same number or symbol as in the description of the test plot, so that following later identification it would be possible to relate the species name to the area. In addition to traditional morphological features other characteristics such as the patterns of the bark of trees, were also recorded. Some plants, particularly those on atolls, were familiar to A.G. Voronov from a previous expedition and in such cases their names were immediately included in the descriptions of the test plots and samples added to the herbarium collection.

The vegetation was characterized on test sites and during all reconnaissance surveys and vegetation transects. The routes for vegetation surveys were chosen on the basis of the distribution of vegetation cover and of relief features which had been identified initially from the available cartographic and aerial photographic materials. The vegetation cover of the islands was examined initially from on board the ship, or by small boat. On the basis of such an examination, vegetation features and patterns were identified enabling the selection of characteristic areas for establishing test sites.

During reconnaissance surveys the patterns of vegetation succession and plant communities were related to external factors such as relief, (in particular the steepness and aspect of slopes), altitude, the shape of the slopes, the pattern of the micro-topography; proximity to the sea; and anthropogenic effects. Preliminary identification of sites for future quantitative description was made.

Occasionally, a particular site was felt to be rather interesting in terms of its vegetation, and was described immediately in case a further visit might be difficult to accomplish. Sites were described in cases when the areas and/or the outline of the plot under the community in question did not permit the establishment of a test site there, or when the time for any detailed description of the test site was obviously too short. In describing such plots it was impossible to calculate plant density or compute the relative importance of different taxa, however all other features of the formation were specified both on the test sites and on the natural areas.

The descriptions of plant formations were made using the standard methods adopted by the Pacific Institute of Geography of the Far East Scientific Center of the USSR Academy of Sciences and at the Geography Department of Moscow State University. Special attention was paid to the following features of the plant community: stratification of landscapes and relief, species composition, canopy layers of the vegetation; in the case of tree storeys, the degree of canopy closure; for grasses, in addition to the percentage cover of each species, abundance was determined in accordance with Drude's scale. The presence of lianas and epiphytes was noted. The undergrowth was assessed within sample plots and specified in two or three height classes. Using Bitterlich's device, we determined the total areas of tree trunks (forestry density). In addition the extent of the undergrowth, its cover, and the composition of the litter-fall were determined. The descriptions of vegetation cover were usually accompanied by soil descriptions which were made by the members of the landscape group.

When describing vegetation cover in the tropics and subtropics it is sometimes necessary to describe certain trees individually; as an example, one may cite huge individual rubber trees, *Pohutukava* (*Metrosideros*), and *Pisonia*, which differ from all other individuals of the species on the sample plot in terms of their community and number of epiphytes, and lianas; or in their size, pattern of growth, and other features. For this reason, descriptions under such conditions are much more difficult to complete than those of typical plots of conifers, deciduous and mixed forests in the temperate zone.

When describing the early stages of vegetation succession as for example along the sea coast, or on the bank of Green Lake on Raoul Island, or across the lava fields on Niuafo'ou, we recorded the width of the zones and determined the species composition, structure and abundance, as well as the vegetation cover at different stages of its development. In this way, our botanical investigations were made at three levels of precision: the most general description was used for reconnaissance surveys and in preparing transect profiles; more detailed characteristics defining separate vegetation layers on some limited plots; and detailed analysis of sample plots totalling 200 to 400 m^2 calculated on the basis of sub-units of 25 to 100 m^2. In addition to the estimates employed in the general description of sample plots, account was taken of maturity and the state of regeneration of the principle species in the forest.

Crown projections for each quadrat under investigation were also surveyed by means of a wide-angle lens with 130° aperture along an inclined plane. Such photographs were useful in detailing the structure and density of the canopy, and in calculating the penetration of solar radiation (Anderson, 1966).

In addition, trees from young and medium-aged stands were examined, and trunk sections of 0.5 m length, were collected for further weighing, ash analysis and calorimetry. Although the number of our samples is not great, practically no information exists in the literature for such parameters, despite their great importance in understanding the passage and storage of energy in natural communities.

FAUNAL METHODS OF RESEARCH

As a rule, zoological investigations were designed to reveal the numbers and distribution of various functional-trophic groups of animals. The most feasible studies for expeditions are investigations of animals and communities whose life-span is short. Such animal groups may yield sufficiently representative data even within rather brief time intervals to provide an understanding of the dynamic components of an animal community of herbivores and their predators. One must be familiar with the population dynamics of the individual species and their reproduction, since without such information the dynamics of the animal community will be difficult to interpret. In this connection, our zoological research was chiefly focused on soil invertebrates which play a very important role in the community. In addition to these main investigations, invertebrates inhabiting grass stands were recorded as were those in dead tree trunks in different stages of decomposition. The numbers of inhabitants of epiphytic micro-habitats and tree crowns were also examined. The reptiles in such micro-habitats were also examined quantitatively as was the species composition of birds and amphibians, and their abundance.

The methods used to quantify estimates of the numbers and biomass of different groups of animals were those adopted for "The Program and Methods of Biogeocenological Investigations, "1974 with some modifications devised for the expedition at the Institute of Geography of the USSR Academy of Sciences (Zlotin and Khodashova, 1974; Zlotin, 1975). In view of this, the data collected by our expedition can be easily compared with similar data for the plain and mountain ecosystems of the temperate belt.

Medium sized soil invertebrates were collected by hand sorting of soil samples, and the microfauna (microarthropods, nematodes, enchytraeids) by funnel extraction techniques. The depth of excavation was regulated by the depth of soil invertebrates' distribution. The accuracy of estimates of such soil fauna is high, the standard error for expedition samples varied between 20 and 30% of the mean. Surface active arthropods were recorded by means of soil traps.

Our estimates and visual records of the invertebrate numbers yielded approximate data on the biomass of individual taxonomic, stratigraphic and trophic groups of animals and the total faunal biomass.

The set of methods used for zoogeographic research did not differ from that employed in the community studies, except for their relative importance. Quantitative estimates, were less important, while broad studies of the area, involving not only typical but also unique habitats were employed; this approach was employed for each island visited. Despite the fact that our observations were made over short time frames, the information gathered on local faunas proved to be quite extensive.

During our zoogeographic investigations special attention was paid to an examination of sub-littoral habitats; deadwood; stream valleys and grassland communities. At the same time observations and collections of various samples from more typical habitats were also made. Easily compared semi-quantitative estimates of animal abundance were frequently made by visual observation during the expedition. When no complete collections were made, such visual semi-quantitative estimates were provided for birds, for a range of phytophagous insects and some insect-predators. The numbers of rodents were assessed using traps, however, this did not prove as effective in the tropics as it has in the temperate zone. Nocturnal insects were sampled by attracting them to lights. In this way, using a combination of methods, we were able to obtain easily correlated quantitative information for the most interesting faunal groups of the ecosystems under study.

SURVEYING OF THE AREAS

As already mentioned above, the particular and typical habitats for each island were simultaneously examined by geologists, botanists, zoologists and pedologists. In this way it was possible to record the ecosystem at both the broadest and most detailed level, as completely as possible. The second, less detailed level of investigation was undertaken through profile studies of the area concerned. During such profile studies, work was undertaken as follows:

1. A measuring tape was laid, preferably across a basic geomorphological structure (along a slope; across an atoll island from the ocean towards the lagoon, and so on) and a transect was established, varying in length from 500 to 1400 m. The island outlines and approximate location of the transects are presented in Figure 2.

2. At ten meter intervals, and at points of abrupt change in slope the atmospheric pressure was measured by means of a microbar levelling instrument, (accuracy within ± 30 to 40 cm standard error). The forest canopy at each levelling point was photographed and the height of the stand was assessed visually.

3. Every 30 m, the vegetation and the soil surface were described, and small soil pits were dug. The following floristic parameters were measured for each layer; stand height; species density; total crown closure; species composition; height of crown attachment; herb layer height; and the development of lianas and epiphytes and their composition.

On Pio island very large trees within a 40 m wide zone were mapped. Thus, by taking into account overlapping photographs, the forest structure was scanned almost totally. The 30 m distance between the descriptions made it possible to assess the spatial elements with linear dimensions over 60 m and permitted the analysis of the spatial structure both qualitatively and quantitatively. As a result, the continuity and discreteness of habitat boundaries, the linear dimensions of homogeneous formations and the extent of their homogeneity; the mutual contiguity of all components of the community, and individual features of the components, were all examined. Based on these data, a reliable and easily compared estimate of the spatial organization of the terrestrial community was obtained.

It should be noted that some of the more detailed descriptions of the ecosystem were effected within the profile, providing direct correlation between the detailed plot studies and the transect observations.

Landscape investigations involving correlated studies of the relief, soils, vegetation and other components were based on mapping of all communities. Each community or "territorial complex" is defined as a section of the overall area within which all landscape components were found to be similar to one another; that is the smallest unit which is homogeneous in terms of the properties of its natural components.

The task of the landscape investigations was to determine the main patterns of spatial differentiation of nature on islands. To accomplish this task, the landscape research planned to: co-ordinate the various types of studies (geomorphological, pedological and botanical); to establish the boundaries of the natural territorial complexes; and to map them. All field work, included three stages:

preliminary survey; work on reference plots; and transect mapping.

PRELIMINARY SURVEY (RECONNAISSANCE)

This aspect was accomplished by a geomorphologist, a botanist and a pedologist, who identified the most important types of natural communities, made a preliminary examination of them and established their boundaries.

RESEARCH ON REFERENCE PLOTS

These plots were described in detail and sampled by soil scientists and botanists. Our landscape investigations were able to establish the boundaries of the appropriate landscape units and to examine the microstructure of soil cover.

LANDSCAPE MAPPING

At this stage the sub-components of the natural communities were studied, by transects describing the vegetation; soil sections and soil pits; and by sampling plants, soils and rocks. Field mapping of the community boundaries was also undertaken.

The level of detail possible in the landscape investigations depended on the availability of maps; the dimensions of the island in question and the length of the visit to the island. From these data, we compiled either landscape schemes or landscape maps as follows (see Table 3 for summary):

1. Landscape observations of the local communities, without any mapping were made on Guadalcanal island in the vicinity of the town of Honiara and on New Zealand in the vicinity of Auckland; on Viti Levu, Fiji; Niue and Motu Koe (Pukapuka Atoll).
2. Landscape sketch maps were produced for the area near Lae in New Guinea; for Bagaman Island in the Louisiades; Pitt Mountain on Norfolk Island; Raoul Island in the Kermadec Islands, Niuafo'ou in Tonga and for the motus of Suwarrow Atoll.

Table 3. Landscape mapping efforts during the 6th trip of the Callisto.

Island	Topographic Mapping Base	Results
Papua New Guinea	1:1,000,000 Topographic map	Landscape sketch map
Bagaman Island	1:20,000 aerial photograph	
Pio Island	None	Two plans of the micro-structure of soil cover
Norfolk	1:25,000 topographic map	Landscape map of Mt. Pitt nature reserve
Raoul	1:16,000 topographic map	Landscape map of island
Niuafo'ou	1:25,000 topographic map and aerial photographs	Landscape map of island
Suwarrow Atoll	None	5 schematic landscape plans of the islands

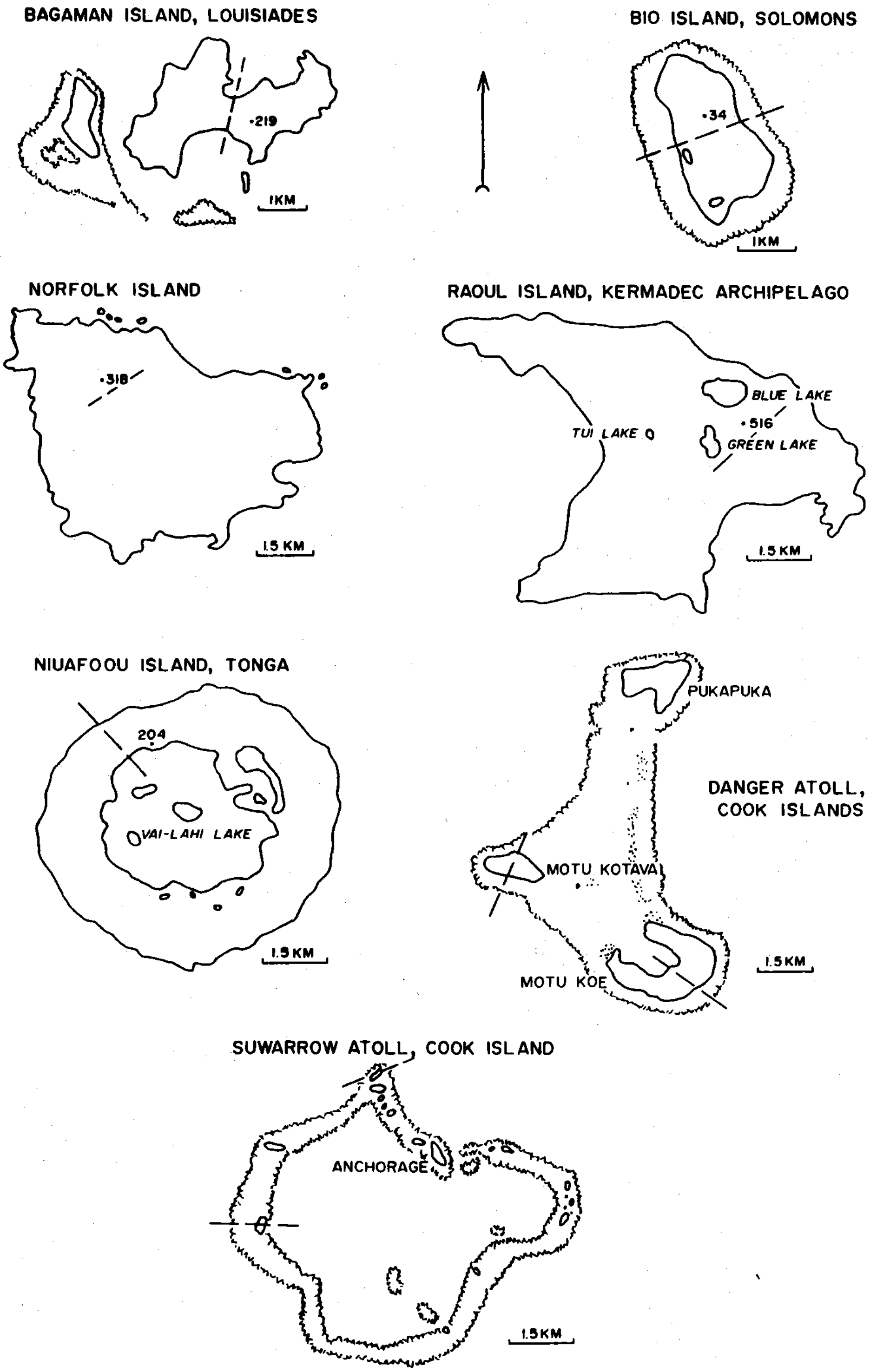

Figure 2. Outline maps of the islands visited. The hatched lines indicate the location and direction of profile transects discussed in the text.

CHAPTER II. GEOMORPHOLOGY, GEOLOGICAL STRUCTURE AND GENETIC TYPES OF ISLANDS IN THE SOUTHWEST PACIFIC

P. A. KAPLIN

INTRODUCTION

Geomorphological studies of islands are of great theoretical and practical importance. The geological structure of islands, their tectonic histories and geomorphological characteristics are indicative of the diversity of structural, lithological and physical geographical conditions of vast areas of the solid earth's surface which lie below sea level. Oceanic (mid-ocean) islands are also good indicators of past changes in sea level (Bloom, 1967; Nunn, 1987)[1].

It is a notable feature of islands, especially small islands, that, compared to continental areas of equivalent size, they are simple in geological structure and composition, and the range of geomorphological processes, although often having profound effects, is quite small (Daly, 1925). In addition, because many islands extend over only small areas and are quite isolated, the major events in their evolution can be determined more easily and generally with greater precision than on continents, where geomorphological characteristics are often influenced by the transfer of energy and materials from outside the landscape unit.

On oceanic islands, particularly those of small size and of recent age, it is often relatively easy to isolate the effects of erosion and tectonic movements. For example, during the sixth voyage of the "Callisto", it was discovered that each of the small volcanic islands examined was of similar composition, each being produced by a single volcano. Every island visited had a simple and easily classifiable structure:

Pio island is a small reef platform composed entirely of coral limestone; Raoul and Niuafo'ou are solitary volcanoes; and Suwarrow (Suvorov) and Pukapuka atolls are reef edifices arising from submerged volcanic piles.

All these islands can be regarded as closed systems in both space and time, the latter stretching from the point that the island first broke the ocean surface to the present day.

The geomorphology of oceanic islands is the outcome of endogenic factors, such as volcanic eruptions, and exogenic factors, such as marine erosion and coral-reef construction. In this sense, oceanic islands are natural models through the use of which one can trace and study all environmental processes, not only geological ones. Of particular interest are processes dealing with environmental degradation related to human activities.

The unique ecological attributes of oceanic islands depend on the following geological and geomorphological factors:

1. The location of the island within the broad structural context of oceanic basins and margins, which leads to a classification such as continental islands, islands of the intermediate zone, and those which rise from the deep ocean floor, considered by many to be the true "oceanic" types.
2. The regional and local tectonic situation, including block faulting, folding, uplift, subsidence and volcanic activity.

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[1] Since the original text of this chapter was written before 1978, Dr. Nunn as the scientific editor for this chapter is responsible for the relevant additions (references) after that date. These additional references and statements, which are indicated by an asterisk (*) have not altered Dr. Kaplin's original theses.

3. The lithology and geochemical character of the rocks forming the island.

4. Age of the island.

5. Geomorphology of the island, terrain, stage of development, process-form relationships, etc.

6. Morphometric indices, such as elevation, relative relief, slope steepness, coastline ruggedness, watershed size, etc.

In our investigations of the islands, we examined these characteristics carefully (Tables 1 and 2).

STRUCTURE AND COMPOSITION OF THE ISLANDS

As a general rule, islands are classified on the basis of the nature of the crust (lithosphere) into three types; continental, oceanic and intermediate islands. Continental islands lie on continental shelves and are parts of the adjoining continental masses. Oceanic islands lie within the main ocean basins and include wholly volcanic islands and most atolls. Islands of the intermediate zone exhibit the most variable structures. Such islands include micro-continents, such as New Guinea, folded islands of intricate structure, volcanoes and atolls.

CONTINENTAL AND INTERMEDIATE ZONE ISLANDS

Large continental islands occurring within the intermediate zone include Viti Levu, Fiji, and Guadalcanal, Solomon Islands. Like almost any large area of land, these islands are far from being homogenous in composition or origin. Alongside young extensive volcanic and sedimentary rocks, one encounters older igneous and metamorphic formations. The central part of Viti Levu for example is built of igneous rocks, the oldest probably being of Eocene age; the Yavuna tonalite stock, which intrudes older sediments in Southwest Viti Levu, has been dated to 34 ± 0.9 ma (Kroenke, 1984)*.

The structure of Guadalcanal is extremely complex. The bulk of the central and western parts are covered with Pliocene sediments (shales, sandstones, conglomerates etc.). The southeast of the island is composed of Upper Mesozoic lavas and intensely folded metamorphosed shales. Throughout the island, the sequences described are intruded by late Cretaceous, Tertiary and Quaternary basalt and andesites. The northern part of Guadalcanal is younger and occupied by a series of ten coral-reef terraces, the highest reaching 800 m. These terraces range in age from Oligocene to Holocene and stretch for about 15km. In the neighborhood of Honiara, the terraces are banked up against an intrusive massif (Coleman, 1970; Coulson, 1985).

Thus, it can be seen that the large islands within the intermediate zone can themselves be divided into parts which have a continental affinity and those which have a typical oceanic, volcanic or coral-limestone character.

Smaller islands within the intermediate zone may also be classified as continental or oceanic. Bagaman Island, for example, is continental. It has a monoclinal structure and is composed of greenstone slates, chlorite and sericitic schists. The Bagaman monocline is part of the huge Calvados anticline, which lies within the Louisiade metamorphic belt of Thompson and Fisher (1965). According to Manser (1973), the greenstone slates of this belt derived from early Mesozoic detrital greywacke sediments. During the Tertiary, this area, together with New Guinea, was involved in orogenic processes and underwent several regional metamorphic transformations. Quartz veins were formed throughout the region 9.67 ± 0.5 million years ago (Pain *et al.*, 1979). The Louisiade metamorphic belt was broken up into blocks during the Tertiary and differential tectonics characterized its later history, some blocks moving up, others down.

Although Pio island is biogenic in origin, it cannot be regarded as truly oceanic or even an atoll for it has the structure of a reef platform. Information from 1:50,000 geological mapping of the center of the nearby island of Uki (Uki ni Masi), where fine- grained Pliocene limestone and siltstones are overlain by reef limestone, suggests that the two islands share an antiform basement, possibly a horst, stretching southeast to northwest. This structure continues to find expression further northwest in Malaita, one of the largest of the Solomon Islands (Coulson, 1985). During the Pleistocene, coral formed on some of the summits of the submarine parts of this structure near the sea surface. The coral colonies gradually coalesced and became covered with reef debris and in this way many of the reef platforms came into being. Elsewhere in the area, uplift caused reef terraces to form (Neef and Veeh, 1977).

OCEANIC ISLANDS

Oceanic islands lie within the Andesite Line, which can be conveniently considered as the boundary between the intermediate zone and the true ocean basins. This expedition examined only two islands in the ocean basins - Suwarrow and Pukapuka, known also as Danger atoll. These are situated in the largest area of block uplift in the central Pacific, known as the Cook Island or Manihiki uplift (Udintsev, 1972). In plan the uplifted block is like a rhomb oriented with its apexes towards the cardinal points. The block includes several northeast-striking ridges which merge in its southwestern part. The highest part of the block is in the southeast and is known as the Manihiki Plateau, the smoothed surface of which lies at depths of around 2,600 m. The Manihiki Plateau is the basement from which the islands of Manihiki, Rakahanga and Suwarrow rise. The southeastern part of the Manihiki uplift block is also a flat-surfaced plateau, reaching depths of more than 3,800 m. Pukapuka rises from the edge of this plateau.

The uplifted block in this part of the Cook Islands is bounded by two fracture zones, one striking northwest, the other northeast. The surface of the uplifted block is covered with a thick mantle of sediments, including carbonaceous foraminiferal oozes and coral sands. There is also material of volcanic origin, such as glasses and lava fragments within this cover. The surfaces of the faults which bound the uplifted block are associated with outcrops of gabbro and serpentinous peridotites, which are characteristic of the oceanic lithosphere (crust). Udintsev and Heezen calculated the thickness and accumulation rate of the sediment cover of this block, and concluded that it was in existence as early as the Cretaceous (Udintsev, 1972).

Suwarrow and Pukapuka are part of the northern group of Cook Islands, which comprise submerged volcanic piles with coral reefs rising from their summits. The best evidence for this is provided by the atoll of Manihiki, in the northwest part of which, reef cover is only 30-40 m, but in the western part of which, it is up to 500 m thick (Hochstein, 1967). Seismic refraction suggests that basalts underlie this reef cover.

According to Wood and Hay (1970), the atolls of the Northern Cooks, including Suwarrow and Pukapuka, originated as fringing reefs around Tertiary volcanoes. As the latter subsided, the reefs grew upwards and have persisted. Hochstein (1967) estimated the beginning of coral limestone formation here as mid-Miocene in age, about 14-22 million years ago. Robertson (1970) mapped the volcanic core of Pukapuka by gravity survey.

Despite their position within the intermediate zone, Niuafo'ou and Norfolk islands can be regarded as typically oceanic. In the region of Niuafo'ou, Hochstein (1967) identified four mega-structural elements, namely: the abyssal Tonga-Kermadec trench; the island arcs lying to the west of this trench from which the Tonga and Kermadec island groups rise; the Lau Basin; and the Lau-Colville Ridge respectively. The entire region is a classic example of an island-arc complex comprising a trench, fore-arc, back-arc basin and remnant arc (Milsom, 1970; Nunn, 1987b).

Niuafo'ou is situated in the Lau Basin which, according to Hockings (1978) is underlain by young theolitic basalts. Chemically and petrologically, these basalts are of a kind normally associated with mid-ocean ridges (Reay *et al.*, 1974). From heat flow data, it was believed long ago that sea-floor spreading was occurring in the center of the Lau Basin (Sclater *et al.*, 1972; Gill, 1976), and that large quantities of basalt magma are rising up, an idea which has recently been confirmed by the identification of a magma chamber beneath the Valu Fa Ridge in the central Lau Basin (Morton and

Sleep, 1985). Repeated eruptions occur along the system of ridges in the central Lau Basin, particularly the Peggy Ridge, and also the apparently isolated submarine volcanoes which include Niuafo'ou. The eruption of basalts signalling sea-floor spreading began in the late Miocene (Hockings, 1978) although Malahoff *et al.* (1982) placed it more recently, at about 2.5 million years ago. The presence of basalts in the Lau Basin leads one to regard Niuafo'ou as an oceanic island, despite its location within the intermediate zone on the 'wrong' side of the andesite line. The geology of Niuafo'ou and other volcanic islands in Tonga was described by Schofield (1970) and Bryan *et al.* (1972).

Norfolk Island is situated within a zone of Mesozoic-Cenozoic folding of oceanic lithosphere and is perhaps even more typically oceanic than Niuafo'ou. Norfolk island rises from the submarine Norfolk Ridge which underwent orogenesis at the same time as New Caledonia, a process which was largely completed by the Oligocene. Although the island rises from a geosynclinal basement, it is a typical oceanic volcano, built from olivine basalts (Jones and McDougall, 1973).

Raoul island is also volcanic although with a different structure compared to Niuafo'ou and Norfolk (Oliver, 1911; Brothers and Searle, 1970). The nucleus of Raoul is composed of andesites, basalts, andesitic tuff and breccia covered by pumice, ash, sand and shingle. This suggests that Raoul experienced more acid vulcanism than true oceanic volcanoes. In addition, the nature of the Raoul vulcanism appears to have been explosive, as manifested by the abundant pyroclastics, in contrast to the volcanic activity which occurs on typical oceanic islands as outflows of lava in sheets and streams.

It is interesting to compare Raoul with Niua Fo'ou. Both islands have vast calderas occupied by lakes, but the caldera on Raoul resulted from a massive outburst of pyroclastic material, which caused the destruction of an existing volcanic pile some 2,170 years ago (Brothers and Searle, 1970). In other words, the Raoul caldera is a typical product of explosive vulcanism. The Niuafo'ou caldera is the typical product of the collapse of a volcanic cone, perhaps into an underlying magma chamber, under the influence of subsidence and/or readjustments in the submarine part of the volcanic pile. The contrasts between Raoul and Niuafo'ou are clear; the former we regard as typical of island arcs and therefore intermediate-zone volcanic islands, the latter we regard as typical of oceanic-zone volcanic islands.

TECTONIC MOVEMENTS

We failed to detect any recent tectonic movements on the majority of islands studied; nor did these islands reveal any traces of Pleistocene or earlier uplift events, which can be recognized elsewhere in the region from successions of ancient shorelines. It can be inferred from the horizontal attitude of basalt lavas on Norfolk and Raoul islands and the absence of any folding that the islands developed under tectonically subdued conditions. The faulting visible on Raoul Island is thought to have resulted from vulcanism and not from regional tectonic activity. It is believed that these islands are presently stable or slowly subsiding, although Schofield (1981) argued that a raised beach at Low Flat on Raoul had been uplifted 3.5 m in the last 440 years.

The surfaces of Suwarrow and Pukapuka atolls do not reveal evidence for any recent uplift (a contrary view is presented by Scoffin *et al.* (1985), although relative uplift, caused by sea-level regression, would have occurred during Quaternary glacial periods and the atolls would have appeared rather like the coral islands of Nauru and Niue do today. During interglacials, Suwarrow and Pukapuka would have reverted to atoll form as they are today. One can see that some recent outward growth of the Suwarrow reef has taken place, which suggests that present- day subsidence is negligible on these atolls. This view is borne out by the observation that many of the morphological features on Pukapuka and especially Suwarrow differ from atolls in Kiribati and Tuvalu (formerly the Gilbert, Ellice and Phoenix island groups) which have recently been subject to relative uplift (Kaplin and Medvediev, 1973; Schofield, 1977)'.

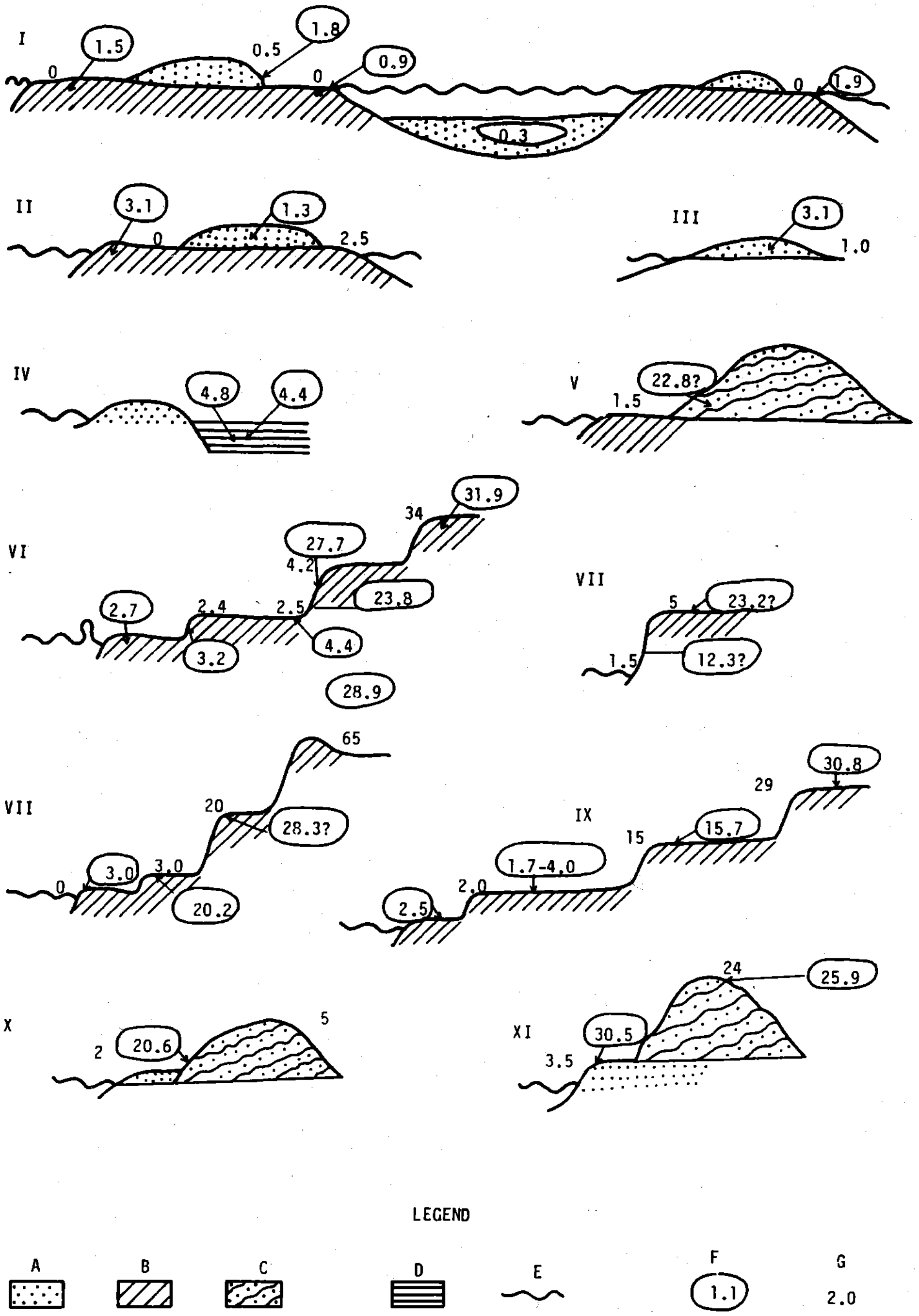

Figure 3. Age (in thousands of years BP) of individual relief elements of oceanic islands.
I. Funafuti Atoll - reef, reef flat, motu, bottom lagoon sediments. II. Suwarow Atoll - reef flat, motu. III. Bagaman Island - old lithified beach. IV. Norfolk Island - old lagoon. V. Norfolk Island - old dune ridge. VI. Pio Island - reef terraces. VII. Misima Island - uplifted fringing reef. VIII. Niue Island - reef terraces. IX. Efate Island - reef terraces. X. Lord Howe Island - old dune ridge. XI. Lord Howe Island - old terrace and dune ridge. Other symbols: A. Accumulative bodies. B. Coral limestone. C. Eolinite. D. Lagoonal sedidment. E. Ocean and lagoon level. F. Absolute ages in thousand years BP (sample recrystallized by over 50%). G. Height above ocean level.

Evidence for upward shoreline displacements was found on Bagaman and Pio islands. It seems, however, that subsidence is presently occurring on Bagaman for the surface of the fringing and barrier reefs is submerged and aggradational beach ridges onshore are being progressively drowned.

On Pio island, there is undoubted evidence for long-term uplift. Three terraces exist at 34 m, 13 m and 2.5 m and their radiocarbon dating has helped determine the uplift history of these islands. The generalized uplift rate is 0.5 m per thousand years, and uplift continues today.

AGE OF ISLAND RELIEF

The islands studied differ in age (Table 2; Figure 3). The youngest are the islands of accumulation, commonly known by the Polynesian word motu, which occur on the reef platforms of the atolls. The atoll foundations are of course much older; the coral limestones of Cook Island atolls began accumulating in the middle Miocene, 14-22 million years ago. In general, most of the coral limestone on oceanic islands is of Cenozoic age, as determined by deep drilling (Stoddart, 1973). None of the boreholes drilled on such islands encountered sediments older than Oligocene (30-40 million years ago) or maybe late Eocene (40-60 million years ago) in age. This is despite sediment thicknesses of as much as 1,000-1,200 m (Kaplin and Medvediev, 1973; Ladd, 1977; Ladd and Schlanger, 1970).

Motus are transient features of atolls which originate on ring-reef structures rising from submerged Cenozoic volcanoes. During the low sea levels of the Quaternary, solution and mechanical erosion of the exposed reef edifices led to the creation of much loose sediment, mostly coral sand, which came to rest on the floor of the lagoon contained by the ring reefs. Once sea level rose again, waves and currents within the lagoon and outside caused much of this sediment to accumulate on the ring-reef surface to form motus during times of high interglacial sea level, such as we are experiencing at present. Most of the present-day motus date only from the time of the mid-Holocene when the sea reached its present after level rising as the result of last-glacial ice melt.

Numerous radiocarbon determinations have been made of specimens from the atolls. A specimen from the central part of the motu known as High Island on Suwarrow allows its formation to be put at 1,261 ± 170 years ago (Moscow State University [MGU] 626). The surface of the ring reef near High Island is understandably older at 3,137 ± 116 years ago (MGU 632).

During the sixth voyage of the SS "Dmitriy Mendelyev", samples were collected from the atoll of Funafuti in Tuvalu. The motu of Amatiku was dated to 1,780 ± 120 years ago (MGU 186) while the associated reef flat yielded dates of 1,530 ± 80 and 1,900 ± 100 years BP (MGU 185 and 191 respectively). These specimens came from the oceanic side of the reef; one from the lagoon side proved younger at 870 ± 50 years ago (MGU 190), and this difference in age supports the idea that atoll rims grow primarily on their lagoon sides.

Abundant data collected by various scientists show that most atoll surfaces are between two and four thousand years old (Kaplin, 1975). For example, as stated by the American CARMARSEL expedition (Curray *et al.*, 1970), the age of the accumulation on Jabor Island (on Jaluit Atoll in the Marshall Islands), which rises to 1.5-2.0 m is 2,290 ± 95 years BP near the surface, 2,730 ± 100 years BP 0.7 m down, and 4,475 ± 103 years BP at 1.25 m depth (0.75 m below mean sea level).

Similar ages were found for material in storm beaches and beach ridges on islands which are not atolls. On Bagaman, the storm beach at Lalaguela Bay is 3,190 ± 170 years old (MGU 639). The age of the reef flat on Pio island is 2,725 ± 84 years BP (MGU 627), that on Niue is 3,070 ± 170 years BP (MGU 589), and that on Efate is 2,540 ± 190 years BP (MGU 177).

It is understandable that accumulative landforms on the ocean facing coasts of atolls should be younger. Many motus, especially at Suwarrow, have been affected by tropical cyclones, including typhoons, in the last decade and have only recovered partially. Despite this, it is possible to state that the time of formation of the present surface of most atolls, intertidal reef platforms, and recent accumulative landforms is from 4000 years BP to the present. The period of most active formation appears to have been between 4000 and 2000 years BP, by which time the ocean level had stabilized following the postglacial transgression in the Pacific (Schofield, 1980; Nunn, 1987c).

A Holocene age is common for the lowest marine terraces on islands which experienced late Quaternary uplift and which are still being uplifted today. For example, the back of the lowest terrace on Pio island rises to 2.5 m above sea level and was dated to 4,439 ± 84 years BP (MGU 618). Material from the seaward scarp of this terrace was dated to 3,180 ± 170 (MGU 519) and 2,446 ± 170 years BP (MGU 624). The lowest terrace on Efate island at 1.5-2.0 m above sea level was dated to between 1,740 ± 70 years BP (MGU 178) and 4,030 ± 150 years BP (MGU 170). The range of dates we obtained for this terrace on Efate is slightly younger overall than that of Bloom *et al.* (1978) for the same location. Such differences are common and not necessarily significant (Kaplin, 1975).

The lowermost terraces on islands which are believed to be (and to have been) tectonically stable are commonly pre-Holocene in age. For example, the U/Th dates obtained by Veeh (1966) for a variety of 2-4 m terraces in the Pacific and Indian Oceans were unexpected since most were referable to the last Interglacial (Sangamon), perhaps 100-120,000 years ago. The lowest terrace (2 m) on Oahu in Hawaii was dated by radiocarbon to 24-26,000 years BP; and the 4 m terrace thereon was dated to 31-32,000 years BP (Shephard, 1963). Such dates suggest interstadial rather than interglacial high sea levels but this remains a subject of debate (Thom, 1973).

In addition to the islands described above, the "Callisto" also visited the upraised atoll of Niue and the island of Misima in the Louisiade Archipelago. Coral from the 3 m terrace on Niue was dated to 20,200 ± 460 (MGU 590), and that from the 5 m terrace on Misima to 23,200 ± 180 years BP (MGU 593). Since both samples were re-crystallized, as shown by x-ray diffraction, the true age of the terraces is likely to be much older.

The tectonically stable atolls of the mid-Pacific have sediments close to present sea level which are referable to littoral deposition during Pleistocene interglacials. This is no surprise since Pleistocene interglacial sea levels were all close to present sea level (Markov and Suetova, 1964). Such observations bear out inferences made already about the stability of these atolls.

We drilled a large number of holes on Eniwetok Atoll in the Marshall Islands from 20-100 m in depth. Analyses of the cores showed that the oceanic side of the atoll consisted of strongly-cemented coral reef, and the lagoonal side of medium to weakly-cemented coral debris and an abundance of the calcareous algae *Halimeda*. Down to 8.5 m, the reef is of Holocene age, and at about 10 m there are corals dated to 132,000 years BP. Five stages of coral growth could be recognized through core dating: at 6, 132, 330, 450 and 550 thousand years ago. These growth stages agree with the periods of ocean-water temperature rises, as found through oxygen-isotope dating (Szabo and Tracey, 1977) and are compatible with results obtained by other scientists from Eniwetok and nearby atolls (Ladd, 1977; Ladd and Schlanger, 1970). Similar structures and growth stages have also been identified on other Pacific atolls, such as Mururoa in the Tuamotu archipelago (Labegrie and Lalon, 1969).

Traces of last interglacial shorelines were found on some volcanic islands surrounded by fringing reefs. Rarotonga, which was visited during the "Callisto" expedition, is a volcano which formed 2.3-2.8 million years ago (Wood and Hay, 1970). The old volcanic center is fringed by a flat terrace 200-300 m wide and up to 6 m above sea level. Although this was not drilled, it is almost certainly the last interglacial shoreline and reef platform. Most of the samples from Rarotonga came from the modern reef surface, showing it to be of Holocene age. Coral sand from dated terraces 8 m above high-tide level was dated to 1,235 ± 57 years BP; at 6 m, it was 2,470 ± 63 years BP; and at 4.5 m, it was 3,510 ± 50 years BP. Coral in growth position 1 m above sea level was dated to 2,030 ± 60 years BP. Similar samples at 3 m were dated to 28,000 ± 850 years BP; and at 2 m, to a minimum of 48,900 years BP. It seems likely that the 28,000 BP date corresponds to the high sea level during the Paudorf Interstadial (Bryansk warming) and the minimum age of 48,000 years to part of the Sangamon Interglacial (Schofield, 1970; Wood and Hay, 1970).

During the visit to Lord Howe Island in 1971, we sampled marine terraces and dune complexes.

Lying 650 km east of the Australian coast, this island is one of the most southerly in which living coral reefs are found; the marine geology was described by Bentz (1974). The island is a coalescence of volcanic massifs, Pliocene or Plio-Pleistocene in age, which are linked by 'bridges' of old dunes. In the northeast of the island, dunes form a barrier 20-25 m high, built of lithified, finely-stratified eolianite. These dunes overlap a 3-5 m terrace composed of coral and shell detritus, which was dated to 27,100 ± 450 years BP (MGU 1841) and 30,500 ± 600 years BP (MGU 1842). The overlapping dunes are 20,600 ± 220 years BP (MGU 179) in age, from which it can be concluded that the terrace developed during the Middle Würm and that the dunes formed later during cold post-Wurm times when the ocean was much lower and corals were dying in great numbers.

Dune complexes on Norfolk Island are contemporaneous with those on Lord Howe Island. Samples from the south coast of Norfolk Island showed that dune accumulation began 22,897 ± 352 years BP (MGU 628). Following the Holocene transgression, this area became a lagoon enclosed by a tombolo; pieces of wood found in lagoonal sediments were dated to 4,400 ± 90 years BP (MGU 594) and 4,440 ± 50 BP (MGU 674).

On reef-fringed coasts which are being uplifted tectonically, it is usual to encounter complexes of fossil reefs (reef terraces) at different elevations and of different ages. The classic studies on the Huon Peninsula in Papua New Guinea (Bloom *et al.*, 1974), on Barbados (Mesolella *et al.*, 1974), in Vanuatu (Jouannic *et al.*, 1980), and on the Ryukyu Islands off the main islands of Japan (Konoshi *et al.*, 1970) exemplify the situation (of tectonically uplifted and complex coral reefs in the Southwest Pacific).

We identified and dated a number of elevated reef complexes during our expeditions to the equatorial, tropical Pacific. On Pio Island, in addition to the Holocene terrace mentioned above, there are also terraces at 6-13 m and 34 m above sea level. The lower of these terraces was dated to 23,894 ± 430 years BP (MGU 631) and 27,700 ± 350 years BP (MGU 592). The surface of the 34 m terrace was dated to 31,930 ± 1,300 years BP (MGU 634) but, since the sample was 80-90% recrystallized, this should be regarded as only a minimum age for this terrace. On the apparently uplifted atoll of Niue, several terraces occur (Schofield, 1959). One terrace at 20 m was dated to 28,333 ± 330 years BP (MGU 622).

The complex of terraces on Efate Island developed as fringing reefs around a group of small volcanoes which experienced a long history of uplift. This uplift is apparent as a series of terraces at 1.5-8 m, 12-20 m, 30-40 m, 80-90 m, 120-140 m, 180-190 m, 225-250 m and 400 m (Kaplin, 1977; Kaplin *et al.*, 1975-1977). The Laboratory of Quaternary Stratigraphy in the Geography Department of Moscow State University determined the age of the three lowest terraces to be 1.5-4.2, 15.7 and 30.8 thousand years old respectively from lowest to highest. These ages allow the average rate of uplift to be calculated at about 1 mm/year. If this rate applied during the time at which the earlier terraces were uplifted, then their ages would be 85, 130, 190, 240 and 400 thousand years old respectively from lowest to highest. These ages agree well with those obtained by Bloom *et al.* (1978) for the Efate terraces. Using the Th/U technique, Bloom dated 11 t at 2-10 m, 55-65 m, 85-95 m, 110-130 m and 180 m to 2.8-6.8, 76-92, 114-130, 131-141 and 174-192 thousand years BP respectively. More recent work on Efate (Lecolle and Bernat, 1985) yielded the following Th/U dates for terraces at the following elevations:

2-10 m	terrace	39.2 ± 2.4 Ka (000 years)
20-70 m	terrace	76.9 ± 4.6 to 86.7 ± 5.2 Ka
70-80 m	terrace	103.5 ± 6.2 to 108.0 ± 6.5 Ka
85-100 m	terrace	121.6 ± 7.3 to 133.5 ± 8.0 Ka
120 m	terrace	175.2 ± 10.5 Ka

On the whole, the dates obtained from the surfaces of coral-limestone terraces show that most of these formed during transgressions which can be linked to either interglacials or interstadials (Kaplin, *et al.*; Kaplin, 1976-1977). Most of the dates fall within the following time periods:

2-6,000 years BP	Holocene
24-35,000 years BP	Paudorf, Plum Point, Bryansk Interstadial
58-64,000 years BP	Amersfort, Breroop, St. Pierre Interstadial
80,000 years BP	Early Wurm Interglacial, Upper Volga warming.
90-110,000 years BP	End of the Riss-Wurm, Eemian, Mikulino Interglacial.

The 114-130,000 year old terrace on Efate can be correlated to the temperature optimum of the last Interglacial. The 130-150,000 year old terrace may also be linked to this time, although the date clearly lacks precision. The 160-180,000 year old terrace can be linked to the early stage of the last Interglacial. The shoreline of 210-230,000 years ago may be correlated with the period of warming which separated Riss I from Riss II.

One can find references to even older terraces in the literature which may be linked to early Pleistocene warming events. However, the difficulties involved in dating samples older than 300,000 years are immense and the dates cannot be considered as reliable as those from younger materials. Further, the correlation of the shorelines on Efate with transgressions during periods of warming should also be regarded as preliminary, not the least because the errors commonly exceed the age intervals between dates from particular terraces (Neef and Veeh, 1977)*.

It should also be remembered that not all the reef terraces which formed during transgressions will have reached above present sea level because the maximum sea level attained in the particular transgressions during which they formed may have been well below today's sea level. For example, terraces formed during the Paudorf Interstadial are linked to a sea level 20-40 m below present sea level; the terrace regarded as being 40-50,000 years old formed around 38-40 m below present sea level; the 60,000 year old terrace formed 20-28 m below present sea level; and the 80,000 year old terrace at a sea level 13-14 m below the present. Hence, terraces of such ages would be found only on islands with a long and reasonably continuous history of tectonic uplift.

Despite problems relating to the accuracy of the data reported above, they can still be employed in the systematic investigation of Pacific island ecosystems. For example, terraces of coral limestone form the bases of many oceanic islands, the time of formation of which clearly coincides (for all practical purposes) with the start of pedologic and biotic development. A terrace complex, comprising reef platforms which emerged in succession, provides an excellent opportunity to study evolution of the ecological environment through time.

There are many difficulties involved in establishing the ages of volcanic islands. According to Menard (1966), the earliest phase of volcanic activity in the Pacific Basin climaxed in late Mesozoic - early Cenozoic times. Some of the islands in the Marshall, Caroline, Kiribati and Tuamotu island groups had developed by the Eocene. An Eocene foundation for many Southwest Pacific island arcs appears probable (Kroenke, 1984; Nunn, 1987b).*

A second phase of Pacific Basin vulcanism began around the end of the Neogene (Menard, 1966) and continues today. All the volcanic islands visited by the SS "Dmitriy Mendeleyev" and "Callisto" expeditions came into being during this second phase. As reported above in Table 2, Norfolk Island formed between 3.1-2.3 million years BP since which time development has been dominated by subaerial denudation. K-Ar dates from Rarotonga suggest that this island formed 2.8-2.3 million years BP. Carney and Macfarlane (1982) suggested that the earliest phase of volcanic activity on Efate in central Vanuatu (New Hebrides) was 1.7-1.1 million years BP; it was followed by a second phase from 0.2 million years BP to the present day*.

The greater parts of the volcanic islands of Niuafo'ou and Raoul are of Quaternary age, the last eruptions having occurred in the 1940s-1960s. According to Brothers and Searle (1970), the bulk of Raoul Island appeared 2,000 years ago as the result of a volcanic eruption which cloaked the island with a thick pumice mantle and brought about collapse of the volcanic pile and resulted in caldera formation. The subsidence caldera on Niuafo'ou also seems to have developed within historical times. The lower part of the resulted in caldera slopes are overlain by lava from peripheral parasitic vents which erupted in 1885, the 1930s, and in 1946. The upper slopes of Niuafo'ou, which are formed from lavas originating in the central crater, probably date from the Pleistocene.

In summary, the land surface of Norfolk, Rarotonga and Efate dates from about 2 million years BP; that of Raoul and Niuafo'ou is several hundred, in some places several thousand, years old.

GEOMORPHOLOGY AND EVOLUTION OF THE ISLANDS AND THEIR EVOLUTION

VOLCANIC ISLANDS

Stearns (1946) and Menard (1966) distinguish several stages in the evolution of volcanic islands, the main ones of which are as follows:

1. Submarine eruption resulting in the formation of a submarine volcano.
2. Exposure of the active volcanic pile above sea level resulting in the formation of an ash or andesitic-basaltic cone of considerable height.
3. Destruction of the top of the cone, resulting in the development of a summit caldera, and of shallow grabens along the main faults.
4. Filling of the caldera and development of an ash cone during subsequent eruptions.

Menard (1966) believed that the time between stages (2) and (3) was usually quite short, the cones formed in (2) surviving for only a few months, sometimes a few days, before destruction resulted in caldera formation.

The volcanic islands described in this report all agree well with this model. The young islands of Niuafo'ou and Raoul (Figure 4) are at the first subaqueous stages of their development, their calderas have just come into being. Subaerial conditions have prevailed on Rarotonga, Efate and Norfolk for over one million years and their calderas have been filled up. On Norfolk Island, the original vents have all been submerged (Jones and McDougall, 1973).

The geomorphological characteristics of volcanic islands depend largely on their structure and age, and can be traced by comparing for example, islands of similar structure but different age and lithology. The main exogenic processes responsible for landform development on volcanic islands are subaerial and coastal erosion.

COASTAL GEOMORPHOLOGY OF VOLCANIC ISLANDS

The stage of landscape evolution on different islands is a function of their age and is best shown by erosional and depositional coastal landforms on the islands studied.

On the oldest island, Norfolk, one can see high, sheer cliffs which are mature erosional forms, as are the erosional embayments, capes, sea-stacks and abrasion platforms extending seawards from the modern shoreline. Cliffs on Norfolk reach 90 m in the north and northwest, and 60 m in the southwest. The lower part of the cliffs rises abruptly and looks like a "layer cake" of interbedded basalt lavas and unconsolidated yellow tuffs, which have been differentially weathered. The upper part of the cliffs consists of a weathering crust dipping seawards at 45°. In places, this crust area is dissected by ravines down to the level of the uppermost lava flow. The foot of the cliffs is commonly strewn with basalt boulders which grade into boulder-shingle beaches at the heads of bays. Only at the head of the funnel-shaped Anson Bay is there a beach of clean yellow sand, over 7 m broad in places.

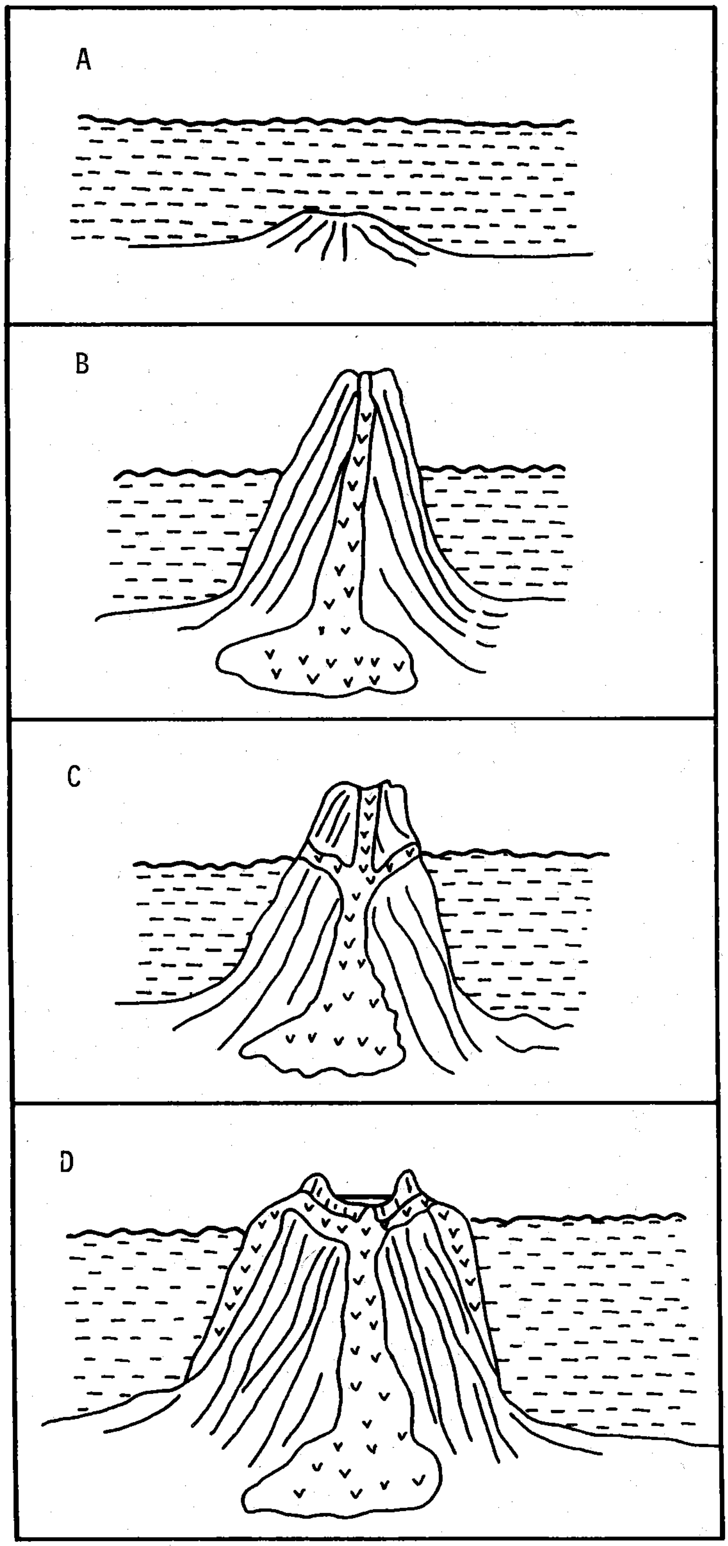

Figure 4. Evolution of Niuafo'ou Island. Legend: A. Pliocene; B. Pleistocene; C. Holocene; D. Recent.

A similar type of erosional volcanic coast is found on Lord Howe Island, which was also formed by coalescence of a number of Pliocene volcanoes. On this island the cliffs, composed of basalts, agglomerates and tuffs, reach 200 m in height.

The shoreline of the young volcanic island of Raoul is also dominated by erosional forms. Its cliffs are cut into the steep slopes of the high massif which forms most of the island and are the result of rock falls and debris slides. Cliff formation on Raoul is exemplified by those at the anchorage off the southeast of the island. This is in a funnel-shaped bay, which appears to have formed through tectonic activity. The shores of the bay rise directly to a prominent watershed ridge. In their upper parts, these slopes are 40° or more, and in their lower parts, cliffs 50-70 m high are found. These cliffs exhibit inter-bedded basalt lavas and tuffs.

Raoul's north coast consists of a 60-80 m high alluvial plain truncated by the shoreline. The plain is built of cemented pebbles of pumice with a matrix of sand and sandy loam; its seaward edge is bordered by a 60 m high cliff fringed by a 100 m broad sand and shingle beach. Notwithstanding the presence of this beach, the erosional profile of the cliff appears fresh and it is thought to be actively developing at present. Wright and Metson (1959) believed this alluvial plain to be a marine terrace but our investigations suggest otherwise. The plain is the result of the coalescence of alluvial fans at the mouths of valleys cutting into the northwestern flanks of the island's central plateau.

The coast of Raoul is not so advanced in its stage of development as that of Norfolk. There are no abrasion platforms or sea-stacks on Raoul's coast which indicates that coastal erosion has not been acting for long. This inference is also borne out by the sharp contours of the topography; lines of primary structure such as tectonic scarps, being clearly visible.

The youngest coastline observed was that of Niuafo'ou; many of the basalts along this coast were formed only in the last few decades. A stepped coastal profile in places is the result of the extent of various lava streams. The shoreline itself is built of chaotically-piled heaps of lava blocks and varies in height between 5 m and 30 m. Some lava tongues protrude offshore as small headlands. In the south of the island, the coast consists of the denuded wall of a secondary crater.

In plan, the coastline of Niuafo'ou is irregular and the dissection of the island's topography is in a very young stage. The volcanic form of the island's submarine slope is little altered although complicated in places by structural irregularities. The absence of a coral reef associated with the present shoreline of Niuafo'ou can be attributed to its youth. The primary volcanic form of the island has not been altered sufficiently to provide a base for reef growth. The youth of the coastline of Niuafo'ou is also suggested by the absence of accumulative landforms. In place of beaches, which are almost wholly absent from the island, one finds heaped debris along the waterline. A few narrow sand and shingle beaches occur in places.

The presence of well developed depositional coastal landforms usually testifies to the maturity of a particular coastline. For example, in Danham Bay on Raoul Island, there is a barrier beach ridge separating the head of the bay from the ocean. This barrier rises to 5 m above ocean level and is 200 m wide in places, and fringed on the ocean side by a broad sand and shingle beach. Landwards of the barrier beach is the old beach 400 m wide with a freshwater swamp in its center.

More complex coastal accumulative forms are encountered on the older islands of Norfolk and Lord Howe.

In the southern part of Norfolk Island there is a triangular coastal plain, the southern apex of which is named Hunter Cape (Figure 5). The northern part of this plain is bounded by a steep scarp which rises to the plateau above. Beneath the surface of the coastal plain are lagoonal deposits about 400 years old. Clearly this coastal plain formed from the merging of two spits or tombolos, behind which infilling occurred. The dunes which characterize Hunter Cape, the point at which the tombolos merged, are about 20,000 years old, and appear to overlie an older surface which may have been formed during the sea-level rise of the Paudorf interstadial.

Palynological analysis of the old lagoon deposit (Boyarskaya, pers. comm.) indicates that the vegetation there 4,000 years ago was similar to the present, as demonstrated by the presence of the woody species of Celastraceae, probably of the genus *Elaeodendron*. Microfossils of the following were also encountered: *Araucaria*, Palmae, *Lagunaria*, *Celtis*, *Nothofagus*, Moraceae, Santalaceae, Euphobiaceae, Sapindaceae, Araliaceae, Passifloraceae, Ranunculaceae, Amarantheaceae and Orchidaceae. The spores revealed the presence of Polypodiaceae (microsporium), and the ferns, *Adiantum* and *Pteris*.

On Lord Howe island, dunes of the same age overlie an aggradational terrace nearly 30,000 years in age. These dunes are made of coral sand which is interesting for these islands now lie close to the southern limit of reef growth. The implications are that 20,000 years ago, reef growth was much more extensive than it is today and that the ocean waters must have been warmer (than today). The dune sand underwent cementation when the climate became drier.

The dune massif on Norfolk Island was once much more extensive than it is today. The island of Nepin, lying 1.3 km south of Hunter Cape, is also built of eolianites which reach 32 m in height. The island is separated from the mainland by a shallow strait which suggests that they were once joined and that the dunes there were formed by the same processes.

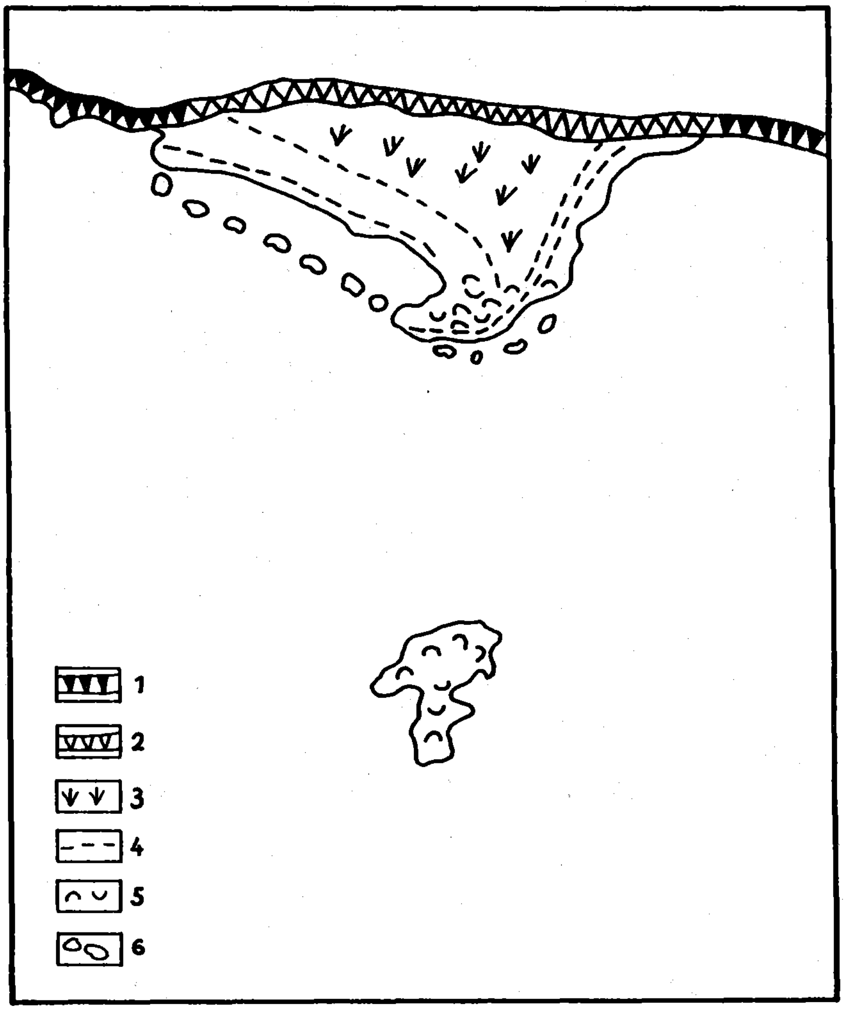

Figure 5. Geomorphology of the southern coastal plain of Norfolk Island. Key: 1. Active cliff; 2. Dead cliff; 3. Relict lagoon; 4. Coastal accumulative forms; 5. Old dunes; 6. Coral colonies.

FLUVIAL GEOMORPHOLOGY OF VOLCANIC ISLANDS

The volcanic islands studied exhibit differing degrees of subaerial and fluvial erosion.

On Norfolk Island the drainage network is poorly developed; there are only ephemeral and no perennial channels. Some of the ephemeral channels have, however, excavated sizeable valleys, the largest of which are Watermill Creek which drains into Sodney Bay, and Cascade Creek which flows into Cascade Bay. These valleys extend 2-3 km and are cut down almost to ocean level. All the other valleys on the island are downcut only slightly and meet the sea in hanging valleys.

The valleys originate from a plateau 90-120 m above sea level which is underlain by horizontal basaltic lavas. A 45-60 m thick mantle of weathering residue, thought to be about 2 million years old, overlies the lavas. Shallow dissection of this residue accounts for the undulating character of the plateau surface. The permeability and depth of the weathering residue also explains the absence of perennial streams on Norfolk Island and the apparent youth of the island surface.

On the other Pliocene volcanic islands studied, Efate and Rarotonga, the effects of fluvial processes are more obvious. On Efate, most valleys are of primary tectonic origin; valley-side slopes are rectilinear, and valleys are arranged in a radial pattern (Kaplin *et al.*, 1976). The areas of most intensive dissection on Efate are confined to its windward slopes which receive the heaviest rainfall. The situation here is exacerbated by the erodability of the bedrock, which is mostly volcanic tuffs and pumaceous rocks. The leeward side of Efate, where basalt lavas and reef limestones outcrop on the surface, is understandably less dissected (Carney *et al.*, 1985).

The high interior of Rarotonga is composed of grey-black basalts, basaltic breccia, nephelinitoid phonolite and phonolitic ash. The area is heavily dissected by radially arranged rivers.

The most heavily-dissected landscape observed was on the young volcanic island of Raoul. The presence of narrow interfluves separating deep valleys with steep valley-side slopes, averaging around 30° in places, is somewhat puzzling. The slopes on the island's western side are generally steeper and shorter. The land surface of Raoul is clearly in a young stage development, characterized by intensive vertical fluvial erosion resulting in V-shaped valley formation. As with the windward side of Efate, the situation on Raoul is exacerbated by its composition, chiefly pumice, ash and weakly cemented volcanic sands and shingle. The future situation on Raoul will involve a reduction in the rate and amount of dissection, a tendency to slope decline rather than valley deepening and an eventual flattening of the topography - the peneplain stage in the well-known Davis' cycle of denudation (erosion).

In contrast to Raoul, the young volcanic island of Niuafo'ou is little affected by erosional processes, the original shape of the volcanic cone (pile) and caldera being easily recognizable. Only on secondary volcanoes within the main caldera are the effects of fluvial erosion clearly seen. The cones of these volcanoes are composed largely of ash, and their slopes dissected by a dense network of deep and narrow ravines. In morphological terms, these ravines resemble their counterparts cut in loess in other parts of the world.

The relative absence of dissection on the ocean-facing slopes of Norfolk Island is the result of lithology. The basalt lavas in the island's lower parts are resistant to erosion, and the ash in the island's upper parts are fine-grained and well-graded, attributes which render them much more erosion-resistant than the "loess-like" ash of Niuafo'ou and the cemented breccia and shingle-sand deposits of Raoul.

On account of its non-volcanic origin, the geomorphology of Bagaman Island is somewhat different to those described above (Pain *et al.*, 1979). Bagaman is composed of metamorphosed greenstone schists and all upstanding elements of the island's topography are related to intrusions. The island slopes are cut by a dense network of small steep-sided valleys: there are few tributary valleys. The fluvial geomorphology of oceanic islands depends on their inclination (relief) and stage of evolution (age) among other factors. The most important determinant, however, appears to be the lithology of rocks composing the island.

VOLCANIC LANDFORMS

As described in the preceding section, the primary volcanic landforms of many of the islands visited have been greatly altered by erosion. Nevertheless, on Raoul and Niuafo'ou, primary volcanic landforms such as calderas and basalt plateaus are also seen. Morphologically, the calderas on Raoul and Niuafo'ou are similar although the former has been formed by explosion, the latter by collapse.

The lower parts of Niuafo'ou comprise a basalt lava plateau; some of the most recent eruptions are associated with a fissure in this plateau marked by a number of small volcanic cones, varying in height from 0-50 m, in basal diameter from 30-300 m, and in summit diameter from 5-30 m. The upper parts of these cones are usually composed of ash, the lower parts from basalt lavas. The western part of Niuafo'ou comprises unvegetated lava fields with highly irregular surfaces resulting from lava eruption associated with outbursts of gas.

BIOGENIC LANDFORMS

Biogenic landforms were found on the atolls of Suwarrow and Pukapuka, on the uplifted atoll of Niue, and on the emerged reef platform of Pio Island.

Many atolls were investigated during the expedition on the "Dmitriy Mendeleyev", including Funafuti in Tuvalu (formerly the Ellice Islands), Marakei, Butaritari and Tarawa in Kiribati (formerly the Gilbert Islands), Gardner in Kiribati (formerly the Phoenix Islands), and the uplifted atoll of Nauru. The geomorphology of these islands was fully described in *Geography of Atolls of the South-western Part of the Pacific Ocean* (Kaplin and Medvediev, 1973) and, for this reason, much detail is not repeated here.

The development of biogenic landforms is controlled by four related factors: the growth of coral, relative changes in ocean level (tectonic or eustatic), coastal process regime (reef destruction and detrital accumulation), and lithification of detrital material. The resulting landforms are depicted in Figure 6.

The main geomorphological components of atolls are as follows.

1. A ring reef or a rim including -

    (a) an external slope facing the ocean.
    (b) an external platform (reef flat).
    (c) central part of the reef platform with depositional islands called motus.
    (d) reef flat.

2. An internal lagoon where the following intra-lagoonal reef forms can be distinguished -

    (a) patch or table reefs, frequently shapeless in plan but having flat surfaces.
    (b) coral pinnacles rising from deeper parts of the lagoon.

Two of the atolls visited by the present writer revealed all these elements. Suwarrow is a typical ring atoll, but Pukapuka is more triangular in shape with large motus at its apices.

Unlike the atolls of Tuvalu and Kiribati, the reef platforms of Suwarrow and Pukapuka are not exposed completely at the lowest tides. On both atolls, the outer part of this platform usually has a well-developed rampart with an inner moat dotted with microatolls; groups of coral of the species *Porites* which form a tabular reef, the inner part of which are dead, the outer parts living. The moat is filled in places by partly cemented coral conglomerate derived from the reef edge.

The central part of the reef platform on Suwarrow and Pukapuka is characterized by high areas built

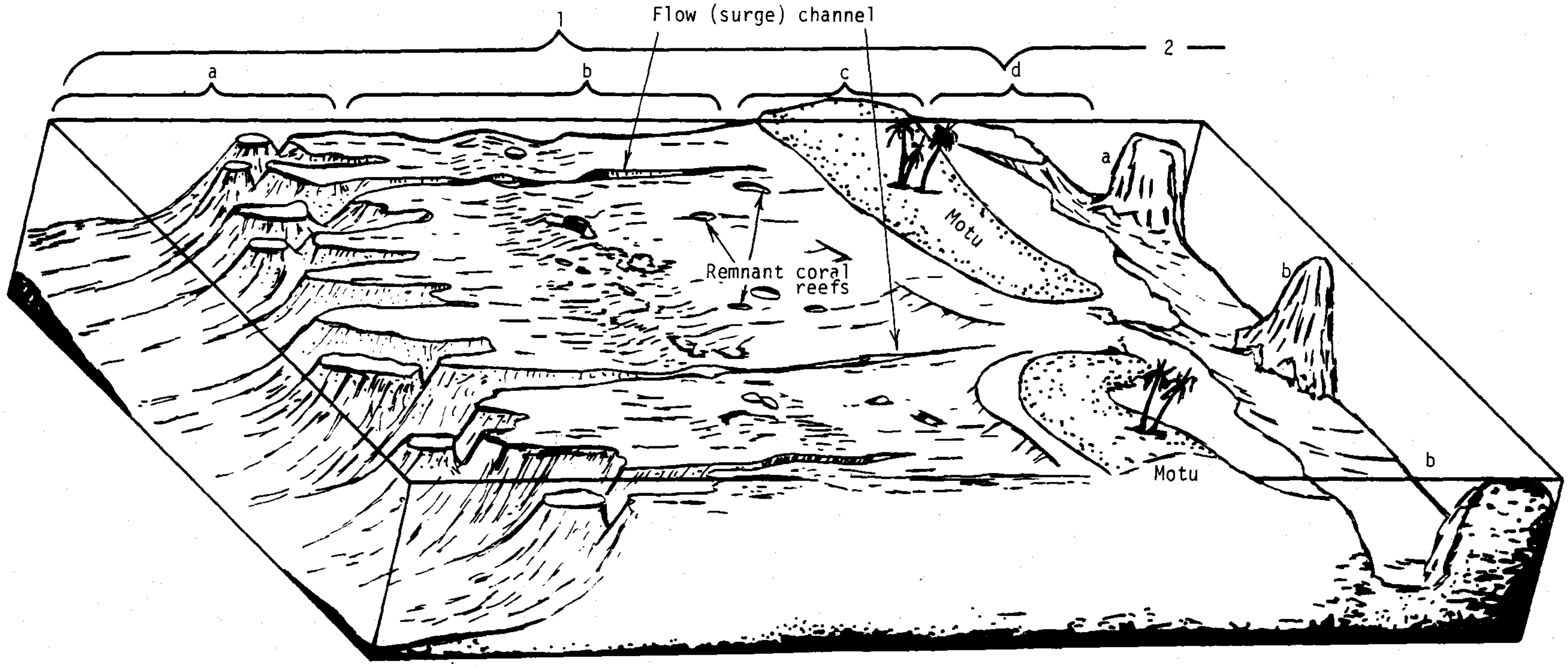

Figure 6. Schematic diagram of the main geomorphological elements of an atoll. Refer to text on previous page for identification of components.

of, or fringed by cemented reef or beachrock. These are the stripped bases of former motus, and their distribution allows convincing palaeogeographic reconstructions of the islands to be made.

On the eastern side of Pukapuka, from Pukapuka to Motu Koe, and on the northeast and east of Suwarrow, from Motu Finau to Anchorage and from Gull Islet to Seven Islands, continuous stretches of motus once existed. It is believed that severe storms in the last few decades have been responsible for the depletion of motus on these atolls. Existing motus have changed their position on the reef so that they are now oriented with their long axes at right angles to the rim.

On Suwarrow, motus occupy only 10% of the rim area. The largest of these, High Island and Anchorage, reach 2.5 m and 3.2 m above the reef flat respectively. These two motus were formed by the coalescence of a series of beach bars, the highest on the ocean side. These bars are built from shingle, angular coral fragments and reef rock in a sand matrix.

Some of the motus on Pukapuka, which occupy about 50% of the rim perimeter, are also unusual. Owing to the triangular shape of the atoll, the motus, lying at the apexes, are typical accumulative shore cusps in origin, formed from clastic material arriving at (other) places on the atoll rim. This material moves along the reef flat to accumulate in the large motus at the apexes. The material is well-rounded and graded as would be expected from longshore (littoral) drift over such comparatively long distances.

Motu Koe, the largest of the Pukapuka motus, is composed of a series of beach bars, whose original forms are still visible in the landscape. The bars are composed of well-rounded shingle and small boulders of coral limestone. Bar height varies from 3.0-5.5 m. A depression with a small lake exists in the interior of Motu Koe.

The lagoons of both Pukapuka and Suwarrow are dotted with patch reefs, mostly consisting of dead coral, even along the lagoonal side of the rim. The reasons for the paucity of living coral are unclear.

The unique structure of the surfaces of Pukapuka and Suwarrow can be attributed to:

1. The effects of tropical cyclones.
2. The low (micro-) tidal range (about 1 m).
3. Negligible or no tectonic subsidence.

The contemporary tectonic condition of these atolls is particularly difficult to assess. Suwarrow is commonly cited as an example of a subsiding atoll (Leontiev and Medvedev, 1972), but this conclusion was based on the observation that motus occupy only a small part of the atoll rim, the inference being that removal of the motus has been assisted by rapid subsidence. However the new data described above suggest that scouring of motus is common during tropical cyclones and that motus may eventually recover their original forms. Weak submergence of this atoll, as suggested by the reef-flat rim protruding seawards, may result from sediment compaction rather than true tectonic subsidence (Badyukova, 1978).* Inconsistencies in the levels and ages of raised reefs on Suwarrow imply recent tectonic disturbance of the atoll (Scoffin *et al.*, 1985). The considerable height (5.5 m) of beach bars on Pukapuka suggests that this atoll may be in the process being uplifted or has at least been stable for a considerable time. The relationship between atoll morphology and tectonics was considered by Montaggioni and Pirazzoli (1984).*

There is clear evidence of uplift on Pio and Niue islands. On Pio, there is a reef platform which has been uplifted 34 m in 50,000 years, in a series of three stages described at the beginning of this chapter. Niue is an uplifted atoll similar to Nauru, which was studied during the expedition on the SS "Dmitriy Mendeleyev" (Kaplin and Medvediev, 1973; Leontiev *et al.*, 1973). Like Nauru, Niue also reveals well-preserved features of an old atoll: its central basinal part corresponds to a former lagoonal floor, and the basin rim to the former ring reef. There are reef terraces on the coast of the island. Niue rises to 91 m above ocean level.

On Nauru, which rises to 67 m, Leontiev *et al.* (1973) identified four reef terraces at 4.5 m, 11-12 m, 22-24 m and 60 m above sea level. The terraces are Holocene, late, middle and early Quaternary respectively in age, and the atoll itself may be of Paleocene age (Leontiev *et al.*, 1973). On Niue, Schofield (1959) identified terraces at 12-15 m, 20-26 m, 60-70 m and, possibly, 40-45 m above sea level. The Holocene accumulative terrace found on Nauru is absent from Niue, where the contemporary reef flat is about 3,000 years old. The three main terraces on Niue were believed by Schofield (1959) to be 100,000, 150,000 and 500,000 years old from lowest to highest but these ages are considered extreme. The Niue terraces probably conform to a similar age sequence as shown by those on Efate (see above).

ISLAND TYPES AND THEIR CLASSIFICATION

Although volcanic and biogenic island types clearly have many points of contrast, they are genetically related and are part of a morphogenetic series, in which each island represents only a stage. The duration (or persistence) of islands in each stage is regulated by the following factors.

1. The patterns of vulcanism in both time and space.

2. The rates of growth and destruction of coral-built edifices.

3. The rates and directions of tectonic movements.

4. The stage of evolution (within a particular evolutionary cycle) and the number of evolutionary cycles a particular island has undergone.

The following genetic classification of islands is based on Darwin's subsidence theory of atoll formation and was first presented by the participants of the 1971 cruise of the SS "Dmitriy Mendeleyev" (Kaplin and Medvediev, 1973). According to this classification, islands are to be regarded as a monocyclic, morphogenetic evolutionary series from young volcanic islands to atolls (Figure 7).

The first in the series is a young island on the shores of which no abrasion (shore) platform has yet developed to allow corals to colonize. Niuafo'ou, as described above, fits this description. Erosion and cliff development will eventually provide a suitable environment for coral-reef development, at first around headlands where the platform is usually widest. Gradually corals will spread over the entire island platform and a volcanic island with a fringing reef such as Rarotonga will eventuate.

The further development of such islands depends on the tectonic subsidence of their volcanic nucleus and the upgrowth of the fringing reef. In this way, the fringing reef becomes converted to a barrier reef which is separated from the island proper by a shallow lagoon as in the case of Borabora in the Society Islands (Guilcher *et al.*, 1969). This situation will occur only when the rate of coral upgrowth can match the rate of subsidence. Obviously, if the latter is too great (perhaps more than 7 mm/year), then the whole structure will be submerged.

In the normal course of events, a further subsidence of the volcanic nucleus and the upgrowth of reef coral will lead to the complete disappearance of the former beneath sea level and the formation of a normal or typical atoll with a fringing reef (rim) supporting separate motus. Examples include Funafuti and Suwarrow, which were visited on our expeditions.

Drilling operations on various atolls have revealed Oligocene and Miocene reef sequences rising from volcanic basements 1,000-1,2000 m below sea level (Stoddart, 1973). This gives an age for atoll development of 20-40 million years. Among the reasons why an atoll may itself became submerged are rapid tectonic subsidence and/or rapid sea-level rise. At least twenty-two submerged atolls are known in the Pacific (Fairbridge and Stewart, 1960; Kaplin and Medvediev, 1973). Among them is Robby Bank, south of Kiribati, where minimum depth above the ring reef is 13 m and maximum depth above the drowned lagoon floor is 54 m. Such submerged atolls will eventually become guyots.

Clearly when a normal atoll becomes transformed into an uplifted atoll, the dominant tectonic trend has been reversed. The first stage in uplift of a normal atoll would appear to be signalled by the coalescence of formerly isolated motus, such as at Gardner Atoll which was visited during the sixth voyage of the SS "Dmitriy Mendeleyev". The next stage in uplift of an atoll would be a low coral island with a lake in its center, such as Vaitupu in Tuvalu. The well-developed uplifted atolls of Niue and Nauru have been discussed above: another example is Makatea (Montaggioni *et* al.,., 1985).

The continued uplift of young volcanic islands with fringing reefs will eventually result in the formation of a fossil reef terrace above sea level and a new fringing reef at a lower level. The latter will also form a terrace if uplift continues and this can lead to the formation of a staircase of reef terraces, each of which marks a stage in uplift history. Among such islands, we can cite Efate (see above) and many other islands characteristic of island arcs, such as the Ryukyus, Palau, Solomon Islands and Vanuatu (Jouannic *et al.*, 1980; Kawana and Pirazzoli, 1984; 1985).

The evolutionary cycle of oceanic islands outside the coral seas appears to be simpler than those within, but for islands of the continental and intermediate zone, the classification given above is inapplicable, and an all-embracing classification needs to be developed in the future.

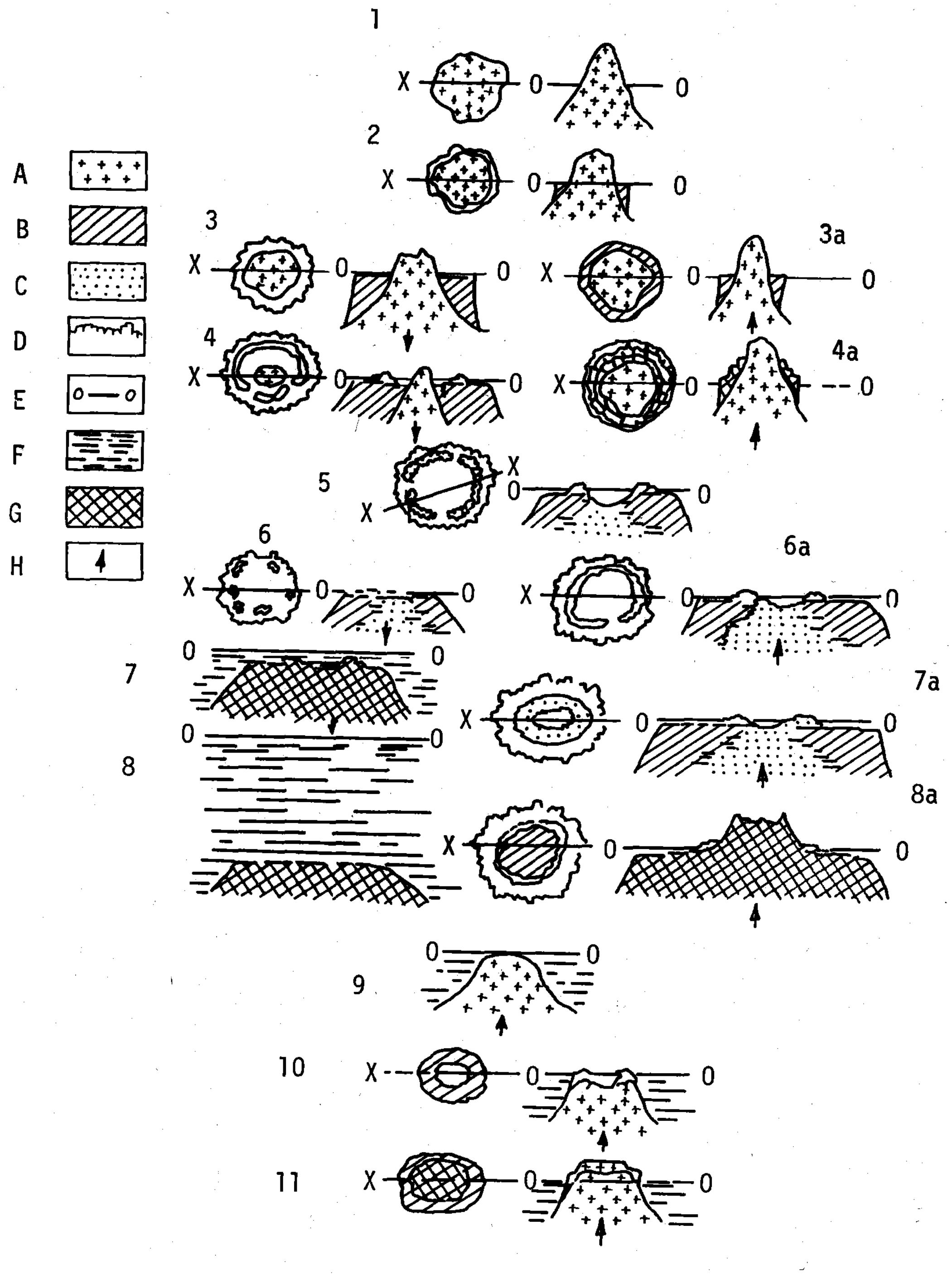

Figure 7. Evolution of oceanic islands. Legend: 1. Young volcanic island (Niuafo'ou); 2. Volcanic island with fringing reef (Rarotonga); 3. Volcanic island with barrier reef (Borabora); 3a. Volcanic with raised fringing reef; 4. Atoll with volcanic nucleus (Oneata Island, Fiji); 4a. Volcanic island with reef terraces (Efate); 5. True atoll (Funafuti); 6. Atoll undergoing submergence (Suwarrow); 7. Submerged atoll (Robby Bank, Tuvalu); 8a. Uplifted limestone island (Nauru); 9. Submarine volcano; 10. Terminal reef structure on an uplifted volcanic base (true atoll); 11. Uplifted atoll (Niue); A. Volcanic rock; B. Coral limestone; C. Unconsolidated sediments; D. Coral reefs; E. Sea level; F. Sequence of ocean levels; G. Old limestone; H. Direction of tectonic movements; X. Direction of profile.

CHAPTER III. SOILS AND SOIL FORMATION ON PACIFIC ISLANDS

V. O. TARGULIAN AND P. V. YELPATIEVSKY

INTRODUCTION

This chapter discusses the origins, geography, evolution and anthropogenic transformation of the soils and ecosystems on some small tropical humid islands of the Pacific Ocean.

A detailed discussion of island ecosystems as integrated formations and of the individual components of their environments is given in other sections of this monograph. The discussion in this chapter is confined, therefore, to a brief review of those factors which directly control the formation and distribution of the main groups of soils.

GEOLOGY, ISLAND RELIEF, AND PARENT ROCKS

To describe the features of pedogenesis on the islands visited, it is convenient to separate them into the three groups as defined in Chapter II:

1. Continental and intermediate islands, (New Guinea, Bagaman, Viti Levu, Guadalcanal).
2. Oceanic, and intermediate volcanic islands (Norfolk, Raoul, Niuafo'ou).
3. Oceanic coral islands, high and low atolls (Pio, Suwarrow, Pukapuka).

The continental islands examined were of mid to low elevation and highly dissected. Characteristics of such islands include: free surface drainage of all landscapes, absence of pronounced features of excessive moisture in geochemically self-contained island landscapes, and a relative absence of gleying and hydromorphism in soils and weathering crusts. On these islands the parent rocks for soils are diverse, with different consolidated sedimentary and metamorphic silicate rocks, basaltic and andesitic eruptive rocks, and coral limestone being common in all coastal areas.

The volcanic islands are clearly subdivided into lava islands of shield volcanoes (Norfok Island) and strato-volcanoes overlain by a series of stratified pyroclastic deposits (Raoul, Niuafo'ou).

Norfolk Island is characterized by a mature, moderately dissected erosional relief, which ensures good surface drainage of the island. The parent rocks are mafic lavas and welded tuffs of basic composition, variable porosity and levels of crystallization.

On the volcanic islands of the pyroclastic type, greater relative relief produced by erosional dissection is combined with free, intra-soil drainage (vertical infiltration of moisture). The loose pyroclastic layers overlaying these islands are composed of aerial or re-deposited volcanic ash, sands, scoria and pumice of moderately mafic composition, which have high porosity, low bulk density, light texture, high proportions of rock debris and sand, and low percentage of clay.

The coral islands include both raised coral islands with heights in tens of meters and low islands, or true atolls, rising only to a few meters above sea level. On the high coral islands, marine terraces are common. Terrace surfaces are flat and weakly dissected. Surface drainage of coral islands is usually imperfect or poor, but overall drainage of such islands is good due to the high permeability of the soils and of the underlying coral substratum. On the coral islands, the soil parent materials are sandy or sandy-rubble (loose layers composed of coral sand and rubble). Sometimes they have admixtures of particles of light, volcanic pumice and ash, which float in water and are brought to beaches by longshore drifting.

Thus, weathering and pedogenesis on the flat interfluves of all the islands studied are mostly characterized by good drainage of the soil profiles, and the absence of clearly pronounced prolonged periods of excessive wetness, gleying, and hydromorphism. This, naturally, does not imply that the phenomena of hydromorphism and gleying are completely absent in island soils. They are clearly important in soils of low lying areas, in small flat-bottomed valleys, streams, and on low marine terraces, and most clearly - in soils of mangrove areas. However, such soils were not studied during this expedition, and are not described in this paper. Signs of excessive wetness in flat interfluvial soils were met only twice: on the ferrallitic, clayey weathering crusts, soils of the high altitude cloud-moss forest of New Guinea, and in brown tropical soils under grasslands on Bagaman.

In the majority of ferrallitic type soils, the loose clay masses are generally well structured providing for free drainage of the profile.

The parent materials of the soils and crusts of the islands visited can be subdivided into three main groups:

1. Dense, mica-quartz-feldspar silicate rocks (e.g. sandstone, schists).

2. Mica-free and quartz-free mafic and intermediate eruptive rocks (lavas, tuff, scoria, pumice, sand and ash).

3. Biogenic, dense coral limestones and their detrital derivatives.

The different composition of these three groups of rocks produces important effects on soil formation which result in different types of mature soil profiles despite similar climate-induced weathering processes. Investigation of the convergence of soil types and of types of weathering crusts should take into account parent rock composition, as well as the age, duration of the processes of pedogenesis and weathering, ferrallitic weathering and further soil formation.

Similar, but more rapid weathering and pedogenesis occurs under anthropogenically induced erosion in montane forest areas on ancient islands. Shifting agriculture, which has been practiced by local peoples for centuries, or even thousands of years, causes destruction of primary forests, development of grasslands and secondary forests. Exposure of the bare or disturbed soil surfaces in the humid climate of the tropics results in extremely heavy sheet, rill and landslide erosion (Gerasimov, 1976; Buringh, 1979; Moormann and Wambeke, 1978).

Due to these factors, humid tropical areas, including the ancient islands of New Guinea, Bagaman, Guadalcanal, Viti Levu, and Norfolk have areas overlain by mature ferrallitic weathering crusts, combined with extensive areas rejuvenated by denudation and erosion.

Another important factor in soil rejuvenation on ancient islands is volcanic activity. In this case old soils and crusts can either be overlain or buried by streams of lava, providing a surface which again undergoes pedogenesis, as for example in areas of Viti Levu and Niuafo'ou, or be rejuvenated through aerial influx of loose pyroclastic matter, ash, sand, and scoria from active volcanoes. Deposition of these completely unweathered products on the surfaces of ancient ferrallitic soils may be of different thickness; from thick layers completely burying the soil to an insignificant dusting.

In general, there are two age classes of soils and weathering crusts on ancient islands: very old soils, aged probably hundreds of thousands or even millions of years-the so called ferrallitic mature soils and weathering crusts with well developed profiles; and young soils, aged from tens and hundreds of years to thousands and tens thousands of years - the immature brown tropical and volcanic soils.

On the young volcanic islands of the Pacific with present-day surfaces datable within the Holocene, volcanic activity, including discharges of ash, scoria, pumice and eruptions of lava (Raoul, Niuafo'ou), is still occurring. On these islands the soils have mostly developed on aerial, volcanogenic layers, where the oldest layers of aerial pyroclastic materials, and correspondingly, the oldest buried soil subprofiles are located in the lower part of the soil, and the most recent, on the present-day surface. Owing to this periodic, regular rejuvenation the soils on such islands become older with depth. However, in general these islands are characterized, by rather young pyroclastic deposits within soil profiles ranging in age from tens of years to thousands of years. Rejuvenation of such soils through erosion is insignificant, since surface erosion on these islands is low, because of the high permeability of soils and pyroclastic rocks.

Coral islands differ in age. High islands up to 20-50 m above sea level, such as Pio, are between 20-50,000 years. The flat relief of these islands, combined with primary forest vegetation (e.g. Pio) suppresses denudation of the loose rock and thus suggests that the age of the marine terraces surfaces on these islands and of the soil are about the same; some terraces on Niue were dated to 20-23,000 years (see Chapter II).

Low coral islands, or atolls are usually several thousands of years old. The low elevations of these islands makes them extremely vulnerable to hurricanes which fell trees, and move sand, rock debris and blocks to the island surface. The age of the soils on such islands can be extremely variable but is often much younger by tens, or hundreds of years than the island itself.

CLIMATE AND LANDSCAPES OF ISLANDS

For elevations from sea level up to 200 m the islands have hot tropical and subtropical climates which are permanently humid or have comparatively short dry periods of around 2 months. Differences in climate (and in temperature and moisture regimes) at these elevations have no significant effect on the genesis and geography of soils. The impact of vertical changes of climate is pronounced in the mountains of New Guinea and on Raoul Island. However, detailed data on climate changes with elevation on these islands were not readily available to the present authors. There is, however, considerable evidence to indicate that moisture levels generally increase with elevation while temperature decreases. Temperature lapse rates in this region are in the range 0.5-1 ° C for each 100 m rise in altitude (see, for example, Curry, 1962).

The biotic components of island ecosystems are linked with the main climatic characteristics of the tropics and subtropics. The flora and fauna of the islands are highly dependent on island age, geology, topography, and lithology.

The most mature and complex communities are found on ancient continental and intermediate islands built of silicate rocks. The younger the island, the greater its remoteness from continents, and the poorer the mineral substratum of the island, the less diverse and simpler is the structure of its climax vegetation.

Pedogenesis on the islands has been and is taking place mainly under different types of primary and secondary forest vegetation. Despite the great diversity of forest vegetation, this was not reflected in the soil profiles determined during the voyage of the Callisto. Silicate rocks of different ages produce morphologically rather similar, dark-colored, thick (up to 15-20 cm) horizons of organic accumulation with mull type humus under primary and secondary closed-canopy forests. No differentiation of the soil profile due to humus translocation was observed. A similar pattern is found in the grassland areas.

On the carbonate coral substrata of young atolls two types of organic material dominate profiles; a dark horizon of humus accumulation is formed under coconut palms, breadfruit and other trees, while under *Pisonia* trees, a very specific peaty-illuvial-humic profile is formed. Thus, with the exception of the *Pisonia* forests on young atolls, the different types of vegetation cover on the other islands produces, by interaction with parent materials of different age and composition, a mull humus accumulation profile.

THE MAIN GROUPS OF SOILS

To identify the principal soil groups on islands which were studied, observations were compared with the available information on soils of humid tropics and subtropics, including those concerned with soils of the Pacific region (Fridland, 1961; Gerasimov, 1976; Zonn, 1974; Glazovskaya, 1973; Mohr, *et al.*, 1972; Soils of humid tropics, 1972; Young, 1976; Moormann and Van Wambeke, 1978; Buringh, 1979; Stephens and Hutton, 1954; Cline, 1955; Wright and Metson, 1959; Dudal and Soepraptohardjo 1960; Sherman and Ikawa, 1968; Wright, 1963; Wright and van Westerndorp, 1965; Twyford and Wright, 1965; Tercinier, 1962; Haantjens *et al.*, 1967; Wiens, 1962; Quantin, 1972, 1975).

As a working morphological-profile grouping for the island soils, the soils were subdivided by groups and named in accordance with the traditional Russian nomenclature and their approximate synonyms of the FAO/UNESCO Legend to the Soil Map of the World (FAO/UNESCO, 1974). This classification is presented below:

1. Ferrallitic (Ferralsols).
2. Brown tropical (Cambisols).
3. Volcanic humus-allophanic (Andosols).
4. Ferrallitic-carbonate (the synonym is not obvious, the former tropical terra rossa, probably Chromic or Calcic Luvisols).
5. Humus-carbonate soils of atolls (Regosols/Rendzinas).
6. Peaty Al-Fe-humic (the synonym is not obvious, probably the Podzols or Humic Cambisols).

However, given the inadequate knowledge of island soils, the incomplete analytical investigation of samples, imperfections of the Soviet classifications for soils of the Pacific island area, and the great diversity of classifications employed by different authorities (FAO, French, New Zealand, USA, Australia) it is difficult to develop an accurate classification of island soils.

In this study the term "group of soils" is used to designate large groups or types of soil unified by similar morphological features of their profiles. Some of the groups are subdivided further into different types of soil profiles.

FERRALLITIC SOILS

Representative soils of this group were studied on New Guinea, Bagaman, Guadalcanal, Viti Levu and Norfolk, which have different climates and vegetation cover. The important factors for the development of ferrallitic soils are their great age, the silicate composition of the parent rock, and their essential morphological features. These soils are characterized by: red or red-yellow colors, high proportions of clay, heavy texture, and absence or low content of rock debris and gravel of parent material origin in the upper and middle horizons of the profile.

Precise ages of the present-day surfaces of these islands and of the ferrallitic layers are not available. According to Kaplin (pers. comm.), such layers are present in those parts of the islands which belong to the Pliocene-Oligocene, or older periods. The soils are probably, somewhat younger due to denudation on mountainous islands or to rejuvenation by lava eruptions on volcanic islands (Norfolk Island). The formation of thick, ferrallitic layers is known to take hundreds of years of subaerial development and weathering of igneous rock surfaces. The depth of the red or red-yellow clay, ferrallitic layers at the six sites examined was usually no more than 1.5-2 m; the lower 0.5-1 m consisted of either lithomarge (argillaceous layers altered by retention of the original rock architecture) or saprolite (produced by rock or fine earth weathering with conservation of the parent rock structure). Deeper in the profile this zone rapidly changes to weakly weathered, compact parent rock. Humid-tropical weathering crusts with full profiles, developed in tectonically stable areas are as a rule, up to tens of meters deep. The shallowness of the ferrallitic layers and their rapid replacement by parent rock suggest that these profiles are incomplete (truncated) when compared to the age of the islands.

The soils examined may be the remnants of thick, formerly full-profiled ferrallitic crusts of ancient age comparable with the age of the islands from which the upper and middle parts have been removed by natural denudation and prolonged anthropogenic erosion, leaving only the lower parts of the original profile *in situ*. Modern soil formation may be superimposed on such eroded ancient layers of ferrallitic material (Gerasimov, 1976; Romashkevich, 1974) however, it should be emphasized that the remaining lower parts of the main profiles consist of thoroughly weathered material which does not display significant morphological changes within the soil profile. This explanation implies at least three major stages in the evolution of ancient crusts and soils on island surfaces: (a) the formation of the full-profile soils and crusts, tens of meters deep; (b) the stage, or stages of denudation and erosion of a considerable portion of the soils and crusts, (c) modern soil formation superimposed on the lower denuded "remains" of the full profile.

An alternative explanation, applicable to tectonically rising islands or areas of dissected relief, is that denudation and erosion are permanent companions of the processes of ferrallitic crust and soil formation, and therefore, no thick full-profile ferrallitic crusts are formed. A dynamic equilibrium is thus established between the processes of ferrallitic alteration of the parent rocks and the processes of erosion-denudation which remove the most weathered (upper) horizons. The soil profile formed in this case would not undergo the above stages as the equilibrium is rapidly stabilised; the profile depth reflects the relationship between the processes of weathering and denudation. Such a process can be very prolonged, and produce in the total period of operation rather shallow (2 to 3 m) ferrallitic layers, which are rapidly replaced by parent rock. At present, insufficient data are available to determine which of these explanations is correct.

Analysis of the ferrallitic soil profiles shows that below the layer of shallow (1 to 3 cm) litter there is usually a dark-colored (dark-grey, dark-brown) A1 horizon with strongly developed granular structure, an abundance of worm-casts and soft accumulative mull humus. Depths of A1 horizons are from 10 to 30 cm below which the transitional AB horizons clearly display the features of red or red-yellow ferrallitic horizons together with signs of humification. Still deeper, uniform red or red-yellow layers with strongly developed blocky or subangular blocky structure are found; these are subdivided into horizons by structure and color (Bw1, Bw2, BC horizons). In these layers practically no signs of differentiation due to material movement are observed; peds have no illuvial cutans, textures are rather uniform, and signs of gleying are absent. Sometimes small dense, dark red concretions are found. Such "soil-like" strata, grade gradually or abruptly into horizons of lithomarge and/or saprolite, which have different structures, but which always retain the structural features of the parent rocks (eruptives, schists, basalts). This common stratigraphy agrees well with the general scheme of vertical zones of eluvial strata in the tropics and subtropics as suggested by Gerasimov (1976).

On one site on Norfolk Island a red ferrallitic soil was observed, which had neither a saprolitic horizon, nor parent rock remains ("krasnozem") above a depth of 2 m. The generally shallow occurrence of the zones of lithomarge, saprolite, and parent rock tend to indicate that these soils have truncated profiles. The thickness of the unconsolidated layers, does not fully reflect the total hypergenic potential (intensity and duration) of weathering and pedogenesis which should have occurred over the life of the island.

Judged by its color and texture, the fine earth fraction is close to the final-equilibrium ferrallitic state, although sometimes does include presumably younger, gravelly material derived from the parent rock. Such a combination of mature and immature features suggests that the soils are probably the remains of denuded, thick, full-profile ferrallitic soils and weathering crusts, rather than the product of ferrallitic soils forming under conditions of permanent denudation. The concept of "dynamic maturity" does not provide an explanation for the existence of strongly weathered fine earth and weakly weathered gravels and other parent rock occurring in the same horizon.

The present soil profile (and in particular, the humus influenced part of the profile) is superimposed on the older ferrallitic (or ferrallitised) materials. Since the main ferrallitic trend of pedogenesis and weathering was, in general, the same during the whole subaerial period, the present stage of soil formation is characterized by comparatively small changes in the inherited ferrallitic part of the ancient profile.

These changes involve the formation of the humus influenced part of the profile. A thick, dark-colored humus horizon is an important feature in ferrallitic soils and thus, its genesis is of considerable interest. This horizon, up to 30 cm deep, is formed under unbroken closed-canopy forests. The main source of organic matter in these soils is provided by tree debris and this depth of litter along with dark color of the humus and its mull type characteristics suggest that the process of decomposition and humification of organic debris is rapid and does not follow the "classical" type of eluvial-illuvial humus profile of closed-canopy forests. No upper residual zone of peaty litter free of mobile humus, and no lower zone of illuvial accumulation of mobile forms of humus are formed. On the contrary, a mull-accumulation (isohumic) type of profile is formed: the organic debris or shallow litter layer is immediately followed by strongly structured humic horizons, where the dark dispersed humus grades into the mineral soil. Further investigations are necessary to determine whether this humus is formed *in situ* from tree roots, surface organic debris and/or the role of soil fauna, which transform the debris and "drag" it down to mineral horizons. The dark color of the humus, and its distribution suggest that, part of the humus profile could probably be formed by the downward translocation of organic matter.

Another specific feature of the ferrallitic soils is the absence of color and particle differentiation as a result of translocation in the mineral profile. The subdivision of horizons in the profile is based essentially on the level of humification, structure and color of the mineral substance, presence of rock debris, and other features. Macro- and mesomorphological studies, (including the bleaching of the mineral mass, elution of silt, illuviation of clay and humus, the amount of oxyhydroxides of Fe and Al in the profiles), all suggest that illuviation and eluviation in profile and horizon formation in these soils is relatively insignificant.

The factors responsible for the lack of eluvial-illuvial differentiation of these ferrallitic soils may be as follows:

1. Good internal soil drainage associated with the strongly developed structure of the loamy-clay fine earth; absence of prolonged periods of saturation, which prevent eluvial-gley and peptisation-suspension differentiation.

2. Accmulative-mull character of humus formation; in this case the production of humic acids capable of chelating and transporting iron and aluminium is low; this prevents humus-acidic differentiation of the profile.

3. High level of weathering of the mineral subsoil fine earth fraction, stability of fine earth and of the silt fraction under the impact of water and humus solutions, and resultant lower differentiation of the profile by mineral alteration and migrational processes.

An interesting phemonenon is the considerable morphological similarity of the humid tropical ferrallitic soils (Bagaman, Viti Levu, Guadalcanal), and of subtropical island ferrallitic soils (Norfolk). Despite different soil parent materials (schists, basalts), types of forest, and climatic regimes, the general morphogenetic features of the profiles of tropical and subtropical soils are very similar. This similarity may be due to the same dominant trend in the processes of pedogenesis and weathering both in the humid tropics and the subtropics. Although different rates of pedogensis and weathering may occur, the outcomes of these processes - mature and equilibrium soils with similar properties result from the length of time over which the processes have occurred.

It is likely that the process of humus formation in such soils is rapid. Given enough time for development the humus influenced parts of tropical and subtropical soils appear mature, and basically the same.

The ferrallitic alteration of the mineral subsoil is essentially completed in the earlier cycles of pedogenesis (before erosion of the full-profile layers). Therefore, the sensitivity of the mineral subsoil to differences in the present intensity of the pedogenic processes is considerably weakened. If during the long period of soil formation and weathering the main portion of fine earth has already been transformed to the ferrallitic state, then the different potential intensities of soil weathering on subtropical and tropical islands may not be reflected in the properties of their fine earth and clays. Generally, the ferrallitic soils of tropical and subtropical islands may be classed as Humic Ferralsols.

The ferrallitic character of these soils is little influenced by present biological and abiotic factors. In this sense, ferrallitic soils are stable formations with respect to the biotic communities developed on them; they do not have a clear evolutionary trend under the influence of biotic factors. Further evolution, development or degradation of ferrallitic soils will depend on possible changes in abiotic factors such as, climate and geological-geomorphological processes, rather than on biotic factors.

BROWN TROPICAL SOILS

These soils were studied on Bagaman Island, but are widespread throughout the humid-tropics on recent surfaces or those rejuvenated by erosion and denudation (Moormann and Van Wambeke, 1978; Buringh, 1979). On Bagaman, brown soils were found in close association with red-yellow ferrallitic soils; the former occupied the surfaces and slopes having northern and north-eastern aspects while the latter were found on slopes of southern aspect. Both types of soils develop in very similar environmental conditions: the same parent rock of grey-greenish mica schists, good surface drainage, similar atmospheric-climatic regimes, and a closed-canopy, multispecies, evergreen forest.

In comparison with neighboring ferrallitic soils, the brown soils have shallower profiles (0.5-1.0 m.) and a higher content of schist debris, which is less weathered than that in ferrallitic profiles.

A typical brown soil profile consists of a thin litter layer mixed with a large amount of large worm casts. The upper part of the mineral profile is represented by a rather thick (10-20 cm) dark-colored, mull humus A horizon. Below the A horizon is a relatively thick, transitional AB horizon, consisting of a mixture of more humified fine loam and of yellow-brown, coarser loam. This transitional horizon is underlain by yellow and brown horizons. On slopes these horizons consist of a mixture of yellow-brown loam and strongly or normally weathered schist debris. On ridges and in the upper parts of slopes, the AB horizons grade into yellow-brown (B-BC) horizons of schist, lithomarge/saprolite. In these horizons the extent of schist weathering varies greatly; heavily weathered layers, which are easily cut by a spade or a knife, lie close to compact layers, which can only be broken with a hammer and a pick. The level of schist weathering declines rapidly with depth; at 0.7-1.0 m the profile reaches a layer of schisty compact light-yellow-brown saprolite.

The profiles of the brown soils suggest that these are rejuvenated soils of ancient islands, which have undergone long periods of weathering and pedogenesis. Unlike the ferrallitic soils, the brown tropical soils are developed on surfaces where denudation has been much greater.

The parent rock with local small enclaves of brown and yellow-brown lithomarge and saprolite zones were exposed at the present-day surface. Judging by their morphology in the former full-profile, ferrallitic weathering crust, these saprolitic layers represented the lowest point of weathering where complete ferrallitic metamorphism has not been achieved. In the final stages of denudation both the material of these zones, and the comparatively more recent parent rock materials were subject to scouring and re-deposition elsewhere. Therefore, the enclaves of saprolite and lithomarge remaining *in situ* (residues of ancient crusts and soils) are often overlapped by a shallow, yellow-brown mantle of loam and hard schist debris. This rejuvenated rock produces the brown tropical soils which have layers of lithomarge and saprolite at depths below 40-50 cm and harder and fresher rock on the surface and in the humus-rich horizons.

Thus, the brown tropical soil on ancient islands is an example of a radically rejuvenated soil profile, where the processes of rock weathering return to the initial and intermediate mostly ferrasiallitic stages, and the new cycle of weathering and soil formation has not yet reached the ferrallitic state.

The abundance of parent rock debris in brown forest soils obviously promotes the ferrallitic weathering character of the mineral substratum of these soils, and delays the onset of the ferrallitic stage.

In terms of morphology brown tropical soils appear quite well-developed and mature. The plant communities formed over these soils appear equally mature in their structure and organization compared to the vegetation on ferrallitic soils. This suggests that the brown soils are not ephemeral in the sequence of humid tropical soils development. They do not represent a short-term phase in the evolution of the ferrallitic soils, but are rather a prolonged and stable stage of a generally very long-term process of "climax" ferrallitic soils formation which takes place under humid tropical, mature climax communities. In order to complete this development, a higher level of weathering of the mineral soil substratum, and a considerable increase in the thickness of soil and of the weathering crust is necessary.

The high degree of similarity in the humus profile of ferrallitic and brown tropical soils suggests also that the humus horizons are mature and in equilibrium with the vegetation. Thus the transition of brown to ferrallitic soils may be controlled not by the humus regime of soils and their biotic stage in general, but by the overall hydrothermic situation in the humid tropics, by the action of water, dissolved carbonic acid, and permanently high temperatures.

Like the ferrallitic soils, the brown tropical soils are characterized by the lack of eluvial-illuvial morphological differentiation of the mineral mass; zones of material outflow are not pronounced, and the signs of illuviation are very vague.

On the whole, the morphological profile of the brown tropical soils (although comparatively young and immature in humid tropical terms) appears as mature as those of the temperate humid brown forest soils. If one compares the soils on similar parent rock and in similar topographic conditions, it appears that the brown forest soils of temperate areas have a slightly shallower humus horizon and a less weathered mineral profile, in situations where they are not based on derivatives of ancient weathering crusts. Generally, the simple development of the profile, the non-differentiated mineral mass, the mull humus-accumulation horizons, shallowness of the solum, and the abundance of rock debris, all make the brown soils ofthe humid tropics very similar to those of temperate (non-tropical) areas.

In this connection there is an interesting problem relating to the soils of humid areas and their age. Brown forest soils are considered the mature "climax" soils in moderately warm humid areas. However these soils are younger, and absolute dating in these non-tropical areas usually gives a maximum age of Holocene or Upper-Pleistocene. Fully developed ferrallitic soils in the humid tropics are usually dated to earlier periods of the Lower Quaternary, Tertiary and even earlier. Despite the fact that they are rarely preserved in full profile, the red-yellow soils are considered the time related homologous forms of the mature soils of higher latitude humid areas.

The brown forest soils of humid subtropics given their occurrence in dissected relief, and the characteristics of parent rock, drainage, and absolute dating, are not homologous with the red-yellow, climax, ferrallitic soils of the tropics, but rather with the brown tropical soils, which are of the same age. Fully developed ferrallitic soils have no comparable homologous forms in temperate humid zones. Even in cases where the ferrallitic soils are considerably rejuvenated by denudation, and have a considerably lower absolute age, no temperate equivalent is known.

The characteristics of brown tropical soils may be interpreted in terms of pedogenetic stages of an acid, eluvial, tialferric type of soil weathering (Targulian et al., 1978). The main preconditions for this trend in soil evolution is a long period of weathering and pedogenesis in an acidic, eluvial situation, and the absence of interference of the processes of rejuvenation and renewal of materials subject to transformation (i.e., without denudation and/or the import of fresh material).

For dissected montane islands, with presently high rates of denudation and anthropogenic erosion, this precondition may be absent. In this case, the brown tropical soils may represent a dynamic equilibrium, or quasi-mature form of pedogenesis, which does not evolve to ferrallitic soils. This dynamic equilibrium can be maintained by similar rates of soil profile formation in contrast to soil denudation. These processes cause the re-establishment of the earlier states of weathering through natural denudation and anthropogenic erosion of the more weathered soil horizons, and continuous "capture" by the soil profile of fresher non-weathered parent rock material. According to this evolutionary model, the brown tropical soil is a permanent self-regenerating stage of the soil cover of humid tropical areas.

In each of the above two evolutionary scenarios, brown soils are considered less mature, less weathered and more sensitive to spatial variations of soil-forming factors than ferrallitic soils. As a result of their higher content of non-weathered silicate materials, the brown tropical soils represent a more eutrophic substratum for plants than ferrallitic soils.

TROPICAL AND SUBTROPICAL VOLCANIC SOILS

These soils were studied on two islands: Niuafo'ou in the humid tropics and Raoul in the humid subtropics. The volcanic soils on these islands display many of the general features found in the whole class of volcanic soils (see Wright and Metson, 1959; Quantin, 1972, 1975; Sokolov, 1973) including:

1. Laminated soil profiles as a result of periodic, regular aerial additions of matter to the present-day surface.

2. The presence of buried, "incised" soil subprofiles or individual soil horizons of varying degrees of preservation in the typical profile.

3. Generally young soil profiles and, as a result, underdevelopment or poor development of many soil forming processes.

4. Inversion of pedogenetic horizons; the surface horizons of volcanic soils are the most recent, and the minimum age of the upper soil horizons under intensive ash falls may be at most, tens of years.

5. Active, recent processes (biological, migrational, etc.) covering the whole soil profile 1-2 m deep, including the systems of incised buried subprofiles.

6. Transformation of the buried subprofiles and horizons in the total profile under impact of recent factors and processes of pedogenesis.

The above features are manifested differently on each island, and in the different parts of the islands, and are dependent on the frequency and intensity of aerial ash-falls on the present-day surface. The western sectors of Raoul and Niuafo'ou were and are, apparently, subject to more frequent and intensive ash-falls than the eastern parts. Correspondingly, the soils in the western sectors of the islands are young, more primitive and have more laminated profiles. On the whole, the tropical and subtropical volcanic soils studied on these islands are characterized by a mineralogy indicative of recent deposition. The dates for the present-day and buried subprofiles range between tens of years and several thousands of years particularly in those subject to intensive ash falls.

Because of their recently developed volcanic soils, these islands lack well developed ferrallitic horizons and strongly-weathered surface deposits within 1-2 m of their present surface. The indications of ferrallitization, rebufaction and argillification are rarely observed in the buried sub-profiles on Niuafo'ou. The recent lava surfaces on this island do not show any visible signs of weathering; the lava block surfaces are devoid of even thin weathering cutans.

The common morphological features of the volcanic soils studied on the above mentioned islands are as follows:

1. Dark-colored and thick (up to 20-30 cm) organic-accumulation horizons ranging in composition from mull to coarse humus depending on soil depth. This feature suggests rapid formation of a comparatively mature humus profile on young, poorly weathered pyroclastic substrates.

2. Light textures of the mineral subsoil - sand, sandy loam, or gravelly (pumice-scorial) sands - upper horizons are the least transformed by pedogenesis and weathering; with depth, the level of transformation of the soil mass becomes greater.

3. Predominance of black, grey and brown colors in the mineral mass associated with the original color of the fresh pyroclastic material and little weathering.

4. Very low amounts of weathering and pedogenic products - fractions of silt, films of iron and aluminium oxyhydroxides, etc. These observations suggest that in volcanically active areas of the humid tropics and sub-tropics, pedogenesis is characterized during the first tens to thousands of years by the rather rapid formation of the humus soil profile on the one hand, and by relatively slow alteration and differentiation of the soil mineral layers, on the other. Judging by the morphology of soils, the rates of pedogenic weathering of the intermediate and basic pyroclastic rocks are quite low and do not greatly differ from the rates of weathering in the boreal and temperate areas of the Pacific volcanic belt (Kamchatka, Kurils, Japan).

The volcanic soils represent a diverse group differentiated by the character of the horizons of organic matter accumulation, by color and composition of the mineral fraction, and by the presence and transformation of buried subprofiles.

Primitive Volcanic Laminated-ash Soils And Primitive Stony Soils On Lavas

These soils are found on the youngest rock, in areas of recent and intensive ash-falls and lava flows on both islands. They are characterized by thin forest litter horizons, below which are humus horizons 5 to 10 cm thick, and practically unaltered black and grey-black ash layers, black porous lavas, and grey or red (burnt) pumice. These are not soils in the full sense of the word.

Volcanic Soils With Well-developed Humus Horizons

These soils display weak weathering in the mineral portion of the profile. The original structure and color of the rock is maintained, or it is light-brown in coloring. They form the largest subgroup of volcanic soils, widespread on Raoul, and are less common on Niuafo'ou. Such soils are found on comparatively younger surfaces and those sections of the islands which have less intensive ash-falls (both in total amount and frequency).

This group is characterized by 20-30 cm thick, dark colored (nearly black, dark brown, dark grey) A horizons of organic matter accumulation. The color and composition of these horizons changes considerably with latitudinal and altitudinal bioclimatic zones of the island ecosystems. Thus further subdivision of this sub-group is possible. Morphological studies established the following profile categories:

1. Volcanic soils with dark-grey and black mull humus horizons, thin litter (1-2 cm) layers, abruptly followed by an A1 horizon with well-humified organic matter, practically devoid of coarse organic residues, dispersed and associated with the mineral ash mass. Depending on the original color of the ash material the humus horizon may have a black color (on the black basalt ash of Niuafo'ou) or dark-grey (on the grey andesite-basalt ash and pumice of Raoul).

With depth these dark mull horizons are gradually or sharply changed by weakly weathered laminated layers of ash, scoria or pumice of black, brown, or grey color without any clear signs of eluvial-illuvial differentiation. The laminated layers often include one, two, or three buried dark brown or dark grey humus horizons which obviously have changed after burial. On Raoul, the laminated ash-pumice layers may not include buried humus horizons. In this case the stratification of the profile is purely lithological without subdivision into buried subprofiles.

Such volcanic soils with black-grey mull horizons were described in the lower part of a sequence on Raoul and in one cross-section with a relatively recent ash layer on Niuafo'ou. They correspond, apparently, to the warmest and most favorable micro-habitats on the islands.

2. Volcanic soils with dark-brown humus horizons, were described on Raoul and found only under closed-canopy forest cover and at higher altitudes than the soils discussed above. They have thick litter layers, which are less decomposed, than those of soils with black or dark-grey humus. The humus horizons are also thick, composed of brown or dark-brown humus, less dispersed and including some elements of coarse humus (probably mull-moder peat or humus). Below the humic horizon, the mineral profile has a varied lithological stratification and the cinnamon-brown color is probably due to some illuviation of humus from the upper horizons. This color disappears with depth and grades into grey-brown colors.

3. Volcanic coarse humus soils. This soil was only seen in the coolest and most humid areas at the summit of the eastern mountainous part of Raoul Island. Below the litter layer these soils have a dark-colored coarse-humus (AO) horizon, where the brown amorphous organic mass is mechanically mixed with ash-pumice material. Under this layer, there is a brown-dark-grey and less coarse-humus (mull-moder) A horizon. Below the A horizons are found the illuvial A-Fe-humus morphological horizons (Bhs) of cinnamon-brown "coffee" color, with brown illuvial organo-mineral cutans on the surfaces of pumice, gravel and ash. Despite a common lithological stratification these soils may, or may not, include buried humus horizons.

In all three variants of volcanic soils the extent of mineral weathering is insignificant; ash particles are rather fresh and contain a few brown-ochre cutans on the surfaces and in micro-pores. Pieces of andesite-basalt and basalt pumice, scoria, and gravel are hard, sometimes coated with very thin weathering cutans on the surfaces, but often without them.

Despite the abundance of iron with its low resistance to weathering, and the low resistance of intermediate and basic pyroclastic rocks to weathering, this subgroup exhibits practically no morphological signs of weathering. As was mentioned above, we interpret this lack of weathering as a result of the youth of the substrate, the short period of hypergenesis and possibly, slow rates of ferrallitization.

Volcanic mild-humus ferrallitized soils represent the third subgroup of volcanic soils studied. They were described for those parts of Niuafo'ou island which have less intensive ash-falls and relatively less thick upper ash layers.

In their most clearly pronounced form these soils have a well developed dark-brown, mull humus A horizon formed within black basalt ash. The general characteristics of this horizon are similar to those discussed previously. Below the humus horizons there is usually a layer of black volcanic ash, pedogenically unchanged and devoid of red or brown iron cutans on the particle surfaces. Under this ash layer are buried subprofiles with more or less pronounced features of ferrallitic alteration of the mineral mass. These buried soils have a dark reddish-brown AB horizon noticeably altered after burial and which contain indications of mull humus accumulation (before burying) and of ferrallitic alteration (measured by an overall increase in texture and a reddening of the mineral mass). There are also signs of a certain "fading" of the humus after burial (compared to the present surface humus horizons).

Lying below the AB horizon are the reddish-brown ferrallitized mineral horizons, which contain an abundance of red, yellow, and brown films on the surfaces of weathered basic ash particles. These horizons often contain completely weathered red-yellow and red ash particles, which are easily triturated by the fingers and exhibit intra-aggregate thixotropy. However, these horizons always contain a considerable amount of weakly weathered ash, suggesting that they are not ferrallitic, but only ferrallitized.

On Niuafo'ou, red and red-yellow, loamy-clay layers formed from ash and scoria and often buried under layers of ash or basalt lavas have been observed in outcrops along coastal cliffs or stream valleys. These soils probably mark stages of island evolution during which volcanic activity was reduced. The duration of these stages was sufficient for development of more mature, weathered ferrallitic layers.

Most of Raoul and Niuafo'ou are now covered by the volcanic soils discussed above. All of these soils are far from equilibrium, as judged by the ferrallitic character of their mineral layers. Their spatial distribution on the islands is controlled by the distance from the centers of eruption, by ash-fall intensity, topography, and prevailing wind pattern.

The above group of volcanic soils is represented, in general, by young soils devoid of ferrallitization. Each possesses a huge potential for further change under the impact of the prevailing bioclimatic factors as these volcanic soils are extremely immature in comparison to the ferrallitic ones. If vulcanism and periodic aerial ash-falls are considered a "normal" feature of the environment then these volcanic soils may be considered to be in equilibrium with the environment, and mature to the extent permitted by the interrelationships of the general bioclimatic factors and the unpredictable factor of volcanic ash-falls.

The brown tropical ferrasiallitic soils, may be interpreted as immature soils, if the level of soil maturity is measured by features and characteristics associated with depth and period of action of bioclimatic factors. But both the volcanic and the brown soils may be interpreted as mature soils in dynamic equilibrium with the specific regular and unpredictable soil forming factors of their environment such as ash fall and denudation. Ferrallitic soils are normally formed under the prolonged action of bioclimatic factors. The pedogenesis of brown ferrasiallitic and volcanic soils, regular rejuvenation by denudation or by ash falls may be considered normal in such cases, and the soils may be considered as "mature".

For brown soils the gradual denudation of the surface soil layers results in the weathering of new and fresh parent rock. In contrast, ash falls increase the total thickness of rock layers, and introduce into the soil profile unweathered pyroclastic materials.

Volcanic soils are less sensitive to temporal and spatial changes in the biotic, climatic and topographic conditions of the islands. We suggest that the diversity of these island soils is more the result of different volcanic impacts (for example ash falls) on soil formation, than differences in the biota and climate.

From an edaphic standpoint, these volcanic soils are a favorable and fertile medium for plants and the soil fauna, since they contain great reserves of base-rich silicate minerals of high weathering potential, and correspondingly high nutrient availability and fertility. The loose soil structure and light texture in combination with high intra-aggregate and "intra-particle" porosity of the pyroclastic layers, provide good soil drainage. In addition the absence of unfavorable periods of saturation and sufficient water-holding capacity favor plant growth (Sokolov, 1973).

These soil factors all account for the high productivity of ecosystems and communities developed on volcanic islands, despite the fact that the age of the ecosystems, the level of their organisation and structural complexity are considerably lower than on ancient islands with ferrallitic soils.

The soils described above also differ in their evolutionary potentials for development. The ferrallitic soils have minimal potential for future development under stable bioclimatic conditions unless radical changes occur. The major factors controlling further evolution or degradation and destruction of these soils are geological/geomorphological ones (changes in the general drainage of the territory, water erosion, burial). By way of contrast the younger volcanic ash soils still have a great potential for development. Such development would be associated with a lessening or cessation of volcanic activity and prolonged and stable bioclimatic conditions.

FERRALLITIC-CARBONATE SOILS

These soils were studied on Pio only, but are widespread on high (uplifted) coral islands of the Pacific. Often described as "tropical terra rosa", these soils represent an interesting, and little understood soil phenomenon (Wiens, 1962; Wright and Van Westendorp, 1965; Twyford and Wright, 1965).

Ferrallitic-carbonate soils are developed only on high (second and third) terraces and are absent on the lower most recent (2-3000 years) Late-Holocene terrace of the island. Ferrallitization of the mineral mass does not occur. According to Kaplin (pers. comm.) the period of subaerial ecosystem development, and correspondingly, of pedogenesis on the high terraces is of the order of the first tens of thousands of years.

For ferrallitic-carbonate soils, three groups of horizons are identified:

1. Organogenic horizons (organic remains, litter, "hanging" aerial-root horizons),

2. Ferrallitic red clay horizons about 20-30 cm thick on average.

3. Underlying horizons of coral limestone.

The organogenic horizons vary greatly in composition and thickness. In closed-canopy forests, this horizon consists of a loose and sparse layer of brown leaf remains covering the mineral surface of soil. Organic material is accumulated near large tree trunks, especially in spaces between large buttress roots. Litter is generally absent, suggesting very rapid mineralization and humification of organic material. Beneath the litter, horizons of moderately decomposed litter and "hanging" horizons formed by the inter-weaving of thin roots are observed. These horizons do not reach the mineral surface of the soil; they seem to hang between the layers of decomposed organic material and litter. Immediately below the organogenic layers are the relatively weakly-differentiated ferrallitic horizons. These consist of dark or brown-red, strongly structured granular clays, which are soft and plastic in the moist state, but very hard when dry. Because of their general shallowness the red ferrallitic horizons are humified down to limestone layers below them. The most humified upper (A1) horizons are up to 10 cm thick and grade into AB horizons. Based on color, texture and structure the boundary between the two ferrallitic horizons is not sharp. The red layers are carbonaceous from the surface down and effervesce with HCl, but neither limestone, nor neogenic carbonate products are visible in the fine earth fraction. The numerous fractures in the block-jointed limestone are filled with red clay fine earth, which forms tongues and pockets reaching down to 40-50 cm in depth. Thin red clay cutans coat the fissures and pores of this limestone. The boundary between the red clay and the white limestone is always very abrupt and nearly linear. There are no transitional zones, which could be considered zones of dissolution and the residual-eluvial accumulation of insoluble ferrallitic materials.

The origin of the ferrallitic, clayey layer which overlies the limestone is perhaps the most interesting and difficult problem of genesis of such soils (Ignat'iev, 1979). Three major hypotheses explaining their origin are available. The first and traditional hypothesis states that the ferrallitic material is an insoluble residue which accumulates in the process of dissolution and leaching of the limestones, and forms a residual-eluvial mantle on the surface. According to the available information, the formation of such a mantle 20-30 cm thick would require, on average, dissolution of 100-300 m of limestone rock. From the geomorphological point of view this rate is impossible if we assume that the initial altitude of such islands was 150-350 m above sea level (the levels of the second and the third terraces); also the primary biogenic-wave formed micro-relief of the terraces should be fully "worn down" and destroyed. Neither of these requirements corresponds to presently known rates of uplift for such islands or to their topography.

The second hypothesis is the aerial-volcanic one: the ferrallitic layer over limestone is allochthonous and is formed by the subaerial weathering of volcanic ash deposited on the surface of the coral island. The soils studied however show no macro- or micro-morphological signs of the original volcanic material (ash particles and accessory minerals transported together with ash) in the ferrallitic horizons.

The third hypothesis is that the ferrallitic layers were deposited over the limestone surface under water and are chemogenic sediments in the lagoons. With uplift of the island the sediment was exposed at the present-day surface where it underwent further transformation through the processes of weathering and pedogenesis.

At present we do not have adequate analytical data to clearly formulate our own concept on the genesis of the ferrallitic layer in ferrallitic-carbonate soils. We can only suggest that the residual-eluvial hypothesis seems the least probable.

Another important problem related to the genesis and evolution of such soils is the fate of carbonates in the soil profile. The ferrallitic layers do not contain limestone remains, but effervesce with HCl, indicating the presence of secondary carbonates. How could such carbonation of the ferrallitic fine earth develop under the humid climatic regimes of tropical rain forests? What processes are occurring at the boundary between the ferrallitic fine earth horizons and rocky limestone horizons in these soils? Is there active dissolution of limestone and the movement of this boundary into the limestone layers, or is the boundary in equilibrium and stabilized such that in dry periods carbonates are transported upward and saturate the ferrallitic layer? Further investigations are necessary in order to answer the above questions and determine whether these soils are stable, and what the patterns of their future evolution may be.

A rough comparison of soils on Pio with soils of other high atolls (e.g. Niue) of the Pacific suggests that soil evolution may parallel processes associated with karst development: re-distribution of a relatively even mantle of ferrallitic material to deep karst cavities, and limestone outcrops. In this case a mottled soil cover may be formed on "older" high coral islands, with a humus-carbonate rock-rubble soil on limestone badlands and outcrops, and ferrallitic soils in the karst cavities.

HUMUS-CARBONATE SOILS

A vast number of soils, all developed on the sandy-rubble coral substrata of young Holocene coral islands and atolls are in this group.

The terrain of low atolls is generally young (2 to 5 thousand years), and even younger. These soils are therefore, young, and form age sequences from the youngest primitive soils (on beaches with/or without pioneer vegetation) to well-developed soils on the surfaces of the first coastal terrace several thousand years old. These soils show no morphological signs of rubefaction (of mineral material) which might be interpreted as the beginning of the process of residual-eluvial ferrallitisation.

Below, a description of only the most developed atoll soils is given. Such soils were studied on the first terrace of Pio Island, and on islets of Suwarrow and Danger atolls in forested sites.

Humus-carbonate soils have comparatively simple soil profiles. Below the litter layer, a dark-grey or black humus horizon is formed in coarse coral sand or sandy rubble. In this layer particles of sand and debris are mixed with fine aggregates of black organic matter with rounded-clotted structures. The horizon is densely packed with roots. The particles of coral sand are not colored by humus, but in combination with organogenic peds they form a loose, even fluffy dark mass.

These humus horizons are up to 10-20 cm thick, beneath which there is usually a transitional horizon, with a rapid or gradual (over 5-15 cm) decrease in the amount of humic, dark-colored aggregates with depth. The color ranges from dark grey or black, to grey-white or white. Still deeper, there are usually non-homogenous, sometimes clearly stratified layers of structure-less white, coral sand or sand and rubble, with evidence of carbonate solution migration (carbonate pendants on lower surfaces of coral rubble). Judging by their morphological characteristics, no material other than coral limestone particles could be detected in the rock layers except in the laminated layers of certain profiles which contained buried humus horizons. These buried layers were similar to those described above, but were lighter in color, and found at depths of about 40-60 cm.

The existence of such horizons may be explained by the periodic rejuvenation of atoll surfaces by wind and wave transport of coral sand and rubble from the open beaches encircling the islands. Due to the unconsolidated nature of much of the coral substrata on these islands, tree root systems are not solidly fixed. During severe storms uprooting of trees and local burial of soil surfaces often occurs.

No relationship exists between the humus-carbonate soils of low atolls and the raised coral islands and the ferrallitic-carbonate soils of the higher terraces of the raised coral islands. The absence of ferrallitisation of the young coral material is noteworthy, since there is no doubt that active dissolution of the coral material in the upper horizons of humus-carbonate soils is taking place. The morphologically corroded surfaces of the rubble in the litter and in the A1 horizons are evidence of this process. This dissolution, does not result in any residual ferrallitic products, thus undermining the residual-eluvial hypothesis concerning the genesis of the ferrallitic mass on raised coral islands.

PEATY Al-FE-HUMIC CARBONATE SOILS

These soils are a vivid illustration of a direct and very strong impact of biogenic factors on pedogenesis. They were observed and studied on the same low atolls, which have humus-carbonate soils (as described earlier) but were found only beneath the closed stands of *Pisonia grandis*. Here the pattern of biological material cycling and the transformation of dead plant debris are radically different from other soils.

Under *Pisonia* forests the soils are formed over the same coral-carbonate sandy-rubble substrata and under the same conditions of topography, drainage and absolute age, as the humus-carbonate soils of atolls. Pedogenic factors differ only in the composition of the plant community.

Below the layer of coarse, poorly decomposed organic debris (O1) composed of large, tough *Pisonia* leaves, there is a rather thick (up to 10-15 cm) reddish-dark brown, peaty horizon (O2) weakly and moderately decomposed in its upper part, and heavily decomposed in its lower portion, overlying the mineral layer.

A shallow coarse-humus horizon (AO) may be found within the mineral carbonate sandy-rubble layers of coral. This horizon is dark-brown to nearly black, and represents a mixture of amorphous matter, coral sand and rubble. Below this horizon, and in cases where it is absent beneath the peaty horizon, there are the morphologically, clearly distinct illuvial-humic (Al-Fe-humic) mineral layers. The parent material of these layers is white coral sand, gravel, and rubble (sometime large blocks of limestone as well). The upper horizons and the components of these layers (from sand to blocks) are covered and colored by red-brown (coffee-colored) Al-Fe-humus cutans. The morphology of these cutans supports the premise of their illuvial origins. Size, abundance, and vividness of color of the cutans are gradually reduced with profile depth and permit the division of the illuvial-humus layers of the profile into Bh, Bht, horizons and so on. The total thickness of the illuvial-humus colored coral layer is up to 50-70 cm. It is underlain by white, sandy-rubble-blocky material.

A specific feature of the *Pisonia* ecosystem is the relatively slow mineralization and humification of the leaf litter when compared with other tropical soils. Rather a "northern" type of oligotrophic decomposition occurs, forming two main groups of products: residual peaty and coarse-humus material accumulated above the surface of mineral layers, and mobile humus, illuviated (in combination with Fe and A1,) into the mineral carbonate layers.

Such humus types and their corresponding horizons (O and Bh) are usually found in soils developed under oligotrophic, humid ecological conditions, and most are observed on poor, difficult to weather silicate rocks. Morphological features of the profile resembles the peaty illuvial-humic, sandy-rubble soils of the northern subarctic and boreal zones (Podburs and Podsols.). The carbonate coral layers in humid tropics are a very unlikely substratum for Al-Fe-humus pedogenesis. The above profile is, apparently developed in response to the chemical composition and pH characteristics of *Pisonia* debris which hinders rapid decomposition of the dead plant mass, and favors peat formation. The illuviation of humus is a result of the type of peat decomposition and of the humid climate. The amount and rates of migration of mobile humus are high, such that not all humus is precipitated on contact with the mineral carbonate surface of soil. This humus is able to "reduce" the carbonate layers. Usually, the illuvial humus is either sedimented at the carbonate barrier and therefore is unable to penetrate through, or it interacts with carbonates and actively dissolves them. No traces of intensive dissolution of carbonate coral fragments were observed in the soils studied as the surface structure of the coral skeleton was well preserved in gravel and rubble particles. Although the high year-round air and soil temperatures in the tropics may be responsible for the reduced carbonate solubility, the combination of a purely carbonate substratum with a deep illuvial-humus process is a unique genetic and biogeochemical problem, which requires further detailed investigation.

CONCLUSIONS

The data and observations discussed here reveal a high diversity of soils on the islands under study, both in morphology and their supposed modes of formation. In humid tropical and subtropical regimes, several radically different patterns of pedogenesis may be used to differentiate soils. These differences are more often due to geological and age factors rather than being products of bioclimatogenic environmental factors, such as climate seasonality, or vegetation type.

We conclude that on the basis of our observations in the humid tropical islands compared with the results of long-term studies in subarctic, boreal and sub-boreal humid areas of the USSR; the geographical diversity of soils is controlled by the imposition and interaction of two independent systems of pedogenic factors: climatogenic factors including (climate, and biota); geogenic factors (rocks, relief, age).

In a broad sense the zonation of soils may be interpreted as the formation of different soils on qualitatively homogenous parent rocks and relief in one and the same time period, but under spatially different climates and biota.

The incomplete convergence of soils may be defined as the formation of different soils formed under the action of qualitatively similar climates and biota, but on parent rocks of different-quality and/or relief in one and the same time period.

On the Pacific islands studied the numerous trends in soil formation within one climatic zone (humid tropical or subtropical) is a result of:

1. Different outcomes of the interaction of one climatic regime with compositionally different parent rocks; and/or

2. Different periods of interaction of climate with these rocks, i.e. different times of soil and crust formation.

In this sense, tropical and subtropical pedogenesis on Pacific islands follows the general pattern of soil diversity found in the polar and boreal humid zones of the USSR where less time, less intensive and slower rates of pedogenesis have not resulted in the convergence of the initial differences of the parent rocks into a single zonal type of soils.

The origin and geography of the principal soil groups on the Southwest Pacific islands, are due to:

1. Different accumulation-denudation trends of pedo- and lithogenesis.

2. Plurality and polyclimax character of the soils resulting from the different composition of parent rocks, and different time periods of pedogenesis (incomplete convergence).

The zonal climate and biota of the humid tropics and subtropics do not have a significant controlling effect on the formation and geography of the groups of soils studied. On ancient islands soils are old and weathered and their mineral layers have been depleted of lime and other nutrients. In contrast, on young volcanic and coral substrates, climatic differences are not fully expressed in the soils because the interaction time between climate and substratum has been rather short. Differences in biotic factors do not have a great impact on the soil type below 300 m altitude.

Altitudinal bioclimatic zonation becomes pronounced at altitudes above 300 m. Although altitude weakly affects mineral alteration, the type of humus and the pattern of humus translocation in the profiles differ significantly. At higher elevations coarse humus and even peat appear in the surface horizons, as do traces of Al-Fe-humus translocation in the mineral layers.

Thus, even in the humid tropics, the potential for the convergence of parent substrates into a single zonal type of weathering crust and soil appears limited.

CHAPTER IV. GENERAL CHARACTERISTICS OF THE ISLANDS AND THEIR VEGETATION

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INTRODUCTION

This chapter presents details of the geological structure and relief of the islands in relation to the vegetation cover. Some of the anthropogenic effects are also described. Detailed data collected during our expedition are provided and serve as the basis for the bulk of our generalizations found later in this volume. The compiled maps give a good idea of the geographic distribution of major habitats and sites (sometimes comparable to first order watersheds) which make up the islands, the delimitation of which is based on associations of soil, topography and vegetation.

RAOUL ISLAND

Raoul Island (29° S, 178° W) is the largest of the 17 islands which make up the Kermadec Archipelago. Many of these are bounded or ringed by cliffs that rise steeply from sea level. The islands are volcanic piles which represent the summits of the submarine Kermadec range, or range system, stretching between New Zealand and Samoa. The Kermadec and Tonga abyssal trenches bound the range system to the east, and the entire zone is a classical island arc exhibiting rather high tectonic activity and frequent volcanic eruptions.

Raoul Island, situated some 1000 km north-northeast of New Zealand is one of the main centers of vulcanism. Its maximum length, from southeast to northwest, is 10.5 km and its area is 29.25 km^2. In plan it resembles a triangle, the central part of which is a volcanic caldera with three ranges radiating outward forming a star-like pattern. The island is 516 m above sea level and over 50% of the island lies at elevations between 270 to 400 m above sea level.

The oldest rocks exposed on the island are olivine basalts of upper Pliocene age, which seem to have erupted as pillow lavas prior to the island's emergence. All other volcanic eruptions on the island have taken place during the Pleistocene as subaerial eruptions. The basaltic foundation of the island is slightly inclined in an east-southeast direction, and overlain by Pleistocene basalts, andesites, gabbro, diorites, quartz-diorites and obsidian. The island's rocks are mainly horizontal or subhorizontal in orientation. The nucleus of the island is composed of andesitic basalts, andesitic tuffs and breccias over which there is a mantle of pumiceous sands and rubble, and andesite ash.

According to Brothers and Searle (1970), during the Pleistocene eruptions a huge volcanic pile evolved in the place of the present-day island of Raoul. These authors suggest on the basis of the islands slope characteristics, that this pile exceeded 1000 m in height. At that time the pile was crossed by a large fault of north-northwest strike. Following a powerful eruption of pumiceous material the Pleistocene volcanic pile was destroyed, forming the present central volcanic caldera, while the rest of the island surface was covered with pumice fragments. Radiocarbon dates for this event, suggest that the present day surface of the island, was formed some 200 years B.C.

Later eruptions which took place in 1814, 1872 and 1964 within the region of the large caldera had local geomorphic significance, covering certain areas, particularly those in the northwestern part of the island with eruptive materials. The mantle of ash and pumice was rather thin in places and was rapidly removed by erosion on steep slopes. Thus, the most recent stage in the evolution of the island's relief and landscape began around 2170 years ago.

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* Deceased

The climate of Raoul Island is subtropical, oceanic with a slightly expressed Mediterranean aspect. Temperature fluctuations during the year are imperceptible, because of the very pronounced oceanic effect; the mean annual air temperature is 18.9°C; Relative humidity averages 75%.

Table 4 presents the precipitation data derived from the records of the weather station, situated on the island's northern coast at 40 m above sea level and 300 m inland. These data are characteristic of the climate in the most arid part of the island.

Table 4. Annual precipitation (in cm) on Raoul Island between 1951-1970.

Month	J	F	M	A	M	J	J	A	S	O	N	D	ANNUAL
Average	10.2	13.1	12.5	11.5	13.7	14.9	17.4	15.7	12.5	9.6	7.9	8.7	147.7
Max'm	34.1	29.3	27.2	24.3	33.5	26.9	32.3	25.0	24.1	22.5	16.4	30.6	326.2
Min'm	0.2	2.6	3.2	1.5	5.1	6.9	5.5	2.8	5.7	1.3	0.7	0.8	36.3

Although the total annual precipitation in some years is high, monthly precipitation may be extremely low in some summer months and very high during the winter. From 20 years of observations, at least one month has total precipitation under 30 mm every 14 years; arid months are characteristic of the warmest time of the year.

The interaction between the humid air masses and the mountain system of the island causes orographic rainfall in the upper parts of the island, resulting in the appearance of relatively arid areas in the rainshadow. The vertical gradient of precipitation on Raoul exceeds the values typical for most continental areas. The heterogeneity of the soil-vegetation cover is influenced by climatic conditions on the island.

The peculiar geological structure of the island, the loose, ash-pumice composition of its surface and the high intensity and periodicity of precipitation all result in the unique hydrological regime of the island. Raoul has no permanent water courses, though its drainage network is well developed and some springs of freshwater are found in three places on the shore. The lakes situated in the crater are recharged by rainfall. Chemical analyses of the caldera water, carried out by P. V. Yelpatievsky, indicate that these lakes are not influenced by the sea. Our expedition worked on the island at the end of the dry period, but despite this fact the soil was found to be moist, especially at elevations over 300 m. The forest litter, particularly in the morning, was damp although the total water holding capacity of the island's soil does not seem great. The low density of the soil and its high and constant moisture favor continuous channel erosion. Streams originate where there are gently sloping (<10°), poorly expressed drainage depressions.

The drainage depressions change rapidly down-slope into V-shaped valleys whose slopes frequently exceed 40°; slope steepness changes abruptly and is distinguished by a well defined break in slope. In the lower third of the valleys the slopes again become more gentle (20-30°); this change is more gradual.

The complicated erosion network, expressed along one profile transect established at right angles to the main valleys in the eastern part of the island, provided representation of all slope exposures (Table 5) and most gradients. No slopes between 30 and 40° were encountered.

The features of relief discussed above demonstrate the young age of the surface and the intensity of recent erosion processes. The significant spatial contrasts in geomorphological conditions have resulted in significant vegetational differences.

Slopes of less than 10° inclination were chiefly observed on, old, weakly eroded surfaces; those of 15° to 30° were found in the lower parts of the valleys; those with steepness exceeding 40° were encountered in the upper parts of the valleys where steep-sided gullies or channels are present.

Table 5. Distribution of slope steepness and direction along the profile on Raoul Island.

Aspect	< 5	10-15	15-20	20-30	> 40	Total
Northern	1		2			3
Northeastern	1	1	2			4
Eastern		1	2	2	1	6
Southeastern		2	1	1	1	5
Southern					1	1
Southwestern		1				1
Western	1	1	1		1	4
Northwestern	1	1		3	2	7
Totals	4	7	8	6	6	

In this way, the relief of the island may be ascribed to three basic factors:

1. Pliocene vulcanism.
2. Recent shore abrasion and accumulation.
3. Recent channel erosion.

Traces of old vulcanism are apparent in the western part of the island,and the slopes of Danham Bay are the remains of an old caldera. The main configuration of the island is determined by Holocene vulcanism. The surfaces directly inherited from the newly formed volcanic pile are relatively smooth watersheds with inclination up to 15 degrees. Younger vulcanism is responsible for the surface inside the crater, which is weakly affected by recent erosion. The intensive shower of volcanic ash in the western sector of the island, related to this vulcanism, did not seriously change the relief but rejuvenated the soil.

The intensive abrasion processes along most of the shoreline have resulted in very steep and occasionally vertical, poorly forested slopes. The processes of deposition are rather limited, and are confined to the old caldera (Danham Bay) or to gently inclined slopes. In the northern part of the island, where the weather station is situated, there is a small section of an old depositional plain which topologically corresponds to the peripheral part of the cone of the old crater.

The fluvial processes on the island are, in the main, erosive; genuine processes of slope denudation seem to be rather poor due to the low density of the rocks composing the slopes. As a result, the valleys are sharply entrenched. Recent deposition is found in the caldera where deluvial trains have formed in the lower reaches of poorly incised intermittent streams.

Thus for Raoul Island, the following main types of relief can be distinguished:

1. The central caldera.
2. Crests of watersheds.
3. Steep slopes.
4. Alluvial terraces.
5. Abrasional shore forms.
6. Accumulative shore forms.

Humans have had an impact on Raoul Island, and a brief history of its colonization is presented here briefly. While Raoul Island has not had a permanent population, attempts by early Polynesians to colonize the island is indirectly evidenced by the widespread distribution of taro (*Alocasia macrorrhiza*). Additionally, herbaceous vegetation representing a post-garden succession, can be found in the southern part of the island.

In the 18th and 19th centuries, goats, rats and the domestic cat were introduced to the island by whalers. The cats and goats adapted well to the island and have become an important functional element in its ecosystems. Attempts to permanently settle on the island were also made in this century. Near the weather station and along roadsides and open spaces, large numbers of fruit trees (e.g., oranges and peaches) can be found. In all likelihood many adventitious herbaceous plants, representing the Old World temperate flora were also introduced at this time.

The flora of the Kermadec Islands has 35 species of lichens, 47 species of mosses and 588 species of vascular plants. Among the latter, 23 are endemics, 152 are introduced and 30 species are feral and/or cultivated; the native element includes 113 species (104 species are encountered on Raoul Island (Sykes, 1977).

According to Sykes (1977), the vegetation may be divided into littoral (coastal) and intra-insular. The coastal vegetation varies as a function of the underlying surface, slope steepness, and the varying extent of goats' grazing. The talus deposits below the slopes are built of soft rocks and are either relatively flat surfaces or inclined fans. All talus deposits are greatly affected by earthquakes, intensive rains, and deposition of salts brought in by storms. For these reasons, the coastal vegetation is largely composed of open clumps of scattered small herbs including *Bromus mollis, Canavalia maritima, Conyza bonariensis, Cyperus ustulatus, Disphyma australe, Gnaphalium luteo-album, Lachnagrostis filiformis*, var. *littoralis; Leontodon taraxacoides, Lobelia anceps, Polycarpon tetraphyllum, Polypodium monospeliensis, Portulaca oleracea, Samolus repense* var. *strictus, Scirpus nodosus, Sonchus littoralis, S. oleraceus,* and *Tetragonia tetragonoides.*

The steep, talus slopes and lower parts of the sea cliffs are usually covered by *Asplenium obtusatum, Cyperus ustulatus, Disphyma australe, Scaevola gracilis,* and *Scirpus nodosus.*

On plots less influenced by the marine environment, the vegetation is thicker and frequently more diverse, closed canopy plant communities, chiefly low forests or shrubs dominated by *Myoporum obscurum*, *Coprosma petiolatum* and *Cyperus ustulatus,* may also develop in these areas.

The inland vegetation can be ecologically subdivided into that of the volcanic caldera and that on the slopes of the volcanic pile. Three principal vertical zones can be distinguished in the vegetation on the slopes which form the bulk of the island's surface. Sykes (1977) specifies two zones on the island, the dry and the moist forests. According to our observations the zone of dry forests generally occurs below 120 m above sea level on the average, and occasionally up to 170-200 m. This belt gives way to that of moist forests which are the most widespread on the island. Beginning at 470 m elevation and up to the highest points, is the zone of dwarf cloud forest.

In general, the upper canopy of both the dry and moist forests, is dominated by *Metrosideros kermadecensis,* which is known here by its Polynesian name "*pohutukava*". The lower canopy and under storey in the dry forests, is dominated by *Myrsine kermadecensis*); the lower canopy of the moist forests is almost always dominated by the palm *Rhopalostylysbauerii* var. *cheesmanii,* and the shrub layer contains abundant *Ascarina lucida* var. *lanceolata.* In the upper part of the moist forest zone the upper canopy is composed of the tree fern *Cyathea* sp. and has increasing numbers of epiphyte mosses.

The belt of dwarf cloud forests is dominated by *Ascarina* with some plants of *Melicytus ramiflorus.* The lower canopy is formed at a level below that of solitary individuals of palms and *pohutukavas.*

Table 6 presents the characteristics of typical plant communities encountered on this island. The spatial structure of vegetation and its more general and physiognomic features within the belt of moist forests are described in the profile (Figure 8). The principal upper canopy species, (*pohutukava*) was 22 to 28 m high, occasionally over 30 m. The lower canopy was formed by palms and solitary trees of *Melicytus* reaching 10 to 16 m in height. The average closure of the upper canopy of *pohutukava* seldom exceeded 0.6, it was usually between 0.4 to 0.5. The closure of the lower canopy varied greatly, averaging 0.7 to 0.8; the total crown closure in the entire stand was over 0.8.

With equal crown closure, the transparency of crowns varies as a function of light demands in the dominant species [(a transparency coefficient (Tselniker, 1969) of 1.00 represents total closure)]. *Pohutukava* had somewhat higher values than palm (0.14 and 0.09, respectively). Using this index, the light demands of *pohutukava* are comparable with *Quercus robur* of the temperate belt; the palm *Rhopalostylis bauerii* is comparable to the shade tolerant *Tilia cordata* and *Acer platanoides.* The potential variation of crown transparency in stands composed purely of *pohutukava* and palm, assuming equal closure, can be assessed from the data below:

Closure	1.0	0.8	0.6	0.4	0.2
Pohutukava	0.14	0.31	0.48	0.66	0.87
Palm	0.09	0.27	0.45	0.64	0.82

The average transparency[1] of the crown canopy (Tr. av.) in the forests on Raoul Island is 0.23, with the most frequent values varying from 0.10 to 0.20[2]. The average data, as well as the closure data presented in Figure 9 which were obtained from processing over 50 wide-angle photographs, are in good agreement with our visual estimation of crown closure in these forests.

Figure 10 shows the variation in canopy transparency (Tr.av.) in different stands, as a function of the zenith angle V. This variation illustrates the inter-relationship between the two main species of the community (*pohutukava* and palm) which can be found both in pure and mixed stands. When *pohutukava* dominates, the crown canopy is most transparent in the zone limited to the sector between 20 and 30° above the horizon. When palm dominates, within the zone near the zenith angle, the transparency is lower; within the range V = 20 to 40°, the average transparency is slightly

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[1] Represented by the Old World temperate zone flora.

[2] According to computations made by Nilson (1977, it is possible to estimate the average transparency (Tr. av) by using photographs made with the objective 130° as that is sufficiently close to the average transparency of the entire hemisphere.

Table 6. Characteristics of the main types of plant communities on Raoul Island (Kermadec Islands).

														Layer Characteristics *			
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
90	NE 250 m N slope 30-35°	9M+1M+1Cr	10Mt+Mr+Cr	20	7.7	263	3.2	3975	86.95	0.9-1.0	0.5-0.6	SS	10	$\frac{\text{Mt(0.6)}}{20}$	$\frac{\text{Mr(0.8)}}{6}$	$\frac{\text{Mr(0.2)}}{0.4}$	$\frac{\text{C(0.0)}}{0.3}$
58	NW 300 m NE slope 35°	10Mt	10Mt	14	10.7	71	5.9	10400	141.25	0.8	0.6	SS	7	$\frac{\text{Mt(0.8)}}{14.0}$	Absent	$\frac{\text{Mr(0.7)}}{2.5}$	$\frac{\text{A1(0.1)}}{0.9}$
65	East 300 m NE slope 10°	8P+1Dp+ 1Mp+1Me	4P3Mt+ 2Dp+1Me	18	18.4	58	15.5	2425	85.26	0.9	0.8-0.9	G	6	$\frac{\text{Mt(0.2)}}{18}$	$\frac{\text{P(0.9)}}{12}$	$\frac{\text{P(0.4)}}{1.5}$	Absent
?	East 300 m N slope 24-30°	8P+1Me+1Ac +M1	7P3Me+Ac+M1	12	16.6	36	14.9	2675	67.75	0.9	0.6-0.8		7	$\frac{\text{Me(0.3)}}{12.0}$	$\frac{\text{P(0.8)}}{10.0}$	$\frac{\text{P(0.2)}}{1.0}$	$\frac{\text{A1(0.0)}}{0.3}$
?	NE 450 m NE slope 12-18°	8Ac+2Mt	----	10-12	15	-	-	-	-	0.9	0.6-0.7	MS	9	$\frac{\text{Mt(0.2)}}{12.0}$	$\frac{\text{Ac(0.8)}}{7.0}$	$\frac{\text{P(0.6)}}{2.5}$	$\frac{\text{A1(0.3)}}{0.6}$
?	Green Lake Terrace	9Mt+1Cor+ 1Mr	9Mt+1Cor+ 1Mr	3-4	2.8	43	1.2	15040	4.45	0.6-0.8	-	SH	6	Absent	$\frac{\text{Cqr(0.1)}}{4.0}$	$\frac{\text{Mt(0.8)}}{3.0}$	Absent
?	Floor of Caldera 50 m	7Mt+3Ac+1Mr	10Mt+Ac+1Mr	16	11.4	86	1.7	2075	33.4	0.6-0.7	0.6	SS	17	$\frac{\text{Mt(0.6)}}{16.0}$	$\frac{\text{Ac(0.1)}}{1.0}$	$\frac{\text{Mr(0.1)}}{3.0}$	$\frac{\text{Al(0.1)}}{0.7}$
?	W Floor of Caldera	5Mt+3Dp +2Ac+1P	10Mt+1DP +PIAC	28	26.5	76	-	700	49.95	0.6	0.4	SS	11	$\frac{\text{Mt(0.5)}}{28.0}$	$\frac{\text{DP(0.2)}}{6.0}$	$\frac{\text{A1(0.1)}}{2.0}$	$\frac{\text{Ac(0.1)}}{1.0}$

* The numerator shows the dominant, the brackets - the closure of the layer; the denominator-the layer height, m.

Table 6. (Continued). Characteristics of the main types of plant communities on Raoul Island (Kermadec Islands).

KEY TO ABBREVIATIONS

A	Site description number
B	Geographic location
	Height above mean sea level
	Slope aspect
	Slope
C	Composition (No. of stems)
D	Composition (No. reserves)
E	Average height of trees (m)
F	Average stem diameter (cm)
G	C %
H	Mo (cm)
I	No. stems/ha
J	Total cross sectional area (m^2/ha)
K	Crown closure
L	Canopy transparency
M	Growth form of *Metrosideros kermacedensis*
	SS - Straight stemmed
	G - Gigantic
	MS -Multi-stemmed
	S - Shrub
N	No. of species per community
O	I tree layer
P	II tree layer
Q	Shrub layer
R	Herb layer

Mt	*Metrosideros kermadecensis*
P	*Rhopalostylis bauerii* var. *cheesemanii*
Me	*Melicytus ramiflorus*
Ac	*Ascarina lucida* var. *kermadecensis*
Ml	*Melycope ternata*
Dp	*Cyathea* sp.
Mr	*Myrsine kermadenensis*
Cr	*Corynecarpus laevigatus*
Cor	*Coriaria arborea* var. *kermadecensis*
Mp	*Myoporum obscurum*
Al	*Alocasia macrorrhiza*
C	*Carex* sp.

higher. It is possible that zones with maximum values of crown transparency coincide with the area of tree stems having high crown, as in the case of palm. The presence of such zones in *pohutukava* forests may be due to the multi-stem form of this tree. In mixed forests the differences in crown transparency are reduced as the distribution of plant species within the crown space approaches uniformity.

The variation in crown closure in the upper canopy of *pohutukava* forests is chiefly due to the local relief. On flat surfaces and gentle slopes, crown closure in the upper canopy of *pohutukava* trees is essentially uniform. Here *pohutukava* is represented by large multi-stemmed trees, over 1 m in diameter and strongly bent over, with numerous supporting roots. Consequently each *pohutukava* tree occupies a large area, up to 40-50 m in diameter. On steep slopes the *pohutukava* is unable to resist slope erosion and in the upper part of slopes the fallen trunks have re-rooted and form a low upper canopy of poor crown closure. In the lower parts of steep slopes, there are no *pohutukava* at all, although occasionally one encounters the uprooted trunks of large (1 m in diameter) fallen individuals. The variation in closure of the lower canopy, of palm, does not depend on the closure of the upper layer. Nevertheless, the greatest numbers of palms and the highest crown closure in palm trees is observed when canopy closure in the upper canopy is low; when the crown closure in the upper canopy is over 0.8, there is practically no lower palm canopy at all.

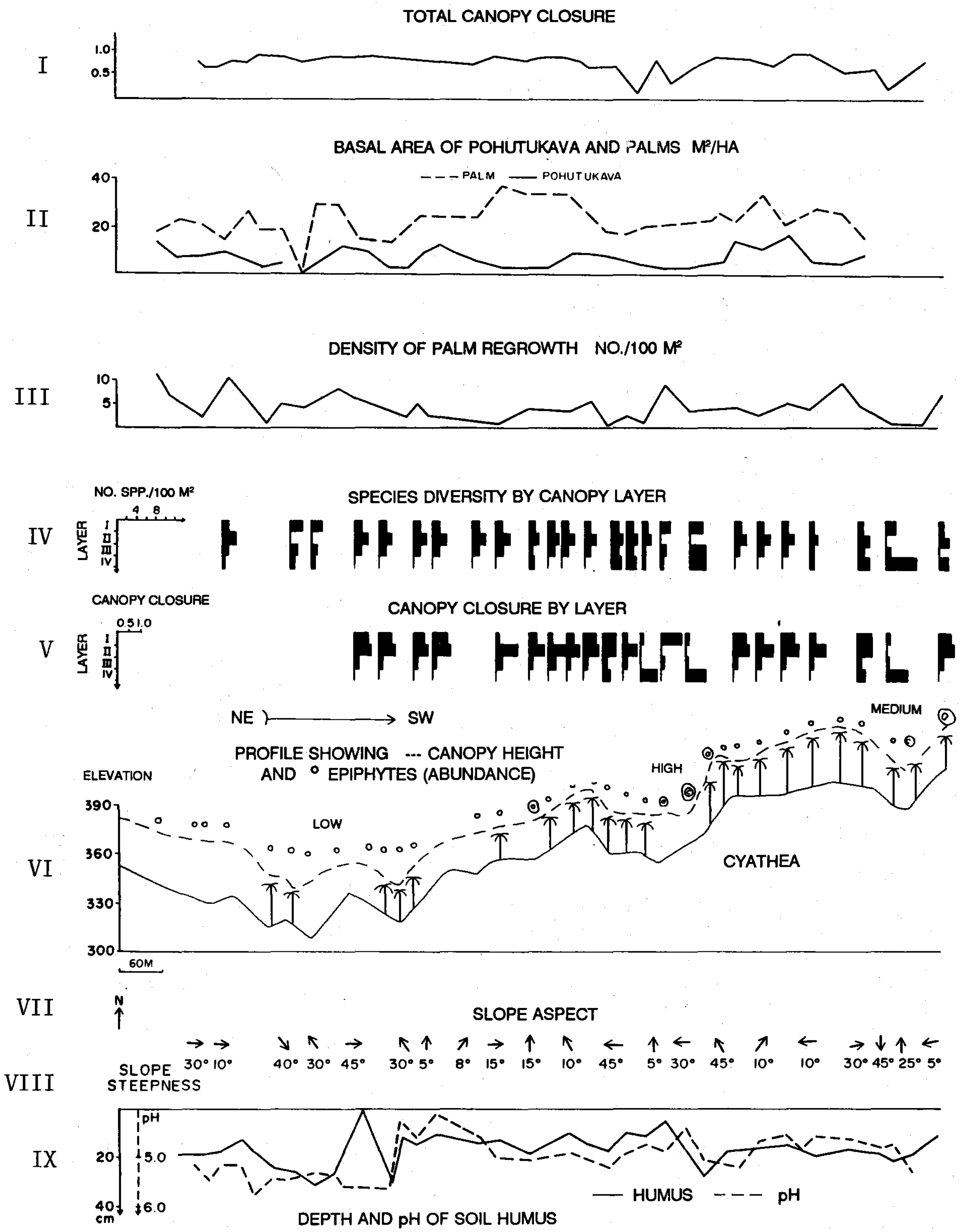

Figure 8. Ecological transect characteristics, Raoul Island. I. Total canopy closure. II. Basal area of *pohutukava* and palms in the crown canopy. III. Density of palm regrowth > 1 m. IV. Species distribution by layers. V. Canopy closure by layers. VI. Hypsometric profile of stand height, abundance of epiphytes, and *Cyathea* presence. VII. Slope aspect. VIII. Slope steepness. IX. Depth of humus layer and its pH.

The number of palm trees in the lower canopy depends on the age of the trees and the extent of their decay. Dead fallen stems of palms at different stages of decay are usually found where the tree canopy is poor. It is these very open places where the abundant regeneration of palm trees, usually occurs. In typical forests of the humid belt, where the total canopy closure exceeded 0.3, the herb layer (and herbaceous plants) was absent and replaced by regenerating palm trees. In the absence of regenerated palm trees of 2-3 m height and under conditions of low closure of the lower canopy, palm seedlings form a continuous carpet, about 15 to 20 cm high and with projective cover as high as 90%. Regenerating palms were encountered everywhere, except on very steep slopes and eroded valley bottoms. In places where the projective cover of regenerating palms was low, the soil surface was thickly mantled with palm seeds.

No other regenerating plants except palms were encountered beneath the canopy of moist tropical forests. The principal plant formation of this island was simple in structure. *Pohutukava*, whose life span seems to be extremely long provides a particular background against which the palm develops, and cyclic changes occur as a result of the succession of generations of *pohutukava.*

Against this background of vegetation, there were certain differences which may be ascribed to differences in atmospheric moisture. Indicators of higher atmospheric moisture are the local tree ferns and epiphytic mosses. Tree ferns occurred at altitudes above 320 m and were more persistent at elevations over 380 m. Between these elevations, the role of epiphytes increased. Although we have no quantitative data on the crown transparency of tree ferns, it is obviously a light demanding plant comparable to *pohutukava.* Tree ferns were found uniformly throughout the upper part of the profile. The crowns of this plant were almost always found above the layer of palms and somewhat below the tops of *pohutukava,* with heights between 16 to 20 m. There were frequent stems of fallen ferns, their numbers exceeding those of living plants. The biochemical decomposition of tree ferns is an extremely slow process and we were unable to find a single rotting tree fern stem. In general, the distribution of tree ferns on this island suggests that this species is a pioneer plant of humid habitats.

Parallel with the changes in vegetation are the changes in soils. These include increased acidity with altitude and, to some extent, resistence to penetration[3]. In the tree fern formation, soils had a pH 6.2-6.4 and a soft humus layer. The area under tree ferns had volcanic, coarse-humus, alpha-humus soils (andosols) with pH 5.8-6.0. These two soil types gradually changed into each other. Soil density generally increased on watersheds near gentle slopes and decreased on steep slopes and valley floors. Nevertheless, the highest value of soil density, (5 kg/m^2) was found on highest watershed surfaces.

The vegetation on the lower parts of the steep slopes of sharply cut valleys contained solitary specimens of tree ferns which were usually short specimens with smaller stems, compared to those beneath the canopy of *pohutukava.* The *pohutukava* crowns can slightly shade the slopes but the stems, as such, usually grow only in the upper parts of all slopes.

In these communities, *Alocasia macrorrhiza* taro reaching 1.5 m in height, dominated the herb layer, its projective cover was 100%. In addition, there were shrubs of *Ascarina* and *Melicytus.* The soils in such areas were usually eroded and lacked a humus horizon. They were frequently less acid and gleyed.

The structure of the vegetation in the western part of the island was similar to that described above. However, the *pohutukava* there was usually straight-stemmed, reaching about 20 m in height.

The vegetation cover in the volcanic caldera represents various stages of an externally generated successional series. The volcanic caldera is circular in shape with steep (over 50°) internal slopes.

Three lakes occupy the floor of the caldera: Blue, Green and Tui. The latter lies at a higher elevation

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[3] Soil pH was determined using a soil tester, while resistence to penetration was determined with a durometer.

and is much older than the two other lakes. In addition, there is a series of small craters, the oldest of which is located near Tui Lake. The watersheds separating the lakes look like low, hilly ridges. There are rather peculiar flat surfaces of low inclination at similar altitudes, situated between the Green and the Tui Lakes. These plains are strongly dissected with deep, V-shaped and U-shaped erosion channels. Their slopes are steep, and occasionally almost vertical. The youngest forms of relief are the small crater in the region of Green Lake, which resulted from the eruption of 1964, and the three terraces of the small lake, which are are truncated by erosion channels up to 1 m in depth.

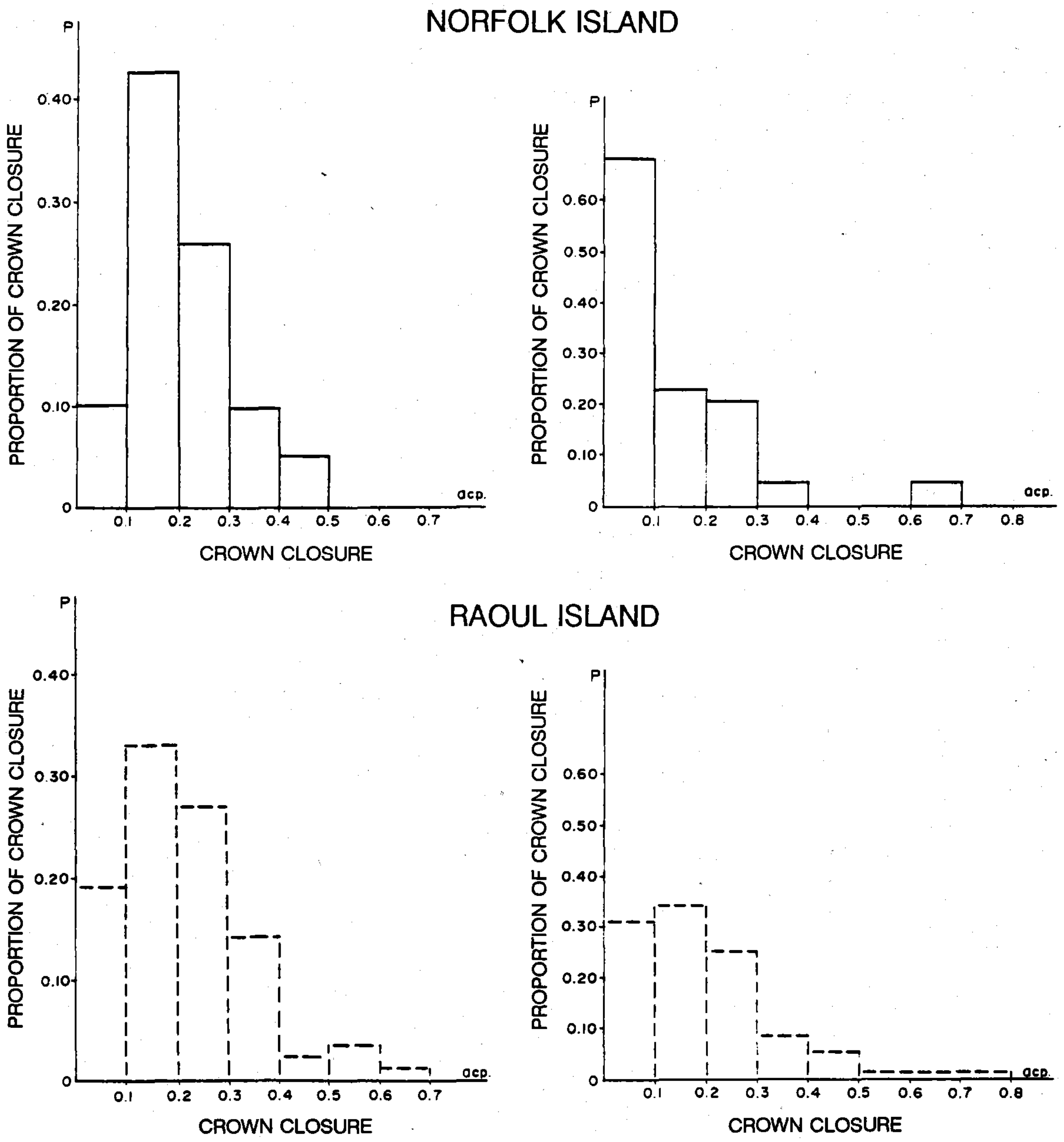

Figure 9. Crown closure distribution in forest stands on Norfolk and Raoul Islands (A and C respectively) and in palm stands on the same islands (B and D respectively).

On the whole, the structure of the vegetation cover in the caldera is very simple. In fact, the entire area, including the slopes and floor, is occupied by one plant formation, namely *Metrosideros kermadecensis* (*pohutukava*); the steep rocky slopes are covered by communities of *Pteris comans*. A small massif in the center of the caldera floor is also covered by herbs. Despite the monotony of the vegetation cover there are considerable differences between the individual plant communities which reflect different stages of succession.

The earliest stages of primary succession after the volcanic eruption of 1964 can be found near Green Lake, where the water level is falling. As a result, terrestrial plants have invaded sites now suitable for their growth, and about 20 m from the lake there were clumps of *Juncus* sp. (0.6 m high) and *Cyperus* sp. (0.8 m high), the latter with individuals reaching 30 cm in diameter. The clumps were between 6 to 10 m apart. Grasses were encountered along the dried water courses entering the lake. Further from the lake, the composition of the local herbaceous plants was richer and individual specimens of *M. kermadecensis* were also found here. The shrub vegetation was 10 m or higher, with heights increasing with distance from the lake.

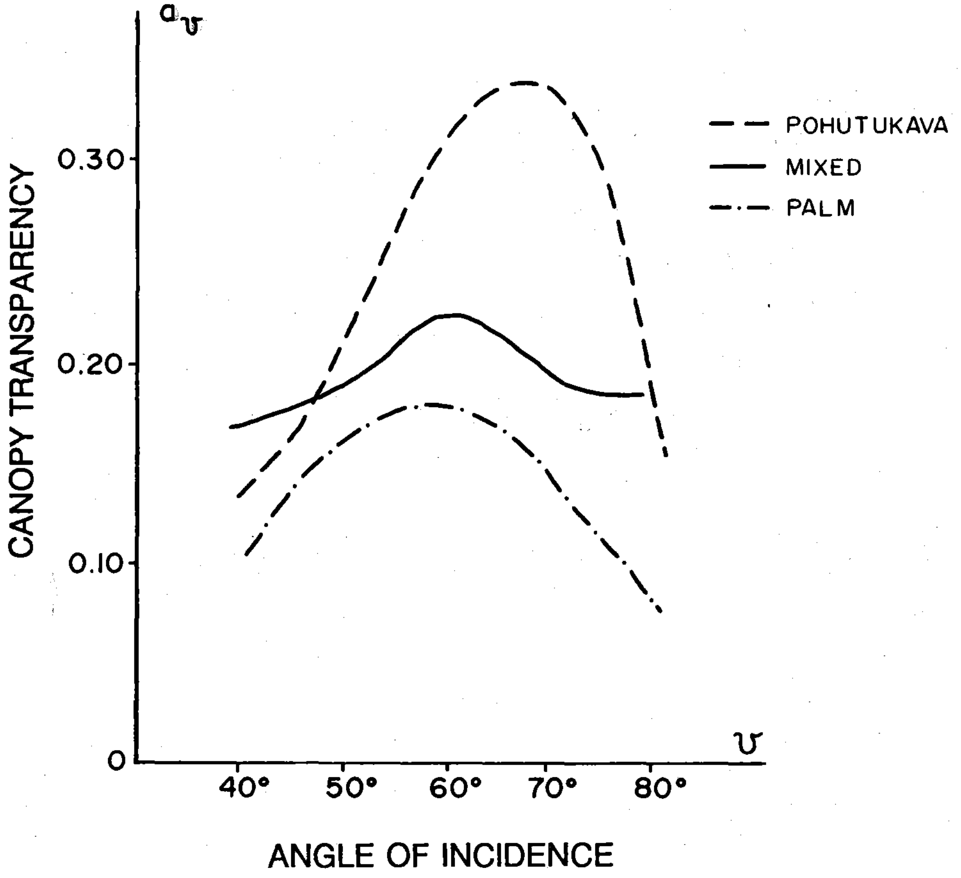

Figure 10. Canopy transparencies in the tree layer of *pohutukava*, mixed *pohutukava* and palm; and in palm forests on Raoul Island.

The second terrace was mainly devoid of vegetation, although along the terrace ridge there were well-regenerated *Metrosideros kermadecensis* shrubs up to 1.2 m in height. The rear part of the territory, which was the largest, was occupied by a shrub association with a canopy closure of 0.4 and a height of 0.7-0.8 m.

The distribution of *Metrosideros kermadecensis* was uniform over the entire area (70 individuals/100 m^2). The crowns of these shrubs reached about 0.6 m in diameter and there were many dead stems of *M.kermadecensis* (approximately 9 individuals per 400 m^2) with diameters averaging 0.4 m and heights of about 8 m; some were standing while others had fallen. In the herb layer, *Juncus* sp. and *Andropogon* sp. had a projective cover of 10% and stood 0.2 m high. Other plant communities, composed of *Scaevola* sp. were scattered over the surface. The areas covered by these shrubs varied in diameter from 0.5 to 50 m^2. Occasionally, the margins of the *M. kermadecensis* shrub community were dominated by *Coriaria arborea* var. *kermadecensis* and *Juncus* sp. *Cyperus* sp. dominated the herb layer, forming clumps up to 1 m in height. There were 20 individuals of these plants per 100 m^2.

Today, the third terrace is covered by a young forest (description 1A, Table 6), which apparently regenerated right after the 1964 volcanic eruption, since the age of the stand, as confirmed by the number of annual rings was 10 to 11 years.

The steep southern slopes of the caldera of Green Lake, some 30 m above the lake level, are occupied by a well-developed forest of *M. kermadecensis* and *Coriaria arborea.* Along paths one can encounter *Schonus* sp., *Pteris* sp. and also *Ageratum conyzoides.* On steep slopes of this caldera and on the ridge separating Green Lake from Blue Lake, there are some dry stems of *M. kermadecensis.*

Near the water's edge of Blue Lake, *Cyperus* sp., *Bidens* sp., and *Alocasia* were found. The lake was surrounded by a wide zone of *Typha orientalis* which lay adjacent to a low forest of *M. kermadecensis.*

The grass cover was poorly developed, which may be a consequence of recent flooding of this area. The level of the Green Lake is known to have risen by 15 m during the last volcanic eruption, and at this time resulted in a confluence of Green and Blue Lakes.

A thicker forest of *M. kermadecensis* and *Myrsine kermadecensis* was found on the slopes of the ridge separating Blue and Green Lakes, with occasional patches covered by abundant *Psilotum nudum* and mosses.

The most mature forests in the caldera were found in the region of the oldest crater near Tui Lake. Two types of forest communities were distinguished (descriptions 92, 93, Table 5):

1. Almost pure straight-stemmed forests of *Metrosideros kermadecensis,* including a few trees of *Ascarina lucida* var. *kermadecensis* and *Pseudopanax* sp.

2. Straight-stemmed forests of *M. kermadecensis* with tree ferns forming a lower canopy.

In most cases, tree ferns were found in more humid habitats. On the very steep ravine side slopes on the caldera floor, tree ferns grew in association with *M. kermadecensis,* and *Ascarina lucida* var. *kermadecensis.* The bottoms of such ravines were usually occupied by *Alocasia macrorrhiza.* At the edge of the old overgrown crater near Tui Lake, the tree fern was found together with *Rhopalostylis* sp. The center of this crater was dominated by *Ascarina lucida* var. *kermadecensis* and some solitary specimens of *Macaranga* sp. were encountered.

The main slopes of the volcanic caldera were almost completely covered by forests of *Metrosideros. kermadecensis,* with a very thick layer of *Myrsine kermadecensis* and a herb layer containing *Blechnum*, *Psilotum*, and *Adiantum* spp.

A general idea of the spatial structure of Raoul Island's vegetation can be determined from our geobotanical map, which was based on the field and laboratory interpretation of aerial photographs (Figure 11). Analysis of the *Metrosideros kermadecensis* communities resulted in typological differences based not only on the role played by other species, but also by the stem shape (form) of the dominant species. These differences may be correlated with the form of the tree stem, tree diameter and height, and the prevalence of certain tree forms in different parts of the island. Based on this correlation, the derived categories can be considered as elements of the seral stages in the formation of mature and senile *pohutukava* forest. The map reveals the presence of altitudinal zones in the *pohutukava* forests; the distinctive vegetation of the recently eroded valleys; some of the seral stages of this vegetation, and a picture of the spatial differentiation of vegetation over the island.

According to Ignat'iev (1979), landscape categories for small islands should be primarily based on the spatial scales of the impact and magnitude of the landscape-forming factors. Three localities are distinguished on Raoul Island:

1. Coastal lowlands and (of) abrasive coasts.

2. Slopes of the stratified cone.

3. Volcanic caldera.

Within each of these localities, the factors of territorial differentiation varied. In coastal localities there are steep erosion slopes covered by herb-shrub light forest. This vegetation was also found on the depositional plains. It was very difficult to identify the first habitat because its facies formed a system or dynamic series reflective of the processes of slope destruction and slope stabilization. Facies differentiation on the depositional plains, depends on the nature of oceanic influences. These facies form an inter-linked series. These include the beach facies which are practically devoid of vegetation, the terrace edges which have herbaceous vegetation, and the central part of the terrace, with a facies of intra-terrace swamp depressions dominated by a swamp vegetation.

The stratovolcanic slopes are differentiated into land units according to erosional effects. Two types of land units are identified here:

1. Weakly eroded watersheds and nearby slopes (the vegetation here is chiefly woody and the soils are humic volcanics.

2. Eroded valleys mainly covered by herbs and shrubs.

Land units of a lower typological rank can be further differentiated according to their hydro-thermal regime. The effect of such changes is most prominent in the watershed land unit. Although the eroded valleys do not reveal any special vegetation zones, at least four types of land units can be specified (within the watershed land unit) on the basis of altitude. Zonal differentiation is the result of changes in soils and vegetation and the land units can be easily distinguished in aerial photographs, as follows:

1. Watershed surfaces and nearby slopes dominated by *Metrosideros* in the upper canopy and by *Myrsine* in the lower canopy; the soils are soft, humic, volcanics; (this land unit is comparable to the dry zone of Sykes).

2. The second land unit has vegetation similar to the first, but the lower canopy is dominated by palms and *Myrsine* is absent; the soils are humic volcanics.

3. The third land unit has tree ferns in the upper canopy; the soils are raw alpha-humic, volcanics.

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[4] For a discussion of the land unit concept and the Russian system of land classification, see Appendix I and II.

4. The fourth land unit encompases the high watershed surfaces and weakly eroded slopes covered by light shrub forests of *Ascarina, Melicytus,* tree ferns, palms and *Metrosideros.*

Within each land unit, facies can be distinguished. In this series, the changes in vegetation are due to cyclic transformations within the community. Regeneration of vegetation and soil seem to result from intense ashfalls which bring these back to earlier seral stages. Such conditions are characteristic of the western sector of the island.

The land units of the eroded valleys are subdivided into slope and valley floor facies, based on the intensity of erosional processes as reflected in the structure of vegetation. With intense erosion, the steep slope facies have denuded and occasionally gleyed soils. The facies of valley floors had thick, alluvial, humic and gley soils covered by light forests of shrubs and herbs dominated by *Alocasia, Ascarina,* tree ferns and palms. When erosion is less intense, one finds facies of tree ferns, *Melicytus* and palms. In the flattest parts of the valley floors there are facies of purely palm forests with highly closed crowns or of straight stemmed *pohutukava* (*Metrosideros*). The valley facies make up a complex series with similar transformations to the land unit of erosive steep slopes.

The caldera is divided into two land units:

1. The extremely steep slopes of the caldera covered by shrubs and herbs.

2. The caldera floor where the soil-vegetation cover reveals a system of externally determined successions.

In the first land unit, and on all eroded steep slopes, there are a number of interlinked facies which correspond to different seral stages.

The facies structure of the caldera floor reflects the stages of volcanic activity, the changing lake levels and the geomorphological forms which result directly from volcanic activity. Surfaces at different elevations inside the caldera floor can be regarded as sub-land units. Facies differentiation within the sub-land units is based on the gradient from the lake to the caldera slope. The variation in vegetation on the upper and older surfaces, is much less than that observed on the lower and Figure younger surfaces.

Thus, the caldera floor reveals a complicated hierarchical structure which reflects the island's repeated volcanic activity and the dynamics of the successional processes. The spatial arrangement of the caldera's vegetation is a miniature reflection of the vegetation pattern on the entire island.

NORFOLK ISLAND

Norfolk Island (20° S, 168° E), and the little island of Philip situated 6 km south are isolated volcanoes. These islands are located in the southern Pacific 672 km from New Caledonia, 768 km from New Zealand and 1361 km from Australia. Norfolk Island extends about 9.5 km in a southeast to northwest direction and is 5.7 km wide from southwest to northeast. Philip Island is 2.2 x 1.8 km in size. These islands are the summits of volcanic mountains of the long, submarine Norfolk Ridge, which has been non-seismic and passive for the last million years.

Among the rocks forming Norfolk Island basaltic lava is the most important; basaltic tuffs play an important role in the geological structure of the Philip Island. In terms of petrography, the lava on both islands is composed of olivine basalts. The rocks of Norfolk Island are not folded, and are almost horizontal, with intervals of basaltic lavas separated by yellow tuffs reaching 20 m in thickness. Using potassium-argon, the dates of the oldest complex range from 3.1 to 3 million years and the youngest from 2.4 to 2.3 million years.

Both islands were formed by submarine eruptions along the Norfolk Ridge axis, and acquired their

Figure 11. Vegetation map of Raoul Island. Refer to next page for identification of symbols.

LEGEND

Formation: *Metrosideros kermadecensis*

A. Shrub forms

▤ Low herbs and shrubs
Coriaria arborea var. *kermadecensis* + *Metrosideros kermadecensis*

▤ Tall shrubs
Coriaria arborea var. *kermadecensis* + *Metrosideros kermadecensis*

B. Trees

▨ Forests dominated by *Myoporum obscurum* + straight form of *Metrosideros kermadecensis*

▨ Forests dominated by *Coriaria arborea* var. *kermadecensis* + straight form of *Metrosideros kermadecensis*

▨ Forests dominated by straight forms of *Metrosideros kermadecensis* + *Myoporum obscurum*

▨ Forests dominated by straight form of *Metrosideros kermadecensis* with *Rhopalostylis baueri* var. *cheesmanii*

▨ Forests dominated by straight form of *Metrosideros kermadecensis* with *Cyathea* sp.

▨ Forests dominated by straight form of *Metrosideros kermadecensis* with *Myrsine kermadecensis*

▨ Forests dominated by straight form of *Metrosideros kermadecensis* and a mixture of herbaceous species on eroded surfaces

▨ Forests dominated by straight form of *Metrosideros kermadecensis* with *Rhopalostylis baueri* var. *cheesmanii*

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis* with *Rhopalostylis baueri* + *Melycitus ramiflorus*

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis* with *R. baueri* var. *cheesmanii*, *M. ramiflorus* + *Cyathea* sp.

▧ Forests dominated by poly-stem form of*Metrosideros kermadecensis* on eroded surfaces

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis*

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis* with second layer composed of *Rhopalostylis baueri* var. *kermadecensis*

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis* with *Rhopalostylis baueri* var. *cheesmanii* on eroded surfaces

▧ Forests dominated by poly-stem form of *Metrosideros kermadecensis* with *Cyathea* sp. + herbs (*Alocasia macrorrhiza)*

Formation: *Ascarina lucida* var. *lanceolata*

▩ Forests dominated by *Ascarina lucida* var. *lanceolata*, *Rhopalostylis baueri* var. *cheesmanii*, + *Cyathea* sp.

▩ Forests dominated by *Ascarina lucida* var. *lanceolata* with dense regeneration of *Rhopalostylis baueri* var. *cheesmanii*

▩ Forests dominated by *Ascarina lucida* var. *lanceolata* + *Metrosideros kermadecensis*

▩ Forests dominated by *Ascarina lucida* var. *lanceolata*, *Metrosideros kermadecensis*, & herbs (*Alocasia macrorrhiza*)

Canopy Closure And Age Of The Forests

	Low	Medium	High
Young			
Medium Aged			
Old			

Figure 11 (Continued). Identification of symbols for vegetation map of Raoul Island.

island status during the last million years. These eruptions originated from the craters which are now below sealevel, and both of these islands are the remains of larger volcanoes which were destroyed by earlier volcanic eruptions and by denudation. At present, only one third of those large volcanoes has survived above the ocean surface.

During the post-volcanic period since the late Pliocene and early Pleistocene, a thick, weathered crust developed on Norfolk Island, reaching 45 and occasionally 60 m in depth. Such deep weathering developed over two million years and is due to the high water permeation of the rocks composing the island, and to the climate which has hardly changed throughout the Pleistocene.

Owing to the high permeability of the rocks, the surface of Norfolk Island is very weakly denuded by erosion. There are no permanent water courses but one encounters intermittent water courses which are not well developed. These valleys have no terraces and floodplains and their longitudinal profiles are poorly developed.

On the whole, three types of relief can be distinguished on Norfolk Island:

1. A volcanic pile with two (Mount Pitt and Mount Bates which are 316 and 318 m high respectively.

2. A slightly rolling plateau with elevations up to 90-120 m.

3. A southern coastal plain, which is an old depositional feature enclosing a lagoon.

The coasts of Norfolk Island, like all volcanic coasts, are picturesque. The towering cliffs are red at the top due to the weathered crust. Their lower parts are black and yellow due to their basalts and tuffs; they have a clear ridge in which the horizontal surface of the plateau borders a vertical cliff. The shore line of Norfolk Island is sinuous and denticulate; it contains numerous abraded outliers ("kekurs") of most intricate sculpturing.

All weather observations on Norfolk Island are carried out at the airport weather station. Its mean annual temperature of 19.1° C, is close to that of Raoul. The annual temperature range is 2.6° C. In winter the temperature is never lower than + 8° C. Strong winds are not typical for this island; as a rule, the wind velocity does not exceed 0.5 m $\sec^{-1}$. Tropical cyclones and hurricanes, very rarely occur near the island. In summer there are prevailing south easterly (?) winds, while westerlies dominate in winter (approximately four months). Thus, the wind regime reflects the peculiar features of the subtropical climate: trade air masses are prevalent in summer and western ones in winter. The annual total precipitation is nearly the same as that on Raoul Island, namely 1272 mm, and corresponds approximately to the value of annual evapotranspiration. The maximum precipitation falls in winter months. On the whole, the climate on Norfolk Island is identical to that of Raoul Island, and can be classified as subtropical oceanic. It has certain features in common with a Mediterranean climate but has no distinctly dry seasonal, though short, dry periods lasting less than a month are rather characteristic of it. This type of climate determines (as it does on Raoul Island) the slightly xerophytic pattern of vegetation on Norfolk Island, as well as the wide distribution of a broad-leaf forest formation.

The island is relatively low, with gentle slopes; the shape of the Pitt massif is dome-like. Given these conditions, rainfall does not vary greatly with altitude and there is little zonation of the recent vegetation cover.

The lower elevations (up to 100-120 m) are potentially arid and have been almost completely changed because of anthropogenic effects.

The erosional network is more developed on the southern slope of Mt. Pitt as this slope receives, a greater rainfall. The greater erosion and channel development seem to have resulted from the island's lithological conditions and geological structure. In winter, the value of evaporation on the northern slopes exceeds that of the southern slopes by 1.5-2 times. With such ratios the landscape has developed asymmetrically on these subtropical mountainous islands. The contrasts in vegetation cover are very great on Norfolk Island, as they are on the Lord Howe Island (Ignatiev, 1973). A weak landscape asymmetry can be also traced in the geobotanical map of Raoul Island.

At the time of European discovery, Norfolk Island had no permanent population. Nevertheless, archaeological finds of tools testify to the fact that Polynesian settlements existed during prehistoric times, at least along the coastline. Norfolk Island was discovered by James Cook on 10/10/1774. Since then the island has been used as a British hard labor prison, a home for the descendents of the H.M.S. Bounty mutineers, and later, a tourist resort. This history has had a tremendous impact on Norfolk Island's vegetation and flora (Turner *et al.*, 1975).

Before 1788 the vegetation on the island was represented by a thick forest of which *Araucaria* sp. was an important component. Later with the advent of European colonization, this forest was reduced in extent and today, remnants can be found only in the Mount Pitt reserve.

The Mount Pitt reserve which comprises 1/4 of the island, embraces 404.8 ha including Mt. Pitt (316 m) and Mt. Bates (318 m). Much of the reserve is covered by natural vegetation. Although the forest was not clear-felled, it was intensely exploited up to 1980 for *Araucaria* and other hard-wood species. There is little evidence of fire but goats and pigs have had a detrimental impact, perhaps evidenced by numerous weedy shrubs, and horned stock can be found wandering and grazing in this forest. Feral cats and the European rat have also affected this forest. The reserve is accessible by good roads, and a 0.4 ha area has been cleared.

Norfolk Island has many weeds of European origin such as *Plantago lanceolata, P. major, Taraxacum officinale, Stellaria media, Malva, Pumax,* and *Cirsium* spp. There are also the typical subtropical weeds, such as *Cenchrus echinatus, Pennisetum* sp., *Sorghum halepense,* and *Cynodon dactylon.* Particularly widespread is *Eupatorium riparium* which grows near roads and also in forests and clearings. This plant may reach over 1 m in height. Another frequent roadside plant is *Ageratum conyzoides. Solanum mauritianum* is often encountered in lighter sections of the forest. One specimen of this plant growing where there was a gap in the tree canopy was 9 m high. As a rule, however, this species is 1.5 to 2.0 m high.

Many introduced shrubs and small trees grow well not only near roads but also in the forest as regular components. Among such plants are *Citrus limon, Olea africana,* and two species of guava (*Psidium guajava, Rhodomyrtus psidioides*) and the widely distributed shrub, *Lantana camara.* On Norfolk Island it forms thick bushes that completely displaces small specimens of local plants. Some stands of *Banksia* sp. lack a herb layer. *Eucalyptus* plantations on Norfolk Island occupy 40 ha. Occasionally, one can encounter *Cedrela odorata* a native of the West Indies. In the grounds of an old monastery, founded over 80 years ago, are various exotics, such as *Grevillea* sp. from Australia, *Syncarpia* sp., *Dillenia* sp., *Persea* sp., *Aleurites* sp., pines and many others.

On the whole, introduced plants play a significant role in the natural communities of Norfolk Island. For example, in the forest with crown closure of 0.6-0.7 the northern main slope is covered with *Araucaria* up to 45 m high. The lower canopy of this forest is composed of 25 to 30 m high white oak (*Lagunaria patersonia*), while the shrub layer is completely made up of introduced species. The herb layer is comprised almost entirely of introduced species such as *Solanum mauritianum, Commelina* sp., *Rumas* sp., and *Stellaria megia.*

On the south-western slope the *Araucaria* forest undergrowth is also dominated by introduced species such as *Bouganvillea spectabilis,* and *Ricinus communis.* It seems likely that the light forests of *Araucaria* are the most favorable habitats for introduced species.

The most important component of the forests on Norfolk Island is *Araucaria heterophylla.* It forms monodominant communities on ridges and on steep slopes. For instance, on the north-eastern slope the upper canopy of such forests consisting wholly of *A. heterophylla,* had a crown closure of 0.3-0.4, was 40 m high and had a stem diameter up to 1.5 m. The lower canopy is composed of white oak with crown closure of 0.4 and between 12-16 m in height. The community has parcels dominated by *Araucaria* (95% of the entire area) and white oak. Most successfully regenerated are the sections bordering the parcels of white oak and along the dents on the slope, in other words, in better lit places.

The herb layer is formed by several species (*Ipomoea cairica, Asplenium obtusatum, Commelina* sp.), where white oak has a projective cover of 30%. On plots dominated by *Araucaria* the grass cover is absent.

The *Araucaria* forests on Norfolk Island have some features typical of tropical rain forests: the wood stand is largely composed of tree ferns (*Cyathea brownii, C. australis*) and by the palm, *Rhopalostylys bauerii*, which is endemic to this island. There are many large lianas. Among epiphytes one finds several species of ferns and orchids. On the main massifs, these forests may be regarded as broad-leaf subtropical and mesophillic forests.

The narrow valleys of the island support a more hydrophyllic forests of tree ferns (*C. australis, C. brownii*), of which *C. australis* is more frequent. These are species-poor tropical forests, having communities of subtropical ferns and fern-palms. It should be noted that tree ferns, in general, are frequently encountered in the subtropics at elevations where the air temperatures are relatively low.

The forests on Norfolk Island include over ten species of woody plants which dominate in the upper canopy. Epiphytic ferns, cormophytic mosses and liverworts are occasionally abundant and the ground cover is rich in ferns. The distribution of species and their role in the communities depend on the aspect and steepness of slopes, and the disturbance pattern of the forests. For example, the upper part of a 15° northeastern facing slope, 200 m above sea level, has a more xerophytic vegetation than that found elsewhere.

The upper layer of the woody stand was composed of *Ungeria floribunda, Araucaria heterophylla* and *Nestegia apetala*, reaching 35, 22-24 and 18 m in height, respectively. The crown closure was under 0.1 and the trunk diameters were up to 1.5 m. At heights from 15 to 22 m the trees were covered with lichens (*Usnea* sp.) which were not present in the canopy.

The lower canopy included *Araucaria* and the palms *Meryta angustifolia, Rapanea crassifolia, Melicytus ramiflorus,* and *Cordyline obtecta*. There were 12 species in this layer which had crown closure of 0.6-0.7, height of 8 m, and mean stem diameter 8 cm with a maximum of 20 cm. Among the shrubs were found *Macropiper excelsum* var. *majus*. Regenerated trees were few with two or three species reaching 1.5 m in height and four species ranging in height from 0.5 to 1 m. The epiphytes in this forest included a few mosses and rarely ferns, with lianas (mainly *Capparis nobilis*) rising to only 20% of stem height in the lower canopy, and seldom reaching the upper canopy. Creeping plants and *Oplismenus* sp dominated in the herb layer with a few rare ferns and orchids.

The forest on the moister southwestern slopes, with inclination of 20° and 200 m above sea level, was quite different. Its upper canopy was 20 m high, formed by white oak and *Nestegis apetala* with an average stem diameter of 0.9 m. The lower canopy was up to 12 m high and formed of tree ferns and palm with *Acronichia simplicifolia, Planchonella costata,* and *Dysoxylum patersonianum* also occurring. The stem height averaged around 6 m and stem diameter was 12 to 15 cm. The total crown closure in the woody stand was 0.8-0.9.

Piper sp. dominated the shrub layer which also included regenerating palms (1-2 m in height) at an average density of 2-3 individuals/100 m^2. The projective cover in the herb layer was only 1%. *Freycinetia baueriana*, a liana which in some places grows as a tree, was abundant in the shrub layer. Epiphytes were few; there were only two species of orchids and a few ferns.

The community of the northeastern slope did not contain a large number of tree ferns and was dominated by white oak. The lower canopy was dominated by palms which were a major component of succession in this area. Crown closure of the upper canopy was 0.2-0.4, and 0.8-0.9 for the lower canopy.

The pattern of the forest on slopes in close proximity to the above plots was somewhat different with *Araucaria* dominating in the upper canopy (35 m high), white oak, *Meryta augustifolia,* and *Cordyline obtecta* the lower canopy (15 m high). Regenerating *Araucaria* were numerous (up to 500 seedlings per 100 m^2) and regenerating palms were also present.

Palm forests dominated in shallow ravines with other species such as tree ferns, *Pittosporum bracteolatum, Pennata endlicheri,* and *Coprosma pilosa,* also present. In steeper sided gorges communities of tree fern (*C. australis*) with some palms and solitary specimens of *Nestegis apetala* were found together with other tree fern species such as *Blechnum norfolkianum, Doodia caudata* (?), *Marrattia frasinea, Diplasium assimile, D. australe.* Three hymenophyllic species of plants were also be found in this moist forest formation.

On southern slopes in the concave upper portions of the watershed, the forest was primarily composed of *Baloghia lucida* (Gillison pers. comm.) with abundant lianas representating a secondary forest in the mid-stages of regeneration. The climax in such areas would be an *Araucaria* dominated forest; and the present formation represents a regeneration following hurricane destruction some 15 years ago. The stand included 14 species and its composition varied spatially with *Celtis panienlata* occurring throughout and *Baloghia lucida* being more common downslope. The total crown closure of the woody stand was 0.9; average height of the main canopy was 14-16 m, while the upper canopy, made up by *Baloghia lucida,* was 35 m high. The average stem diameter was 25 cm and the maximum stem diameter, 40 cm. *Piper* sp. up to 2.5 m high, dominated the shrub layer and in some places completely covered the ground.

Unlike other communities, this one had a herb layer dominated by 5 species of ferns; *Lasteriopsis calantha, Arachnoides diaphanum, Doodia caudata* var. *media, Adiantum diaphanum* and one orchid, *Tropidium viridi-fuscum.* Lianas such as *Millettia australis, Melodinum baueri,* and *Heitonoplazum cymosum* were numerous. On average, there were 2-3 lianas on each trunk and occurred on 95% of all trees. Epiphytes were represented by solitary mosses.

Of the dominants, the most light demanding species was the white oak while the most shade-tolerant was the palm. The transparency coefficient with equal crown closure for 13 wood stands having different dominants is shown below.

From these data it may be seen that the palm on Norfolk Island is much more shade-tolerant than its relative on Raoul Island; its transparency coefficient is close to that of Norway spruce (*Picea excelsa* Link) (Tselniker, 1969). The white oak forms more transparent crowns, compared to the hard-leaf *pohutukava* on Raoul Island. *Araucaria* (the Norfolk pine) a representative of Coniferales, forms less transparent crowns than the Scots pine (*Pinus sylvestris* L.) in the forests of the temperate zone and the slash pine (*P. caribaea*) in the artificial plantations on New Guinea (for the latter, the transparency coefficient with C = 1.0 is 0.32, according to Tselniker (1969), and 0.44 according to our data).

Transparency Coefficients

Stands	1.0	0.8	0.6	0.4	0.2
White Oak	0.35	0.48	0.61	0.87	
Araucaria	0.22	0.38	0.53	0.69	0.84
Palm	0.03	0.22	0.42	0.61	0.81

When the stand included the hard-leaf species of palms and of tree ferns, the crown transparency coefficient with the crown closure of 1.0 decreased to 0.11. The mixed forests on Raoul Island, were more transparent, having an average transperancy coefficient of 0.17.

On the whole, the average transparency for the forests on Norfolk Island was lower than that on Raoul Island (0.16 and 0.23 respectively). The differences in crown transparency can be also traced in the histograms in (Figure 9). The lower crown transparency in the forests on Norfolk Island is due to than more complicated structure of these forests, and to their domination by shade-tolerant palms in the lower canopy.

The peculiar vertical structure of the hard-leaved forests on Norfolk Island provides for maximum crown transparency in the circumzenithal zone (Figure 12). The variation in the value of average transparency as function of the zenith angle in palm dominated forests is similar to that on Raoul Island (Figures 9 and 10).

The crown transparency values suggest that the amount of solar radiation beneath the subtropical forest canopy on Norfolk Island is lower than than on Raoul Island, except for plots under hard-leaved forests dominated by the white oak.

In conclusion, except for beach and coastal cliff vegetation, which are the least specific, there are several successive series of changes in the vegetation cover, from more arid to more humid plots on Norfolk Island. On steep slopes, especially those facing the sea, there are forests of *Araucaria*, occassionally with white oak in the lower canopy. The composition of the *Araucaria* forests on the flat areas is more complex; the lower canopy contains not only white oak but also other hard-leaved species. On drier but not too steep slopes of northern and north-eastern aspect there are subtropical broad-leaved, polydominant forests with *Araucaria* and palms. The upper canopy in such forests may include *Ungeria*; and *Araucaria* is sometimes observed in the upper and canopy second. Such layer-to-layer distribution of *Araucaria* may relate to the age of the forest. The upper sections of slopes are sometimes dominated by palms, while the lower parts are covered with tree ferns.

On south and southwest facing slopes *Araucaria* forms subtropical broad-leaved forests only if the slopes are very steep and close to the sea. The more gently slopes, particularly those in the interior of the island, are occupied by a more mesophytic vegetation. The slopes of northern and eastern aspect are characterized by a polydominant subtropical hard-leaved forest with tree ferns and palms, the upper layer of which is poor in species. Among the latter are the white oak (*Lagunaria*), *Nestegia, Baloghia*, and *Celtis*. The lower canopy in these forests was diverse having over ten species of trees and palms were abundant, forming palm-fern-broad-leaved forests. Finally, the valley floors, and especially the bottom of steep sided gorges, had a characteristic fern-palm and palm-fern (deeper gorges) formation. The herb layer of the latter included numerous species of ferns, and herbs of the family Urticaceae.

Thus, as one moves from more arid to more humid conditions the monodominant forests on the island are replaced by polydominant ones; this transformation follows the following set of formations first Coniferrales; Coniferale, broad-leaved mixture; broad-leaved; broad-leaved, fern-palm mixture; fern palm mixture; and finally palm-fern forests.

The herb cover on the island is generally associated with secondary successional areas and is dominated by grasses and numerous introduced species. The latter are encountered not only along roads and in clearings but also in natural forest communities, primarily in better lit sections. Some native plants, such as many grasses, representatives of the Cyperaceae, and *Euphorbia norfolkiana* which had a restricted distribution prior to human impacts have become rather widespread now.

The landscape structure of Norfolk Island is characterized by hilly and gently dissected relief, and sharply cut valleys with steep slopes are rather rare. The watershed ridges are generally flattened and gradually change into slopes. The poor contrast in relief combined with the ferralitic weathering crust and monotonous soils lead to some uniformity in vegetational patterns. At the same time, the contrasts in vegetation on slopes with different exposures are quite marked, and the shape and profile of the slope plays a very important role in such contrasts.

The mountainous region of Norfolk Island has two land units; the southern windward (moist) slope and northern leeward (dry) slope, differing primarily in their aridity and hence in the relative proportion of xeromorphic and mesomorphic communities. The internal structure of vegetation is primarily regulated by the drainage of the soil which in turn is caused by differences in slope steepness and profile. The variation of vegetation within each facies may be due both to the varying forms of relief and to the successional stage of the vegetation.

Philip Island located about 7.3 km south of the Norfolk Island is a cliffed island of volcanic origin. It rises to 280 m above sea level and approximately 1.8 x 1.8 km in size. About 200 years ago, when the first British settlements were established on Norfolk Island, domestic pigs, sheep and rabbits were introduced to Philip Island. These animals practically destroyed its woody vegetation. The rabbits

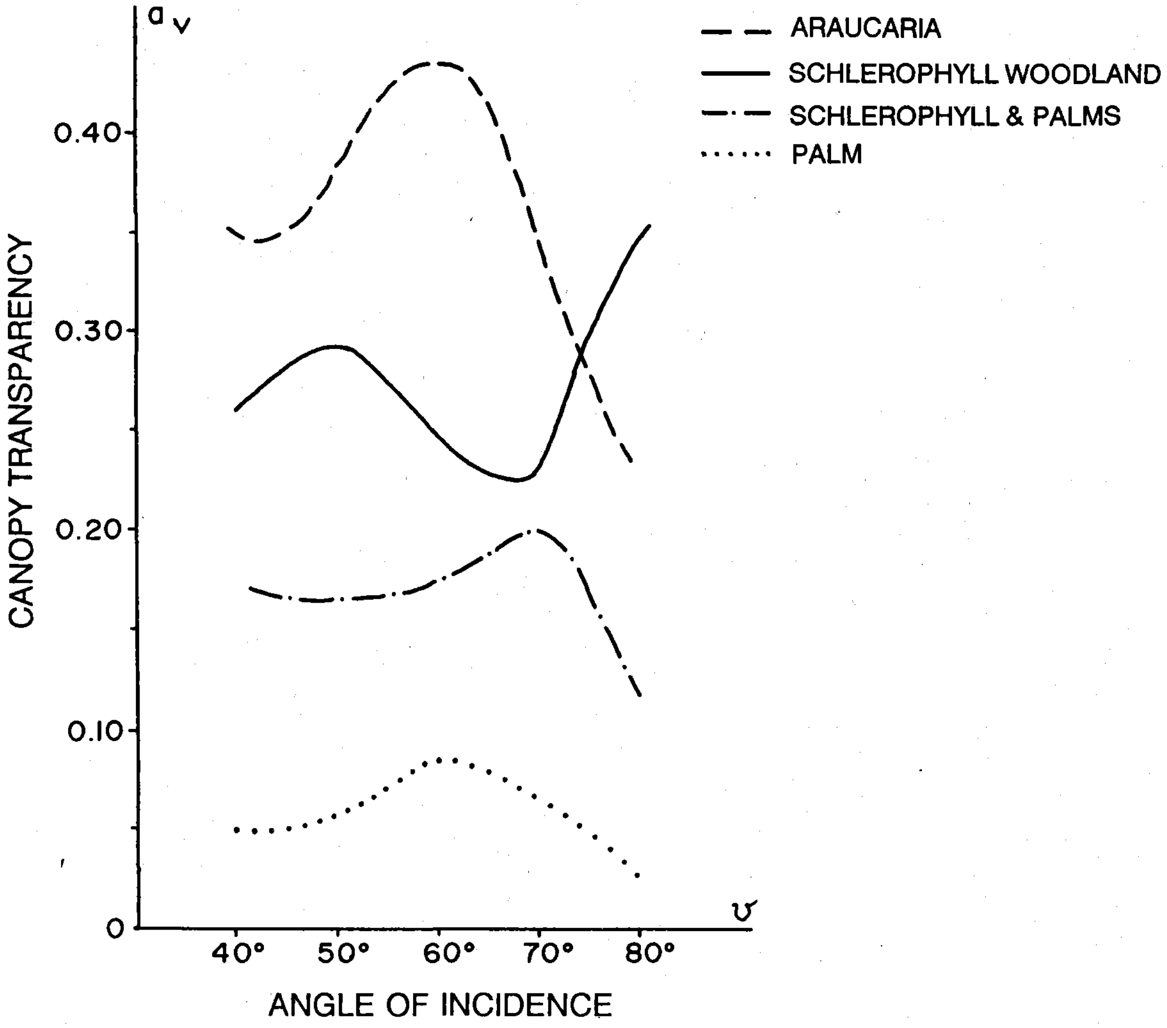

Figure 12. Crown transparencies of *Araucaria*, hard-leaved (sclerophyllous), hard-leaved and palm, and palm forest canopies on Norfolk Island.

have survived to the present. According to Turner *et al.* (1975), the plants which grew on Philip were:

Araucaria - In 1788 there were about 150 trees. Only 10 trees or so are present today.
Asplenium obtusatum - Found on steep coastal cliffs.
Cyperus haematodes - Found on coastal cliffs.
Phormium tenax - Found in coastal ravines.
Celtis paniculata - Now present by very few trees.
Strebloriza sp. - The genus and the species are endemic to Philip Island but may be extinct.
Hibiscus insularis - An endemic species. Only a few are present today.
Nestegia spetala - Only one tree has survived.
Coprosma baueri - Encountered on coastal bluffs.
Lobelia alata - Found on bluffs.
Cotula australis - Grows along the sea coast.
Wedelia biflora - Encountered at elevations up to 200 m.
White oak - Has survived as solitary trees up to 6 m in height.

Among introduced species to this island are *Olea africana, Gomphocarpus physocarpus,* and *Gnaphalium luteo-album.*

The natural vegetation is scarce on Philip Island and has been preserved only along the sea coasts, on certain slopes and cliffs as well as in the upper parts of valleys of temporary streams channels. This vegetation is represented by different clumps of varying species composition and, as a rule, of low crown closure. The clumps are dominated by single species with abundant Cop I, with participation of 2-5 solitary individuals of other species. Among the dominants are *Phytolacca octandra, Gomphocarpus physocarpus* and some others. The herb layer included *Commelina* sp., *Cyperus haematodes*; the degree of projective cover varied from 30 to 80%, although even in the latter cases a closed canopy was not present.

NIUAFO'OU ISLAND

Niuafo'ou Island (15° 30′ S. 175° 30′ W) a solitary island-volcano is located 425 km southwest of Upolu Island (Western Samoa), and 360 km northeast of Lau Island on the periphery of the Tonga-Kermadec-Lau transition zone. Niuafo'ou Island is a classical volcanic pile with a large caldera in its centre. The diameter of the caldera is about 5 km; that of the island proper is about 8.5 km.

The island originated within the Lau Basin as a submarine volcano no earlier than the Late Miocene. It is difficult to say when the volcano rose above sea level to form an island, perhaps during the Late Pleistocene or early Holocene. Eruptions from the peripheral craters were frequent. A great eruption of basalt is known to have taken place in 1885, another in the 1930s, and the last in 1953. As a result, the lower part of the volcanic slopes are overlapped by a basaltic plateau. The surface of the lava plateau is not homogeneous. It was largely formed by the eruptions of 1885 and those of 1912, 1929, 1946 and 1953. Local inhabititants showed us some of the lava fields of the 1929, 1936 and 1946 eruptions. These eruptions were responsible for at least 50% of the lava plateau area. In this discussion of these lava plateaus we shall treat them as very young (1946-1953), young (1912-1929), and old (Pre 1900).

These eruptions, were accompanied by intensive lava outflows and eruptions of ash, which settled on the surface in a very irregular way. As a result, lava plateaus of the same age may be overlain by ash of different thickness, varying from several cm to meters.

The following types of relief can be distinguished on this island:

1. The central caldera formed by subsidence.

2. The relatively old slopes of the strato-volcano; the upper zone of the island slopes.

3. The lava plateaus at the volcanic base and the lower part of the slopes.

The caldera and the lava plateau are young in age and the upper part of the slope is much older. On the whole, the entire relief of the island shows little denudation.

The old lava plateaus are overlain almost universally by ash of different thickness. The geomorphology of old and young plateaus differs slightly. The former are more frequent at higher elevations and usually begin directly beneath the upper zone of the slopes. In the northern and eastern sectors of the island they almost reach the ocean. On the southern and western parts of the island the older plateaus are separated from the ocean by young lava plateaus. Their relief conforms to the shape of the solidified lava, and comprise a system of more or less distinct ridges or disconnected fields. Facing seaward, the margins of the old lava plateaus and ridges are rather steep. Craters of various sizes are characteristic of the old lava plateaus.

In contrast, the young lava plateaus, have a smoother surface although some ridges are also present. Occasionally, a small crater rises above the weakly inclined, lava surface.

The older, upper part of the slopes in the main crater are completely overlapped by a multi-layer thickness of ash. Basaltic outcrops are found only along the ridge. In the western and northern parts of the island, the upper part of the main crater slopes is separated from the bottom by a horizon 70 m thick. In the southern and eastern sectors, the horizon is 40 m above sea level. This horizon occupies nearly 20% of the islands' area. The transition from the lava plateau to the crater slope is always very sharp, and clearly fixed in the relief. The slope steepness increases to 15-25° and is devoid of any traces of erosion. A sharp break in slope separates the cone from the surrounding plateau and the rim forms a narrow ridge between the external and internal slopes of the crater. The highest plateau is small, and is situated in the north-western section; its highest absolute point is 204 m above sea level. Smoothed watershed surfaces usually have their slopes inclined at 5°; like the slopes, these surfaces are overlapped by a heavy layer of ash.

The geomorphology of the caldera is complicated. The internal slope is almost vertical and the width of the rim seldom exceeds 100-150 m. The level of the internal lake exceeds that of the external watershed by 100-200 m. Despite its steepness, the caldera's internal slope is not eroded and transits sharply into an ash-lava plain inside the caldera. Talus deposits are practically absent because the slope is composed of dense basaltic lavas which strongly resist weathering. Near the watershed ridge at the pass in the southern sector of the island we found a four-meter thick old ferrallitic weathered crust overlapped by a 0.5-1 m layer of dense basaltic lava from a later eruption. This lava, in turn, is overlapped by a heavy ash layer of still later date. The internal slope of the caldera seems to be the oldest surface on the island, and is the least changed by later volcanic activity. Thick deposits of ash are observed only on the internal slopes close to the crater rim; downward on the slope they are completely absent. The scarps have fragments of recent soils with a typical ferrallitic horizon; these soils occurred on the basalt outcrops. On the whole, the caldera slope is a gigantic basaltic staircase with chaotically arranged steps, reaching several meters in height and width. The steps are overlapped occasionally by a soil layer. The part of the caldera floor unoccupied by lakes is formed into a series of ash-slag hilly plains of three levels; 100-120 m, 40-60 and 10-20 m. The hilly pattern of this relief is due to craters some of which are filled with water. The ash-slag ratio is not consistent, some hills are almost entirely made of ash, and on such hills one sees traces of recent channel erosion which are unique for this island. The ash is often of different thickness, from .01 to 1 m and underlain by slag.

The age of the ash is hard to establish, but, judging from the state of vegetation and the extent of weathering on the lower soil horizons, there are both relatively young and rather old surfaces present in close proximity to each other.

Niuafo'ou Island, does not have a weather station; the closest are those on Rotuma some 300 km northwest of Niuafo'ou, and on Matatutu Island which is 150 km to the east. Data on the mean monthly and mean annual air temperature are available for these two islands (Table 7). The pattern of temperatures on these two islands is practically identical; the warmest months occur in summer, November-March; the coldest in winter, August-October. Both islands have an absolute maximum temperature in March and the months with absolute minimum temperatures also coincide. The weather station on Matatutu Island, which is situated somewhat more to the east, recorded higher mean and absolute maximum temperatures, as well as much lower temperature.

On the whole, compared to Rotuma, Matatutu has probably a more oceanic pattern of climate and a smaller amount of precipitation. The duration of solar radiation indirectly suggests a relatively dry period during winter from July to September and wetter period in summer, from December to February-April. It may be suggested that the periodicity in atmospheric precipitation on Matatutu island is similar. According to Brookfield *et al.* (1966), the climate on Rotuma island is variable, dominated by a humid period (over 50 mm precipitation per week), with a short dry period (precipitation under 25 mm per week), and total annual precipitation 2000-2500 mm at the onset of the maximum in late December till the onset of the minimum in late June.

Maximum precipitation differs from the mean by about 100 mm per week, and minimum precipitation is 25 mm per week less than the mean. Even in the wettest time of the year the sun is not covered by clouds for 50% of the day and most rain falls as showers at night. The amount of precipitation during trade wind conditions varies according to island relief. Bhumralcar (1973) hasdescribed a model of air mass transformation above this island. According to this model, the amount of precipitation essentially increases with altitude on the windward, eastern part of the island. In the leeward part, the air is usually much drier. A similar pattern is observed for small islands situated near the eastern part of the Viti Levu which receive 1800 to 3000 mm precipitation per year. The eastern part of the island receives between 3000 to 3750 mm, with 4000 mm on its highest parts while the western coast receives less than 1800 mm. In this way, precipitation increases approximately 200 mm for every 200 m altitude in the windward sector while in the leeward part the vertical gradient of precipitation is much greater. On small islands, like Niuafo'ou, these contrasts are considerably weaker, however there is every reason to believe that on islands with summits over 150-200 m these effects can be quite noticeable.

The vegetation structure on Niuafo'ou Island varies in relation to the age of the surface and site specific characteristics. Uhe (1974) described the processes of succession on lavas of the last eruptions based on his observations conducted in 1966 (Table 8).

By 1966 the lava surfaces of the 1946 eruption had a diverse vegetation cover. One could find "habitat islands" of vegetation up to 1.5 m in diameter, dominated by *Morinda citrifolia* (0.15-1.50 m) and *Pipturus argenteus* (0.75), with solitary specimens of *Casuarina equisetifolia* varying in height from 4 to 9 m. In total 27 species were recorded.

The vegetation of the island is in a permanent state of regeneration because of periodic eruptions, although on some plots without lava flows, there were communities of plants which seem to have been preserved from the effects of the more recent eruptions. These "habitat islands" of vegetation are peculiar in that their centre is a depression (1.0 -1.5 m) without lava. These "habitat islands" are comparable to the *kipukas* of Hawaiian lava flows.

These "islands" of vegetation differ slightly from one another and are now occupied by a 15-20 m high, two-layered forest of *Casuarina* and occasionally *Rhus taitensis* which has an upper canopy crown closure of 0.4-0.7 and stand height 14-20 m. The stand had two canopy layers with the lower canopy composed of 4 to 6 species. Shrubs were represented by *Jasminium didymum* and *Scaevola* sp. The projective cover of regenerating *Casuarina* seedlings in the grass-herb layer was 30-40%.

The open lava plateaus were colonised by lichens of the genus *Cladonia*, by algae, and occasionally ferns in deep crevices. *Morinda citrifolia*, as a pioneer species, reaches 2-3 m in height and in some areas the lavas are overgrown by plants such as 3-5 m high *Casuarina*. Solitary specimens of *Ficus elastica* were occasionally encountered.

Table 7. Climatic characteristics of Rotuma and Matatutu Islands (Lebedev, 1973).

Island	J	F	M	A	M	J	J	A	S	O	N	D	Annual
Rotuma													
Mean Monthly Temperature	27.2	27.2	26.9	26.9	26.9	26.7	26.1	26.1	26.4	28.5	26.9	26.9	26.7
Absolute Maximum Temperature	32.8	32.8	33.3	32.2	32.2	31.7	31.1	31.7	31.7	31.7	31.7	32.2	33.3
Absolute Minimum Temperature	30.0	21.7	21.1	22.2	20.6	20.6	19.4	21.1	20.6	21.1	20.0	20.6	19.4
Mean Monthly Duration of Solar Aurora	197	167	202	204	220	195	212	232	221	227	217	177	2473
Matatutu													
Mean Monthly Temperature	27.2	26.8	27.1	27.4	27.2	26.8	26.4	26.3	26.6	26.8	27.0	27.2	26.9
Absolute Maximum Temperature	32.1	34.5	34.0	32.2	33.9	32.1	33.5	30.6	30.2	34.1	32.8	33.1	34.5
Absolute Minimum Temperature	20.0	21.2	22.0	22.0	20.5	21.0	21.0	20.1	20.0	20.0	21.5	21.1	20.0
Mean Daily Temperature Range	5.6	6.4	5.1	4.4	4.4	3.4	3.8	3.8	3.4	4.1	4.7	5.0	4.7

Table 8. Floristic diversity in vegetation on lava flows of different ages on Niuafo'ou Island (Uhe, 1974).

Taxonomic Group, Lifeform	Numbers Of Species On Lava Eruptions By Year			
	1912	1929	1946	1953
Lichens		1		
Mosses	1	1	1	1
Psilophytes	1	1	1	
Ferns	3	3	3	3
Monocotyledons	1	1	6	
Dicotyledons	10	20	16	4
Total	16	27	27	8
Among them:				
Grasses	1	2	6	
Subshrubs		3	5	
Shrubs	1	3	1	
Shrubs-small trees	3	4	4	3
Trees	5	7	4	1
Lianas	1	2	2	

On the lava outflows from the 1929 eruption, the "islands" of vegetation were between 30 to 60 cm in diameter and plants were less than 30 cm in height. On some plots the "islands" were between 2 and 9 m in diameter, with three "emergent" species; *Macaranga harveyana* at 3 m, *Pipturus argenteus* 1.5m, and *Rhus taitensis* 1.8 m. Many plants, including 3 species of ferns and *Premna taitensis,* grew in vast colonies. Accumulations of ash and/or slag in the depressions supported such weeds as *Digitaria pruriens, Eragrostis amabilis, Desmodium trifolium, Borreria laevis, Triumfetta bertramia, Sida* sp., and *Euphorbia hirta.* Near the road crossing the lava field, on sand and ashes were also found *Hibiscus* sp., *Stachytarpheta* sp., *Sporobolus* sp., *Indigofera* sp., *Ipomoea* sp., *Dacteyloctenium* sp., and *Fimbristylis* sp.

On the lava flows of the 1912 eruption the "islands" of vegetation usually did not exceed 1.5 m in diameter. The height of the plants seldom exceeded 4.5 m, except in the case of *Casuarina equisetifolia.* Only the ferns, *Nephrolepis hirsultula* and *Davallia soldia* grew in small groups. All other species were usually solitary.

The craters of the 1953 eruption contained only 8 species. Seven of these, observed on all five plots examined, were *Pipturus argenteus, Tacca leontopetaloides, Premna taitensis, Davallia solida, Nephrolepis hirsutula, Polypodium scolopendria,* and *Philonotus* sp. It would appear that these plants are the most important pioneers in the vegetational succession of lava flows. The sections of lava overgrown with plants were usually the uneven lava surfaces. There were numerous fissures of different depths and widths, as well as shallow water channels and rills (hollows) along which one found accumulations of mineral and organic residues sufficient for the rooting of small plants.

Much more overgrown with vegetation was the flat ridge surrounding the crater of 1929. The projective cover there was 70% and among the plants one found *Triumfetta* sp., *Dactyloctenium* sp., *Portulaca* sp., and *Morinda citrifolia.* The latter was represented by small specimens with flowers and fruits.

The regrowth on the lavas affected by ocean salt spray was quite different. Closer to the sea, the plots on the lava plateau were covered with *Casuarina* which had a projective cover up to 10%. Further from the shore, the same species was observed in association with *Ipomoea* sp. The projective coverage was 20%; above the highest coastal scarp it was 30%. In more sheltered places, the fern *Acrostichum* sp. and patches of *Scirpus* sp. were found. The higher scarps along the shore also contained *Pandanus* sp. Above the *Pandanus* sp. the natural vegetation had been partially destroyed and replaced by vegetable gardens. *Morinda citrifolia, Scaevola* sp., *Pandanus,* and regrowth coconut palms were abundant there. The bulk of the island's periphery was occupied by *Casuarina.*

The data presented by Uhe (1974) demonstrate that small differences in the age of the local lavas do not determine the pattern of regrowth by plants. Plants colonize different sections of lavas, depending on the variations in substrate and its proximity to areas already colonized by plants.

The lavas were chiefly colonized by light seeking trees and shrubs, and by grasses. *Casuarina,* which can withstand even the most arid conditions, is an important colonising species. However it is almost never encountered in the pioneer stages of succession under moist conditions. *Casuarina* forests are very characteristic of the island. They occupy considerable areas of the old lava plateaus, but always the relatively xeromorphic habitats, such as areas where the ash is thin or well drained hills.

The crown transparency and closure of *Casuarina* was respectively, 0.44 and 1.0, demonstrating the high light demands of this species. The crown transparency of *Pinus silvestris* by way of comparison is 0.32 (Tselniker 1969). We were unable to find regenerating *Casuarina* beneath forest canopy even of the lowest closure. Other trees typical of the young lava plateau are quite common under conditions of medium crown closure. All species of trees and shrubs found on the young lavas required high light intensities. Many of these were also characteristic of the entire region, being also found in the vegetation of raised coral islands and motus.

The development of vegetation on the old lava plateau and on the slopes of the strato-volcano can be easily traced in the profile laid out in the northeastern part of the island, from the shore to the upper slopes of the caldera (Figure 13). Three surfaces, differing in their origins, can be distinguished within the profile. The first two surfaces are connected to the old lava plateau and reflect various stages of volcanic activity.

In close proximity to the shore is a lava surface of low inclination, which is continuous with a small crater situated some two hundred metres offshore. Here the thin layer of ash was underlain by lavas and slag (scoria) at depth of 8 to 20 cm with the scoria outcroping occasionally. The soils were weakly developed and can be classified as soft humus, volcanic, and ash-slaggy. While the age of the surface is constant, the structure of the vegetation varies with the thickness of the ash layers and distance from the ocean. On the steep lava shore there was a *Casuarina* forest up to 20 m in height and of high closure (about 0.8). A thin layer of *Scaevola* shrubs was found beneath the canopy and the ground cover was composed of grasses and *Tacca leontopetaloides* where the ash layer was thickest (about 20 cm).

Although the ash layer thickness was unchanged for a distance of 80 to 100 m, the height and crown closure of the *Casuarina* forest decreased with increasing distance from the ocean. The forest gradually changed into open woodland with a well developed layer of *Scaevola, Morinda,* and *Cassytha,* and an almost continuous cover composed of grasses, *Mimosa* and *Tacca.* This light forest (open woodland) was characteristic of the entire plot where the ash layer was usually 10 cm thick. The trees and shrubs were found in microhabitats having thicker ash layers, while grasses were chiefly found where the scoria outcropped at the surface. It should be noted that fires which retard the rate of forest regeneration, occur in this territory.

The lateral crater in the profile, despite its small dimensions, formed a special micro-topographic feature; its ash covered floor and steep slopes were well covered with vegetation characteristic of humid conditions. The crown closure here was about 0.8 and the tree layer was 22 m high. There were no shrub or herbaceous forms present, and the two layered forest included five or six species of trees. The vegetation of the external crater walls was an open woodland. Thus, moisture conditions as determined by ash thickness, distance from ocean and the specific conditions in the crater funnel, were the leading factors regulating the regrowth of the old lava plateau. It is clear that the combination of intermittent dry periods and the low water holding capacity of the young, thin ash soils is unfavourable for forest regeneration, and lengthens the regeneration time for the climax vegetation.

An older surface of the old lava plateau occurred at heights of 40 to 80 m. The origin of this older surface was similar to that of the ancient crater situated slightly off the profile. This surface was composed of lava overlain by ash for 20 cm, with ash and scoria being encountered at depths of 30 to 40 cm. This surface is extensive in the northwestern part of the island. Its very old age is indirectly indicated by the development of soils with distinct horizons. The humus horizon was distinct, varying in thickness from 10 to 20 cm; the AB horizon was ocherous or brown in colour and showed obvious traces of ferrallitization. One could easily see the difference in the resistence to penetration values for the horizons. The A layer had a durometer resistence of 1.2 kg/cm^2 while the AB layer had a resistence of 2.1 kg/cm^2. Field pH (6.0), did not necessarily depend on the nature of the horizon. Vegetation structure was apparently not regulated by the thickness of the ash layer, but more so by anthropogenic factors, in particular agriculture.

Slash and burn monoculture particularly of taro was widely distributed on this surface. There were also more diverse mixed vegetable and fruit gardens, recently cleared garden plots and abandoned vegetable gardens which had been quickly invaded by regrowth species. As a rule, when these forests are cleared, regenerated trees with stem diameters up to 10 cm are cut down while larger trees are ring barked. The dried and cut-out material is piled beneath large trees and burnt. The area of each garden was up to one hectare. Such gardens are usually cleared in forests of the later stages of succession.

Unfortunately, no complete identification of plants was possible; nevertheless, we noted the wide distribution of *Rhus taitensis, Barringtonia* sp., and *Hibiscus* sp. (Table 9). These were characteristic pioneer species. The coconut palm was rather rare here, growing only on relatively open better-lit plots. The species diversity on each plot was quite rich with between 5 and 8 species in every layer; plants of each species were encountered in most layers. The crowns were in the main, highly closed (0.8-0.9) although the stand was relatively low, averaging 20 m in height. Stem diameters rarely exceeded 30 cm. Buttresses and prop roots were rarely developed, and there were no emergents typical of true tropical rain forests. All of these features suggested a young age for these communities.

On the whole, the forests are polydominant, although in some places several species dominated simultaneously. Adjacent points along the profile transect usually had 5-6 species in common, which comprised 40 to 50% of the species diversity. On this basis, we considered all descriptions as those of one community type irrespective of their stage of succession.

Figure 14 shows the distribution of crown transparency within the island's forests. The most characteristic value was between 0.1-0.2, and the clearances between the crowns within the forest canopy was rather evenly distributed (Figure 15). The vegetation corresponds to one of the initial stages of forest regeneration in an abandoned food garden.

Older forests with taller trees and larger stem diameters, were encountered on the same surface. Unfortunately it was impossible to provide an absolute dating of this successional stage, although its structural features were recognisably distinct.

More mature stages of regeneration were noticed on the ash-slaggy plains in the crater of the island (Description 100, Table 9). The soils were developed on ash which, at a depth of 50 cm, overlay lava and slag. The soils were volcanic, of soft humus and strongly ferruginous. The pH of the A1 layer was 6.6. The penetration resistence of the humus horizon (0-10 cm) was only 0.5 kg/cm^2, while at 10-20 cm depth it was 1.3 kg/cm^2, at 20 cm, 3 kg/cm^2. This plot was about 50-60 m from the vertical

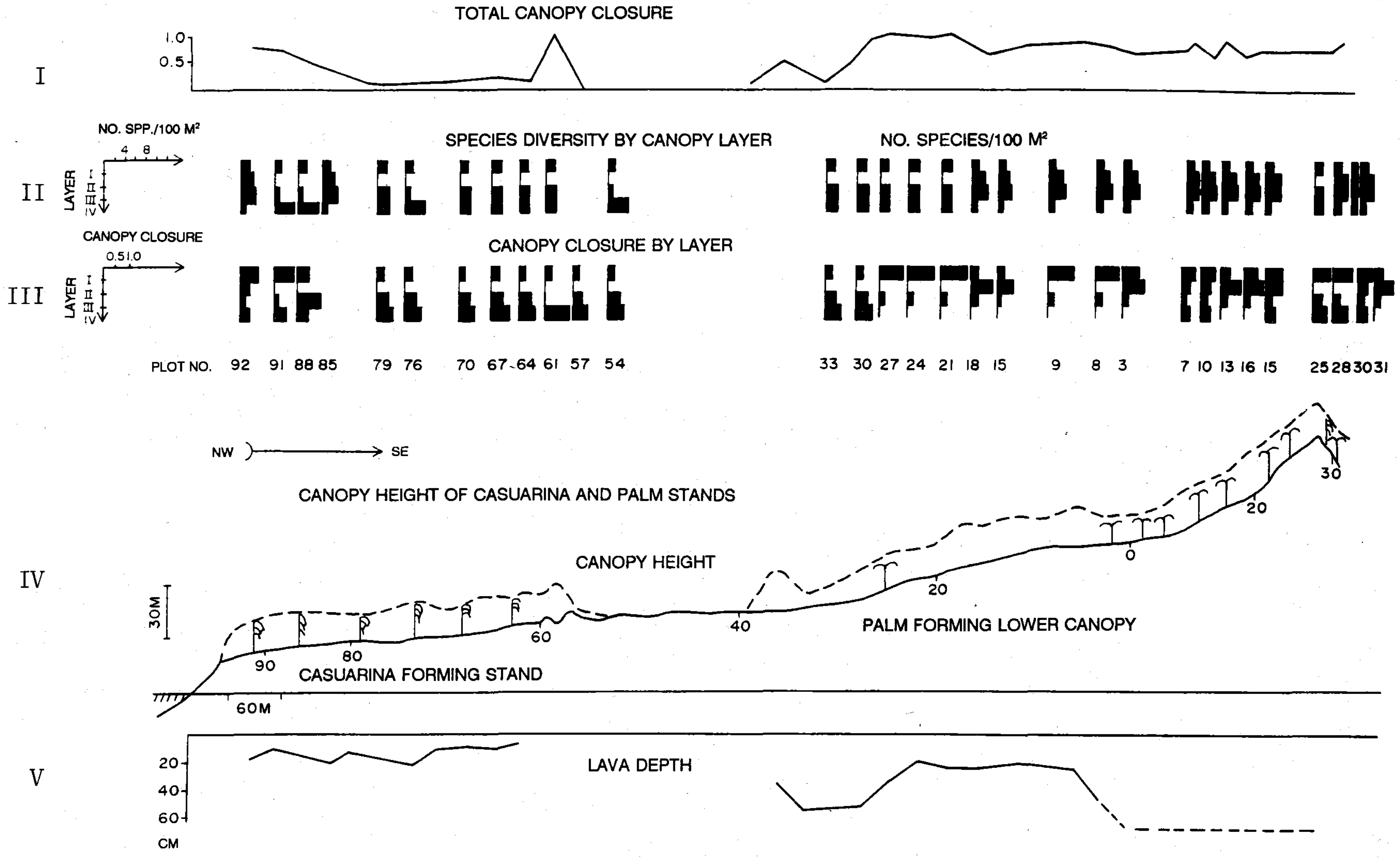

Figure 13. Ecological transect characteristics, Niuafo'ou Island. I. Total canopy closure. II. Species distribution by layers. III. Canopy closure by layers. IV. Hypsometric profile of stand height, abundance of *Casuarina* in layer I, and palm dominance. V. Depth of lava.

wall of the caldera, and had an unfavorable soil moisture conditions and no traces of human activities. Crown closure in the first three layers was relatively uniform, although the emergents at this site were not strongly developed. Species diversity was high in the second and third layers. This description probably represents the most mature community of those observed on the old lava plateaus, both inside and outside the caldera.

The external slope of the main crater can be distinguished from the lava plateau by its steeper ash covered slope and its volcanic soft-humus ferruginous soils. The soil sections revealed several stages of ash falls, which were particularly well represented in the upper parts of the slope and on the watershed surfaces. No slag or lava were found down to a depth of 60 cm. The humus horizon was usually about 10 cm thick with a penetration resistence of 1.2 kg/cm^2 at a depth of 20 cm the average resistence was 3 kg/cm^2 reaching in some sections, 5 kg/cm^2. The pH varied from 5.7 to 6.2 with the AB horizon having a higher pH than the A horizon.

The vegetation of the slope has been greatly affected by man as the entire slope, except for its uppermost part was once a coconut plantation. In addition, the area contained all the species found on the old plateau. The coconut palm was represented by mature trees and regenerated individuals 1-2 m high. Natural regeneration of the vegetation was hindered by constant cutting of regenerating woody species (stem diameters up to 5-10 cm).

As a result of constant anthropogenic effects, canopy closure of these forests averaged 0.6-0.8. The canopy height was 18-19 m. Sunshine was constant here, and therefore crown closure was similar in all layers. Only in the upper third of the slope, where the palms are slightly smaller and the anthropogenic effect is weaker, did the tree stand display increased height and canopy closure. On better-lit plots the natural regeneration of the trees was much greater and the closure of these forests averaged 0.26; although there were some areas of very high and some of very low crown closure (see Figure 14).

The coconut was peculiar in its transparency coefficient, averaging 0.22 in terms of light demand. Therefore, it is comparable to trees growing on subtropical islands. On the upper part of the slope the proportion of palms was less, and species which were characteristic of the lava plateau were again dominant. However, here the forests were mainly of one or two layers. Species diversity in all layers averaged 8.

The vegetation of the caldera slope was distinctive, with old *Casuarina* trees in the upper canopy reaching 18-20 m high, being characteristic of the upper part of the slopes. These trees reached 80 cm in diameter, and had a low crown closure (about 0.4). The coconut palm was represented by a few solitary trees. Many fallen stems covered the soil surface. This *Casuarina* forest occurred on very steep slopes exceeding 45°. Under such conditions the soil cover was shallow and a patchy in distribution with obvious traces of intensive weathering. This forest represented a successional stage developed from a pioneer *Casuarina* forest while the huge size of these trees and the large diameters of their stems indicated a high absolute age for this community.

The most mature forests on the island were found on the lower crater slopes (Description 99). Trees reached heights up to 30 m and trunk diameters up to 1.5 m. Buttress root systems were well developed. Species diversity did not differ greatly from the preceding successional stages, although frequently such forests contained many layers with great spatial differentiation and frequent dead and decaying trees.

The vegetation on this island was dominated by pioneering species and early stages of succession. The course of succession and the speed of the process seemed to depend primarily on edaphic conditions. Species diversity and number of communities on the island were high. The main factor responsible for diversity of communities was relief, or to be more exact, the diversity of volcanic surface forms. As on the other volcanic islands, there was a clear differentiation of the natural-territorial complexes into two types:

Table 9. Characteristics of the main types of plant communities on Niuafo'ou.

											Layer Characteristics *			
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
Caldera, Neck Between Lakes Vai Sii & Vai Lahi	5S4C1Su	9C1S+Su	16.8	82	200	7.49	15	0.1	-	16	$\frac{C(0.1)}{1.5}$	$\frac{S(0.1)}{6}$	$\frac{U(0.1)}{1.5}$	$\frac{E(0.3)}{0.1}$
Caldera, NW Sector, Terrace At Vai Lahi	6S3St1D +2R+Pr	6St4S+D +Pr+R	9.8	62	2625	28.51	16	0.9	0.7	7	$\frac{S(0.9)}{16}$	Absent	$\frac{S(0.7)}{0.6}$	Absent
Caldera, SE Sector, S Of Sulfate Lake, On Flat Scarp	3St2T2Op 1B1Hi	8R2St+B+S +Op+N+Nt+ St+T+Hi	6.5	139	2875	27.93	24	0.8	0.6	10	$\frac{R(0.5)}{24}$	$\frac{B(0.8)}{12}$	$\frac{Op(0.3)}{3}$	$\frac{Bl(0.2)}{0.3}$
Caldera, SE Aspect Internal Slope	4N3S1Co+ +Hi+St+T +Un+U+1Ep	5Co4S1St +T+Ep+Un +Nl+N	7.3	114	5750	55.32	17	0.9	0.7	15	$\frac{S(0.4)}{17}$	$\frac{N(0.4)}{3}$	$\frac{Op(0.1)}{1}$	$\frac{F(0.1)}{0.4}$
Caldera, SE Aspect, 25-30° Slope	6S2StBl +R+T+Al+ 1Un+Pl6	3St3S2Un+ T+Al+Pl+B	10.2	130	2575	63.76	23	0.9	0.7	11	$\frac{S(0.3)}{23}$	$\frac{Sm(0.7)}{20}$	$\frac{S(0.5)}{0.5}$	$\frac{F(0.2)}{0.2}$
NW Sector Of Island & High Oceanic Coast	10C	10C	32.6	56	313	34.56	17	0.4	0.2	-	$\frac{C(04)}{17}$	Absent	Absent	$\frac{D(0.1)}{0.3}$
NW Sector Of Island, Upper Slope, N Aspect 20-25° Slope	5Co1R1U1St 1S+T+Dy	3N2U1St Pl2S1Co T+Dy	11.9	91	2400	43.76	25	0.4	-	17	$\frac{Co(0.4)}{25}$	$\frac{R(0.6)}{15}$	$\frac{Op(0.2)}{7.2}$	$\frac{F1(0.1)}{0.3}$
S Sector Of Island, SE Aspect, 5-8° Slope, Upper 1/3 Of Slope	3B3N1S1St 1A+R+T+Op +Bi+5U+Dy +Hi	2St2B1A1T 1NS+R+Op+ BI+Dy+Hi+Sc	6.5	85	4450	25.71	13	0.8	0.6	14	$\frac{B(0.5)}{73}$	$\frac{N(0.5)}{8}$	$\frac{S(0.4)}{0.7}$	Absent

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* The numerator shows the dominant, the brackets - the closure of the layer, the denominator-the layer height, m.

Table 9. (Continued). Characteristics of the main types of plant communities on Niuafo'ou.

LEGEND

A	Site descriptors
B	Composition (No. of stems)
C	Composition (No. reserves)
D	Average stem diameter (cm)
E	CV %
F	No. stems/ha
G	Total cross sectional area (m²/ha)
H	Average height of trees (m)
I	Crown closure
J	Canopy transparency
K	No. of species per community
L	I tree layer
M	II tree layer
N	Shrub layer
O	Herb layer

S	*Syzigium* sp.
C	*Casuarina equisetifolia*
Su	Undefined
St	*Sterculia* sp.
N	Undefined
R	*Rhus taitensis*
T	*Thespesia populnea*
D	Undefined
B	*Barringtonia* sp.
N	*Notopanax* sp.
Bl	*Blechnum* sp.
Sc	*Scaevola* sp.
Mo	*Morinda* sp.
E	*Eleusine indica*
Sl	Undefined
F	Fern (undefined)
M	*Mangifera indica*
Di	*Digitaria* sp.
Op	Undefined
Al	*Aleurites* sp.
A	*Alphitonia* sp.
Pr	Undefined
Bi	*Bischofia* sp.
Hi	*Hibiscus* sp.
Ep	Undefined
Co	*Cocos nucifera*
U	Undefined
Dy	*Diospyros* sp.

1. The communities of the external surface of the crater.

2. Those of the internal surfaces of the caldera.

The external slopes usually experience lava flows, which destroy vegetation and soils, thus favouring the continuous renewal of the vegetation. During this process, sections which were not directly affected by volcanic activity are able to maintain their soil and vegetation and seem to serve as seed sources for sections buried under lava. Inside the crater, volcanic forms are quite different and heavy ash accumulations prevail. Buried soils testify to numerous interruptions in the biogenic processes caused by such strong ashfalls. Unlike the interruptions on the external slopes of volcanoes, these ashfalls may be extensive, resulting in a complete devastation of all life on the caldera floor. In this case the vegetation can only regenerate via propagules from plants that have survived on the walls of the caldera, or in areas subject to lower ashfall.

Each of these two localities has its own specific micro-climate. The external slopes of the crater have varied micro-climates which result in the differentiation of vegetation throughout the area. This differentiation seemed to be absent in the caldera.

The landscape structure of the external slope of the volcanic crater depends on the age and pattern of volcanic activity, with pahoehoe lava of black colour either absolutely devoid of vegetation or having a very impoverished and transformed plant communities. Within the young lava fields (Figure 16) the following types of facies are recognisable: lava fields devoid of vegetation; ash fields without vegetation; ash-lava fields with pioneer vegetation along crevices and fractures; lava fields with thin pioneering vegetation of shrubs and herbs; forested "islands".

Old lava fields have a rather characteristic thick, slaggy-ash, soft-humus volcanic soil and both the soils. The vegetation within this land unit varies greatly because of the complicated history of these complexes. The soils may include ash horizons of different thickness, weathered red lavas and even weathering crusts. The vegetation on these old lava fields represents different stages of succession following subsistence agriculture. The speed of forest regeneration differs as a function of edaphic conditions. A number of facies were identified within this complex land unit (including lava plateau with thin ash-slag layers covered by vegetation of herbs and shrubs; open woodland; coastal facies consisting of shrubs and *Casuarina*).

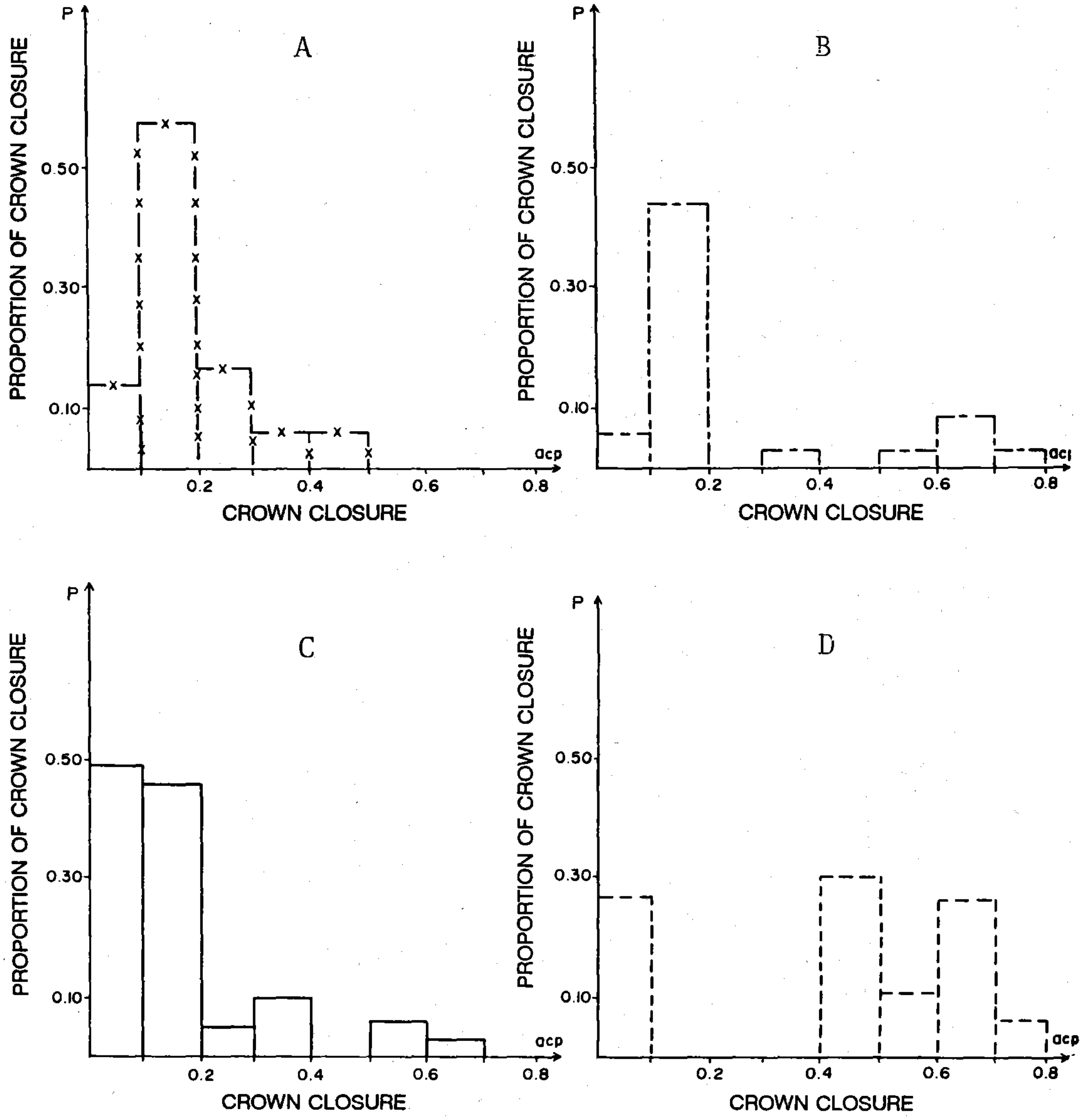

Figure 14. Distribution of forest closure on Niuafo'ou Island. A. *Casuarina* forest; B. Palm forest; C. All forests; D. Mixed forest.

The land unit of the strato-volcano slopes reveals older and more mature complexes. Their greater age is evidenced by red-colored crusts or buried eluvial horizons. Within the volcanic slopes there are two facies, differentiated on the basis of their moisture regimes. On the upper moister slopes, the coconut palm does not grow as well as on the drier lower slopes. Conditions in the upper parts of the slopes are also unfavourable for gardening since the excessive moisture and high frequency of mists, although not affecting the native vegetation, apparently adversely affects the efficiency of agriculture.

The center of the caldera is almost entirely filled by Lake Lahi. Only 10% of the total area is covered with terrestrial vegetation. There are three land units: the steep (50-60°) slopes of the caldera sides; ash-slaggy hills; and the caldera bottom. Each land unit has a different soil and vegetation. The caldera is characterized by dynamic processes of landscape formation with frequently changing conditions. This is demonstrated by the widespread distribution of *Casuarina*, normally a tree of early seral stages, but which is found in the upper canopy of all caldera associations.

The ash-slag hills are steeply sloping (40-50°) and usually 40-50 m high. On the islands in the lake and in the southern part of the crater, these hills have retained their original shape. In the eastern part, the hills are deeply incised by ravines. These differences may have resulted from differences in land use; the eastern part, where the hills are covered by open *Casuarina* woodland, is grazed by horses. Consequently, the eastern part has higher rates of erosion.

Closed canopy *Casuarina* forest up to 18 m high is widely distributed throughout the island. These forests contain representatives of woody species characteristic of the initial stages of successions in equatorial-tropical forests.

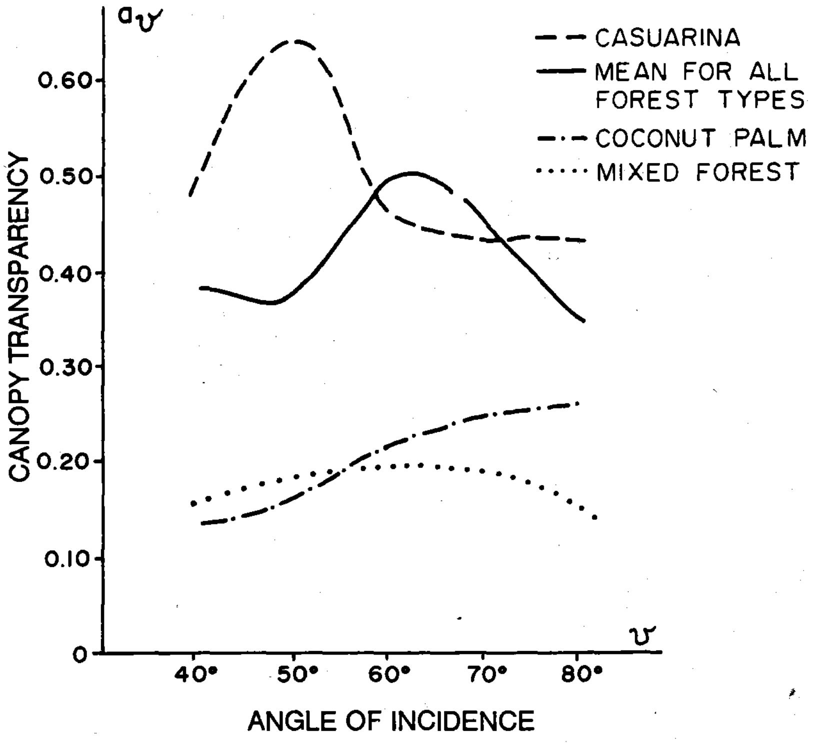

Figure 15. Canopy transparency in the woody layer of forests on Niuafo'ou Island. A. All forests; B. *Casuarina* forest; C. Palm forest; D. Mixed forest.

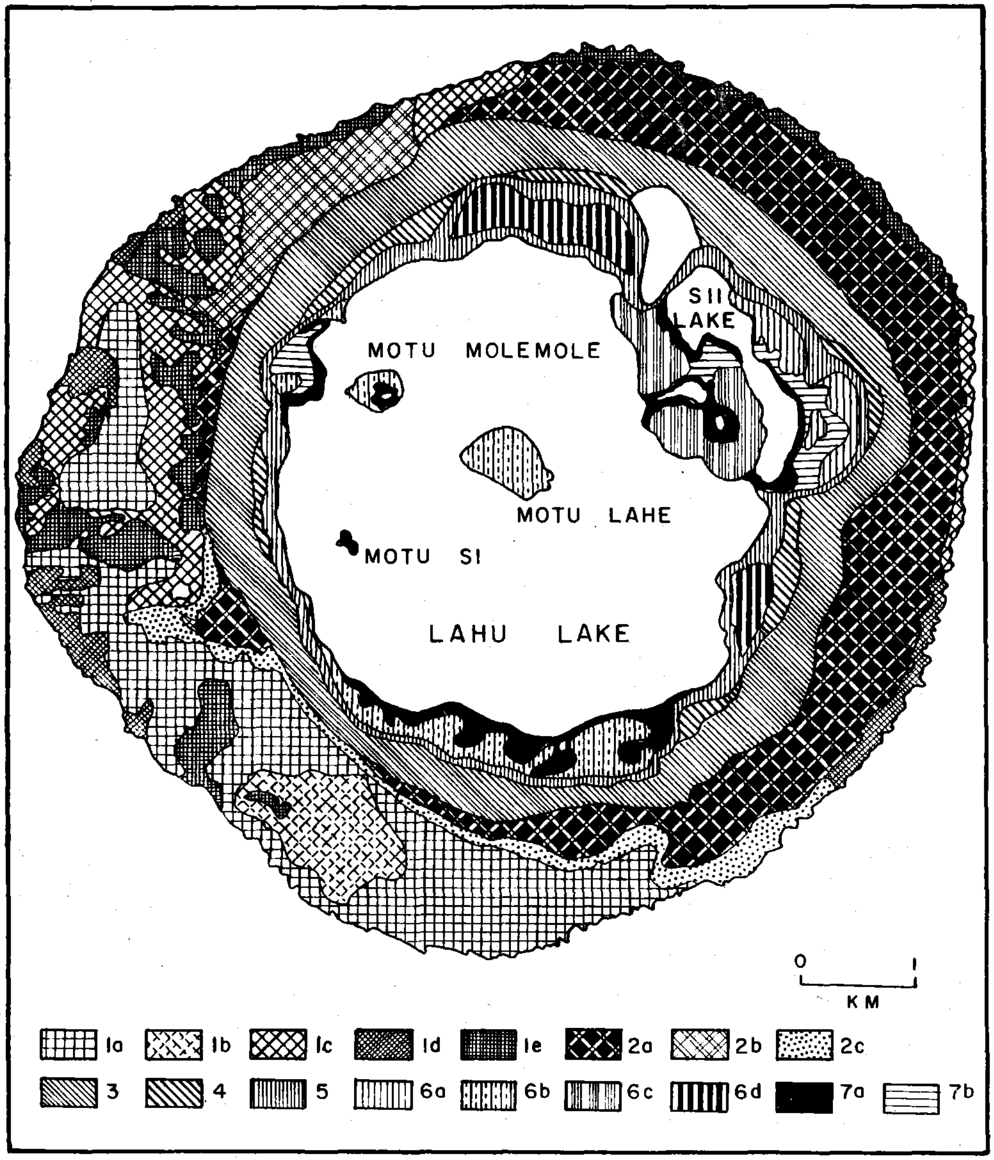

Figure 16. Landscape map of Niuafo'ou Island. Legend. I. External volcano slopes and plains. 1. Ash or lava plain, 2-4° slope; 1a. Lava field with no vegetation; 1b. Ash fields with no vegetation; 1c. Lava field with pioneer vegetation and immature soils in crevices; 1d. Lava field with maritime shrub-herb vegetation, young soils; 1e. Forest "islands". 2. Old lava fields with ash-slaggy soils with developed humus horizons; 2a. Vegetable gardens, plantations, secondary forest and shrub succession in abandoned gardens; 2b. Herb-shrub vegetation; 2c. Coastal shrub vegetation; 3. Strato-volcano mid-level slopes with red andosols, coconut plantations, vegetable gardens, post-garden forest and shrub successions; 4. Upper strato-volcano slopes with polydominant forests on thick ash soils; II. Inner crater slopes and plains. 5. Steep (50-60°) internal crater slopes with oligodominant forests (mainly of *Casuarina* in the upper layer) on laminated ash soils with old humus horizons; 6. Ash-slaggy hills and plateaus of crater with laminated ash soils; 6a. Undissected hills covered by mature monodominant forest with *Casuarina* in the upper layer; 6b. Weakly dissected hills covered by young forest of *Casuarina*; 6c. Strongly dissected hills covered by *Casuarina* in open woodlands and pastures; 6d. Plateaus with *Casuarina* forests; 7a. Lacustrine-ash plain (low level) covered by shrubs; 7b. Lacustrine-ash plains (high level).

The two terraces supported slightly different formations. The lower terrace was characterized by *Casuarina* forests with *Hibiscus* and *Terminalia* present, and in more open areas by *Pandanus, Morinda,* and *Scaevola.* The upper terraces, depending upon edaphic conditions, are occupied either by complex *Casuarina* forests or by a regenerated vegetation typical of more humid conditions. A multi-layer sequence of ash was usual for the soil sections on the upper terrace. A section 1.5 m in depth revealed 25 layers of ash reflecting the dynamic conditions under which the vegetation cover was formed.

In summary, it is worth noting that vegetation regeneration, both on the ash and on the lava surfaces takes a long time, even when conditions are most favorable: 100 years is insufficient time to permit the development of the climax vegetation. Although there are no firm dates for the island's volcanic events, no serious eruptions have apparently occurred during the last 100 years. The endemic *Megapodius* was known in the last century to nest in the same area of the caldera where we found it during our expedition. The nest holes of this bird are found near the warm sulfate lake in the southern part of the caldera. The forest around the lake also has features which testify to its young age. It may be that the edaphic conditions here are unfavorable for succession, and pioneer communities of forest vegetation and open woodlands may be stable for a long time.

BAGAMAN ISLAND

Bagaman Island (11° 8′ S, 152° 40′E) lies in the Louisiade Archipelago in southeast New Guinea. The island is small; it extends west to east for about 5 km, and north to south for 2-2.5 km. The highest point of the island is only 219 m above sea level. The coastline is strongly dissected. In the northeast the coastline is interrupted by Ulubala Bay, and in the south by Lalagela Bay.

Like the other islands of the Archipelago, Bagaman Island is part of an underwater extension of the Owen Stanley Mountains, and thus of continental origins. Other islands in the Archipelago lie in close proximity to Bagaman Island. Thus, it is highly likely that the island was separated from the landmass of Papua New Guinea in the not too distant past.

Geologically, Bagaman Island is composed of greenstone slates, schists and sericitic schists with graphite intrusions. The schists were intruded by quartz-reefs 9.67 ± 0.5 million years ago. The beds of schists commonly dip towards the NNE and NE at 45° and form a monoclinal structure which determines the geomorphological structure of the island. Thus the island has steep southern slopes and gentle northern slopes.

The axial ridge of the island is arc-shaped and convex to the south. The ridge is also displaced towards the southern coast. The main south facing slope occupies about 2 km^2, those of northern aspect-about 6 km^2. The average steepness of the southern slope is 16°, while that of the northern slope is 11°. Spurs extend northward of the main crest.

The island is of dissected relief, composed of steep erosive slopes of different exposure, and divided by clearly pronounced ridges. The strikes of the ridges follow fault lines punctuated by intrusive bodies and quartz-reefs. Considerable metamorphism in these zones has resulted in weather resistant ridge strips, below which are rather gentle slopes which rapidly become steeper. The middle parts of the slopes are inclined at 30°. The geomorphology of the island is presented in Figure 17.

The slopes are cut by a thick network of small valleys slightly entrenched in the upper slope, with their incisions becoming much sharper down slope. In the middle parts of the slopes, the valleys reveal a canyon-like transverse profile, and owing to their steepness the erosive valleys have no lateral tributaries, but are rectilinear across the lower lying land. The relief of this island is presented in Figure 18, which shows a profile starting at the beach ridge 6, running through the coastal lowland, and then through the northern slope across to the southern slope. Near the beach ridge there is a 70 m wide marine terrace built of rock debris and coral fragments.

A small stream separates this terrace from the mangrove lowland which occupies former lagoon now covered by thin deposits of dove-colored ooze. Depending on the micro-relief, small soil pits revealed water at depths of 0.3 to 0.5 m. The coastal terrace to the east and north of the profile is interrupted by channels which are tidal and carry stream water from the slopes during rains. The twisting channels of the lowland begin directly at the erosive hollows on the higher slopes. It should be noted that, there are practically no permanent water courses on this island, although in the lowermost part of the stream channels one may see very weak and constant springs of ground water. The lowland rises towards the slope very gently. At a distance of 170 m from the shore line, small fragments of corals in very low quantities are found together with ooze. The mangrove lowland is 10 m wide and changes abruptly into the slope. Almost no talus is present.

The direction of slope inclination coincides with that of the schists. However, on the slope one can see a clearly delimited scarp at the same elevation as the spur to the west of the profile. Outcropping bedrock was found only in the mid part of the profile. The loose slope soil was thin, loamy, and weakly detrital. The uppermost soil horizon was enriched with rock debris. The slope was mainly covered with brown ferrallitic soils, particularly in the upper parts of the slope. Down slope, the ochreous-brown shades of the B horizon give way to yellow and yellow-brown shades.

From 0 to 10 cm the average resistence of the soil to penetration was 3 kg/cm^2; from 10 to 20 cm it was 3 to 10 kg/cm^2. One has an impression that slope processes chiefly involve intensive evacuation of some finer fractions during plane washout. The great penetration resistence of the 10-20 cm horizon and its heavy texture form an impermeable layer. Since rain-showers here are typically of great intensity, they cause some washout of oozy material which is carried along this impermeable layer. The abundance of rock debris in the surface horizon supports this hypothesis. Given the negligible fluctuations of temperatures and the thinness of the slope mantle, solifluctional and defluctional processes must be of rather limited scale.

On the south facing, slope beginning at the watershed ridge, the soil resistence at 0 to 10 cm was 10 kg/cm^2, and 14 kg/cm^2 between 10 to 20 cm depth. The soils on this slope are not brown, but typically ferrallitic and thick (1 m and more). The slope is 35-40°, and erosion channels are found in the upper third of the slope. These are ravine shaped up to two meters in depth. This asymmetry of the slopes can be explained by the direction of dip in the schists. The dip of the southern slope is perpendicular to that of the schists. As a result, the washout of the loose mantle of the slope seems to be limited. To some extent, one can explain the greater laterization of soils and the higher soil density on this slope in terms of a less intensive washout.

The greater intensity of soil laterization on the southern slope may be also partially explained by the specific climatic characteristics for these slopes of different exposure.

Climate data for Bagaman Island are not available. However, data from the Bwagoya Inlet weather station, near the southern coast of Misima Island and some 100 km northward of Bagaman Island are probably representative of Bagaman (Lebedev, 1973). The station is 30 m above sea level and has a mean annual temperature of 26.7 °C. The coldest month is August (25 °C), the warmest is December (27.8 °C).

Precipitation within the Louisiade Archipelago occurs most unevenly (Brookfield and Hart, 1966). The western islands of this archipelago receive only 1250-1700 mm of rainfall annually. Misima and Togul Islands, which lie eastward of Bagaman Island, receive 1800-3000 mm per annum. As Bagaman Island lies almost midway between these two points, one could suggest an annual precipitation on this island of about 2000 mm. This amount is relatively small for an equatorial-tropical zone. In parts of New Guinea, which receive the same precipitation, numerous grasslands, possibly of secondary origin have developed. Unlike these regions, however, Bagaman Island has practically no dry season.

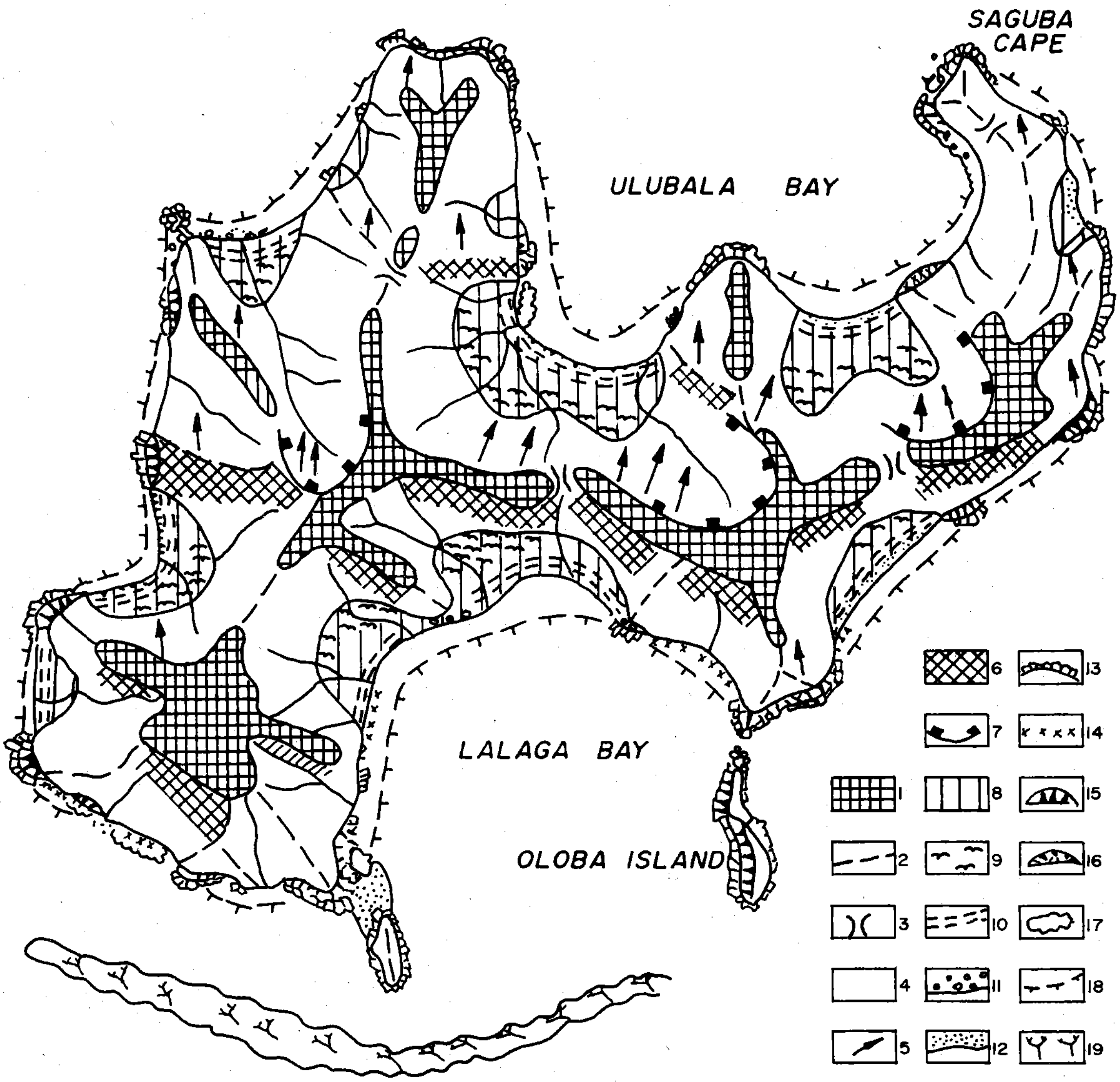

Figure 17. Geomorphology of Bagaman Island after Pain, *et al* (1979). Legend. 1. Smooth crest slopes (0-15°). 2. Sharply pronounced divides. 3. Saddles. 4. Steep slopes (30-45°). 5. Dipping slates accordant with slope surfaces. 6. Scarps of tectonic faults. 7. Erosive semicircuses. 8. Coastal lowlands. 9. Lagoon relicts. 10. Seaside walls. 11. Pebble beaches. 12. Sandy beaches. 13. Lithified beach deposits. 14. Benches. 15. Active cliffs. 16. Stable cliffs. 17. Mangroves. 18. Outer edge of fringing reef. 19. Barrier reef.

The climate has a fairly constant temperature and humidity regime. Bagaman Island does have two relatively small maxima of precipitation, one of which occurs in December-March and the second in May-August. These two maxima are due to the monsoons (from northwest) and trade winds (from southeast), respectively.

The interaction between the island's landmass and the air masses is especially clear when we compare Bagaman Island with nearby Panavan Island. Bagaman Island is almost completely forested while Panavan Island, only 110 m in height and five times smaller, is forested only along the terraces. Panavan's slopes are absolutely devoid of trees. A general feature of the Louisiade Archipelago is the absence of forests on small islands. Small areas of grassland are found on Bagaman Island's northern slope, and along the low watershed ridges (spurs) which branch off the main axial ridge. On the whole, this pattern of vegetation testifies to a relative aridity. The southern slopes have more forests. This asymmetry reflects the rainshadow effect during the tradewind season.

Bagaman Island is rather heavily populated with several hundred people living in five villages, each located on a bay. The village at Ulubula Bay has a coconut plantation in the eastern part of the terrace (the profile passed through this plantation), while food gardens occupy the northeastern and eastern slopes, and in particular the relatively flat surface near the watershed. These food gardens are arranged in small plots cleared from forest. Each plot averages 400 m^2 and contains bananas, pineapples, sweet potato, cassava, sugar cane, papaya, breadfruit and maize. Near such food gardens are plots of young regenerated (secondary) forests 5-6 m in height and overgrown by thickly intertwined lianas. These sites represent a secondary successional sequence on abandoned food gardens. In a mature secondary forest (18 m high), located on the northeastern part of the slope, we encountered an old overgrown plot with a coconut palm and several *Pandanus* trees.

However, not all plots are reforested. Near the watershed ridge on the western slope we found an abandoned plot, quadratic in shape and 1-2 ha in area which was overgrown with the grass *Themeda*. Shrubs were absent. Along the northern slope, plots of savannah vegetation are found both on the slopes and ridges at heights of 50-100 m above sea level. These seem to have the same origin as the quadratic-shaped plot described earlier.

The main vegetation types on this island are illustrated by the profile description in Figure 18. At the coast, on the first terrace, there is a narrow strip of shrub vegetation that includes *Scaevola, Ipomoea, Hibiscus,* and a number of salt tolerant mangroves species. The bulk of the terrace area was planted with coconut palms which in many places grew near the shore. In the interior of this terrace, where coral fragments were largely covered with ooze, there were plots under high-trunk single canopy forests with canopy closure of 0.9, heights of 30-35 m, and trunk diameters of 1 m. The interior of the mangrove lowland was covered by very shallow water, silty soils, and a typical mangrove vegetation. The trees were about 12-15 m high; their stem diameters were about 50 cm, and the canopy closure was nearly 0.9. The pneumatophores rose 20-30 cm above the soil surface.

On the narrow and rearward portion of the lowland, adjacent to the slope, the ooze was mixed with coral fragments. Here, in addition to the 3 species of typical mangroves, there were small coconut palms up to 6 m in height in the lower canopy. The true mangrove forests, as a rule, are single canopied. Plots on relict lagoon terraces are larger in area and have taller trees such as *Ficus* which form essentially one-layered forest.

Relatively simple forests of *Casuarina eqisetifolia* were found on parts of the slope. The upper canopy had *Casuarina* trees 16-18 m high with trunk diameters reaching 10-15 cm, and canopy closure between 0.1-0.3. The lower canopy was 11-14 m high and dominated by *Hibiscus.* The total closure of the stand which contained 9 species was about 0.8. Regenerated trees were from 2 to 2.5 m high and their closure was from 0.5 to 1.0. This layer contained four species of which three were not encountered in the poorly expressed herb/scrub layers. This type of forest is characteristic of the slopes of northern aspect where soils are thin. The origin of this type of community is still not clear, although it may be an successional stage. At present *Hibiscus* and

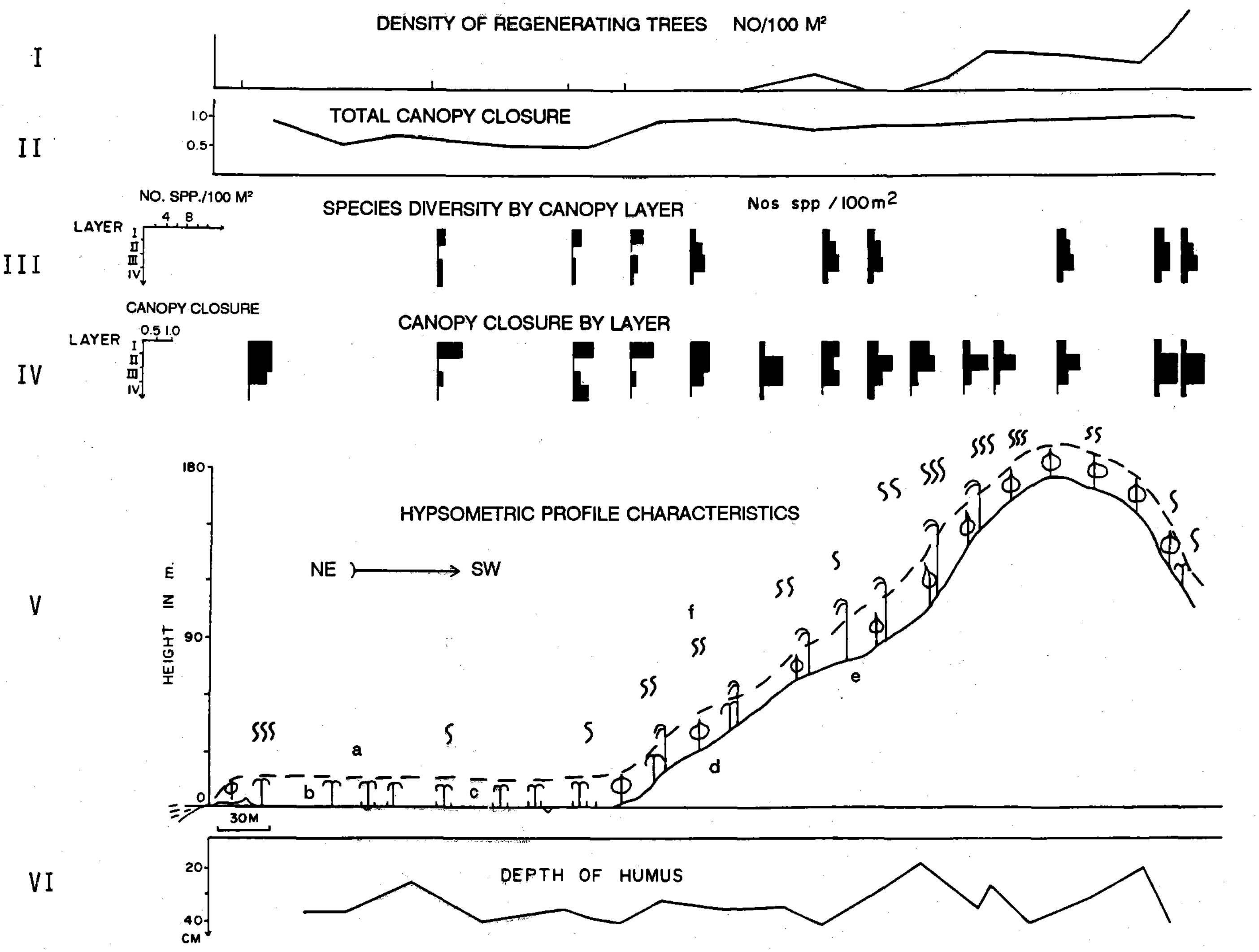

Figure 18. Ecological transect of Bagaman Island. I. Density of regenerating trees/100 m². II. Total canopy closure. III. Species diversity by canopy layer (number of species/100 m². IV. Canopy closure by layer. V. Hypsometric profile of canopy height: a. upper limit of canopy; b. coconut palms; c. mangroves; d. notomesophyllous forest; e. microphylls in the upper canopy; f. abundance of lianas. VI. Depth of humus horizon.

Albizia are being replaced by more shade-tolerant species. In contrast, the fact that all layers in this forest were quite well expressed may suggest that it is a rather late stage of succession. No traces of an anthropogenic impact were observed in this forest type.

The middle third of the northern slope contains forests in which the upper canopy was dominated by *Albizia* sp. The closure of the upper canopy was 0.3-0.5 at a height of about 30 m. Trunk directions averaged 40 cm. The closure in the lower canopy reached 0.9 at 13-16 m in height. The closure in the regenerating tree layer (3 m high), did not exceed 0.5. This layer was dominated by *Terminalia*, which in some cases was also found in the lower canopy where it reached a height of 9-10 m. Total species diversity in these forests was low, only 10-15 species being present. No species were common to both the tree and regeneration layers. In general, the community under consideration may be regarded as a simplified tropical rain forest in which *Albizia* functions to some extent, as an emergent tree. Analogues of this community were observed during our expedition to Viti Levu Island (Fiji) and in all such forests, the grass cover was rare, being often replaced by tree seedlings.

Near the watershed ridge was a 16-18 m high community dominated by *Hibiscus* sp. (with stem diameters of 40 cm). The lower canopy was composed of shade-tolerant species. This community had an upper canopy dominated by tree species characteristic of the lower canopies of *Albizia* and *Casuarina* forests. Maximum closure was encountered in the lower canopy and regeneration was high. Among the regenerating trees, one finds the same species that are common in the tree layer. A total of 10-15 species were encountered. The upper canopy had a low closure (about 0.1-0.3); the trees were 14-16 m high and their stems reached 20 cm in diameter. The lower canopy closure was about 0.9 and the fallen trunks of the second and upper canopy layer trees were present.

Communities of tropical rain forest of low species diversity and a two or three layered canopy were typical for the entire island. However, these forests displayed a complicated series of seral stages which were dependent on ecological conditions. High-stem forests with emergents were mainly confined to terraces; *Casuarina* forests to slopes with shallow soil; and *Albizia* forests to the northern slopes. The moist southern slope was covered by forests composed of many species of which one species may dominate slightly over the others.

In all formations lianas were quite common, although not at high density. A characteristic feature of these communities was a surface root system which penetrated the first ten centimeters of the soil. Epiphytes were not numerous in these forests, but were more frequently found on the southern slope. The average crown transparency in these forests was very low (Tr. av. 0.13) (Figure 19), indicating the presence of many upper canopy species with high light requirements. Canopy closure values for these forests are presented in Figure 20.

ATOLLS OF THE NORTHERN COOK ISLANDS

The expedition visited Suwarrow Atoll and Pukapuka Atoll, which are separated by over 300 km of ocean. Nevertheless, the islands of both atolls have many common natural features, and in view of this, the results for both atolls will be discussed together.

Suwarrow Atoll (13° 17′ S, 163° 07′ W) is the second largest atoll of the Northern Cook Islands. It has a typical ring-shape, stretching 15.5 km from north to south and 17.5 km west to east. The annular reef of the atoll supports over 20 islets (motus) built of coral limestone fragments. Most of these islets are concentrated in the northeastern concavity of the rim, with two islets in the northwestern and two in its southeastern quadrants. The largest motu, called Anchorage, is situated along the northeastern part of the reef and is 1 km long and 200 m wide. Two rather large motus, Manu and High Island, lie on the northwestern side of the atoll and are 700-800 m long and 150-200 m wide. Motu Fanu, the northernmost islet, has nearly the same dimensions. All other motus are smaller and do not exceed 200-300 m in length and only a few tens of meters in width.

In total, the motus occupy less than 10% of the perimeter of the annular reef. On Gardner and Mara Atolls in contrast, the motus occupy 95% of the perimeter; on Tarawa Atoll, 60%; on Butariki Atoll, 40%; on Funafuti Atoll, 25%. According to Wood and Hay (1970), the small number of motus and their low dimensions on Suwarrow Atoll are due to the devastating effects of hurricanes within the last hundred years. The atoll suffered a severe hurricane in 1942 when half of the motus were washed out. On a 1926 map, High Island is shown as strip of land elongated along the reef; today it lies almost perpendicularly to the reef. The present dimensions and configurations of other motus are also different from those shown on the 1926 map.

The annular reef of Suwarrow Atoll has just one passage (situated on the northeastern part of the atoll) from the lagoon to the ocean. The passage is 450 m wide and at its shallowest, 7-8 m deep. The interior of the atoll rim encloses a vast lagoon which reaches a depth of 80 m depth in places, although it is generally between 40 and 60 m deep. The lagoon has many patch reefs, many reaching up to sea level.

Pukapuka Atoll (10° 55'S, 165° 50'W) is the westernmost atoll in the Northern Cook Islands. The atoll has the shape of an irregular triangle, with three motus at its apices. Tearai Reef, with a section stretching westwards, is a peculiar morphological part of the atoll. The reef is submerged, 500 m wide and about 7 km long. Only the western end of the reef dries out during extreme low tides. Excluding Tearai Reef, Pukapuka Atoll stretches from north to south for over 9 km, and 4.5 km from east to west. All three sides of the reef are concave on their oceanic faces.

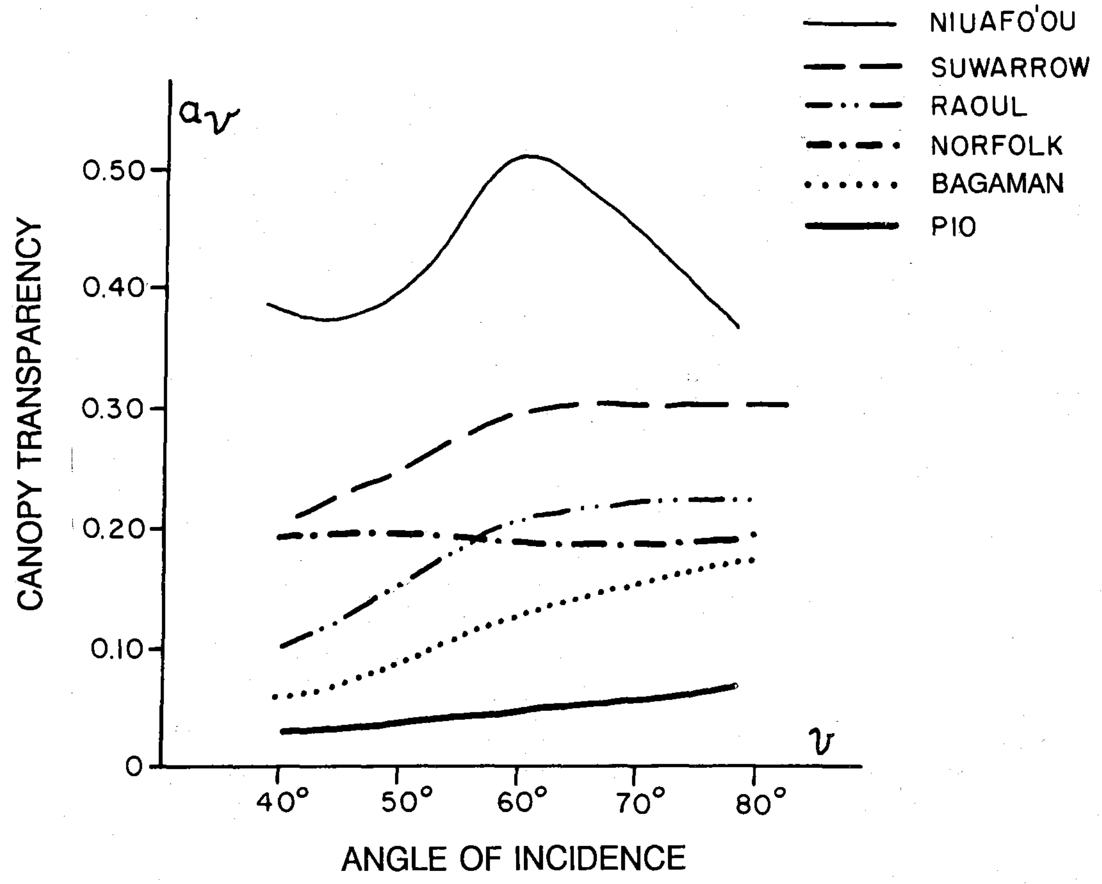

Figure 19. Variation in tree canopy transparency for island forests.

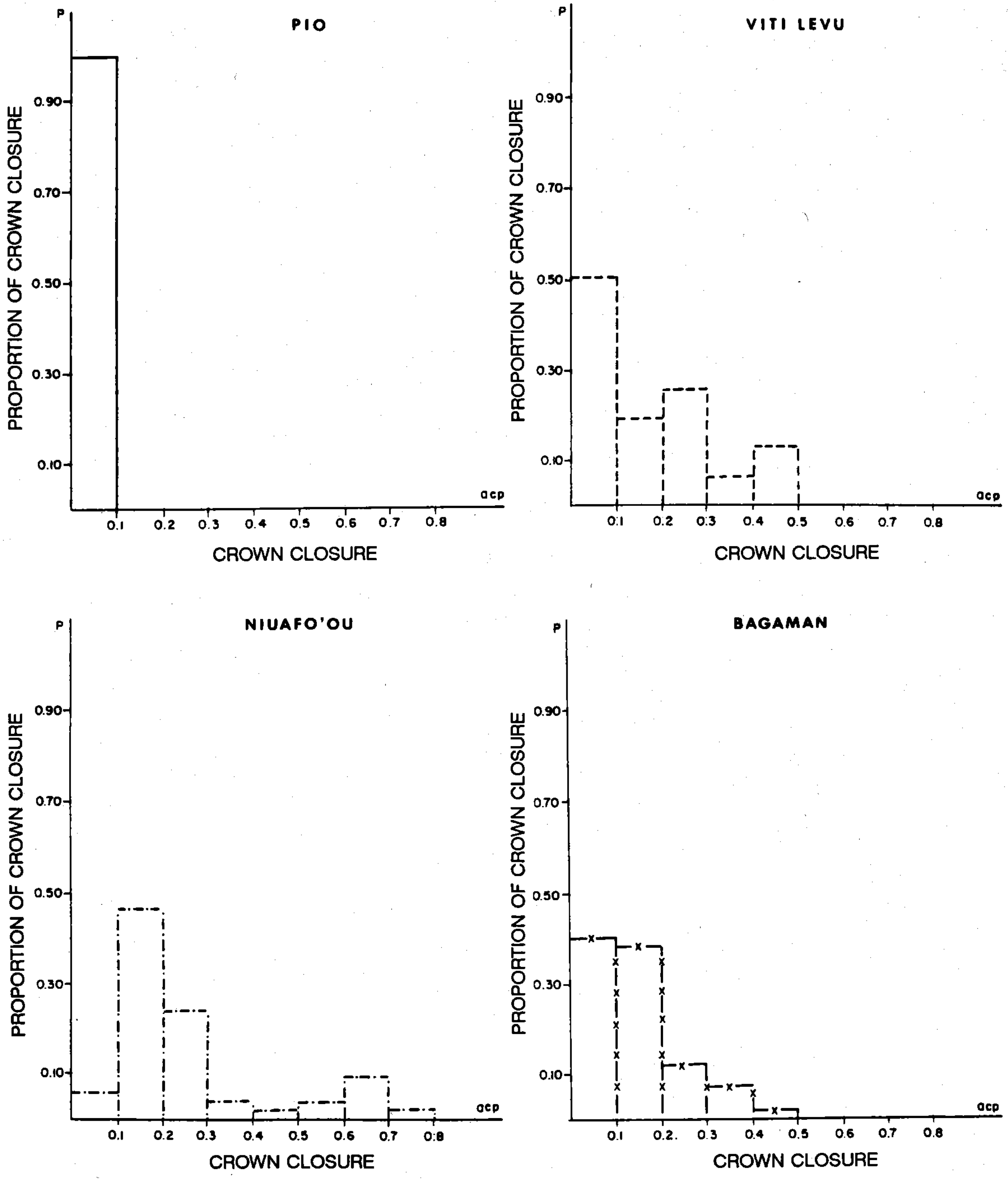

Figure 20. Distribution of canopy closure for the tree layer of island forests.

The three motus of the atoll occupy an area of 384 ha (the area of all motus on the Suwarrow Atoll is only 40 ha). The northern motu, Pukapuka and the southern motu, Motu Koe, resemble huge parabolic dunes, with their "heads" lying in the tips of the atoll triangle, and their "branches" spreading along its sides. The total length of Motu Koe exceeds 6 km; its width is nearly 1 km. The length of Pukapuka Motu is about 4 km; its width is close to 1 km. The third motu, Motu-Kavata, is shaped like a rhomb, and elongated almost 2 km from west to east. From north to south, the axis of this rhomb is only 1 km. In their total extensions the motus of Pukapuka Atoll occupy almost 50% of the reef perimeter.

The surface of the reef on the northwestern side of the atoll is slightly below sea level. Here the reef does not dry up even in the lowest ebbs, and flat-bottomed boats can cross the reef flat into the lagoon. There is no passage cutting through the rim of the atoll. The depths inside the lagoon vary from 15 to 36 m, and patch reefs are abundant.

The climate in the Northern Cook Islands is classified as a marine, temperate, humid climate (Ignatiev, 1973). This region is dominated by easterly winds, with wind velocity changing according to season and time of day. The strongest winds are observed in July and August, and are more violent in the afternoon (Wiens, 1962).

Based on data from Tongareva Atoll (Lebedev, 1973) the mean annual temperature is 28.4 °C, ranging from a mean maximum temperature in April of 28.9 °C to a minimum of 27.8 °C during June-July.

The Northern Cook Islands are a region of high precipitation. On average, Pukapuka Atoll annually receives 2736 mm of precipitation (Wiens, 1962), with a range between 2200 to 3225 mm per annum. The greatest amount of precipitation falls in summer (Table 10). Winters are relatively dry.

Table 10. Mean monthly precipitation (in mm) on Pukapuka Atoll (Meterological observations for 1959-1962).

Month	J	F	M	A	M	J	J	A	S	O	N	D
Precipitation	409	518	344	118	109	105	98	212	126	122	115	174

Suwarrow Atoll is practically uninhabited. Only Anchorage Island was inhabited between 1952 to 1954 and again from 1960. In 1964 Pukapuka Atoll had a population of 718 (Wood and Hay, 1970). The other motus are uninhabited, but are used as coconut plantations and vegetable gardens.

The flora on the atolls is species poor. Six species were encountered on all of the motus of both atolls. *Cocos nucifera, Pisonia grandis, Pandanus* sp., *Scaevola* sp. and two ferns - *Asplenium nidus* and *Phymatodes* sp. *Tournefortia argenta, Boerhavia diffusa, Guettarda speciosa,* and *Morinda citrifolia* were found on five of the six motus that we visited; these may have been missed on the sixth motu. Other species were encountered on four and even fewer islets.

The total number of species found on the motus varied between 14 to 30, except on Pukapuka where the list of plants is obviously incomplete (Table 11).

Among the introduced species are taro (*Colocasia esculenta*), papaya (*Carica papaya*), breadfruit (*Artocarpus* sp.), banana (*Musa* sp.) tomato (*Lycopersicon esculentum*), and red pepper (*Capsicum* sp.). Decorative plants include (*Hibiscus tiliaceus*), *Cassia* sp., *Araucaria heterophylla, Plumeria* sp., a Liliaceae and *Barringtonia* sp. Weed species include *Eragrostis* sp. and *Ageratum conyzoides.* The parasitic plant, *Cassytha filiformis,* is particularly widespread on inhabited island although this

Table 11. Number of recorded species on Suwarrow and Pukapuka Atolls.

Atoll	Name of motu	Number of Species
Suwarrow	High Island	17
	Fanu	14
	Anchorage	30
Pukapuka	Pukapuka	12
	Motu Koe	28
	Motu Kavata	20

plant may not be introduced as Carlquist (1974) notes that the seeds of this plant can be dispersed by ocean currents.

The islands have a poor flora (see Table 12). The number of woody species does not exceed five, and grass species also number five. In some descriptions a grass stand is absent. Lianas were encountered only in one out of eight descriptions. In total, the number of species in any description was less than 10 and each woody community constituted between 18 and 71% of the flora of a given motu. Shrub and herbaceous communities frequently had an even poorer composition consisting of only one or two species. Regenerating stands were composed of one (*Pisonia*), two, three and four species in the four stands examined. In four other cases the regrowth did not contain all the tree species present in the canopy. The number of woody species varied from 1 to 5, while the regrowth contained between 2 to 6 species. The total number of species was between 3 to 10, with the highest number of species being found in the community dominated by *Messerschmidia.*

The structure of the forest was simple, often consisting of one or two woody stories with occasionally a fragmentary third story and one or two fragmentary herb/scrub layers only one of which may be well expressed. There were no lianas. Two species of ferns, namely *Asplenium nidus* and *Phymatodes* sp., which are normally epiphytic, grew on the soil surface and formed a layer which occasionally had a high projective cover. Much less frequently they were found on trees from 1.2 to 9.0 m above ground. *Phymatodes,* a ground species, was found on the soil surface, while *Asplenium* grew more frequently on the rotten nuts of coconut, large dead branches and trunks of trees.

The spatial structure of vegetation at the facies and phytocoenotic level, as well as the factors determining it, can be well traced through the analysis of profiles established on the motus.

High Island Motu is divided into two parts (Figure 21). The western part near the ocean is an upraised limestone platform with surface depressions, while the lower part near the lagoon is built of coral fragments. The relief is undulating with depressions filled with large limestone debris over much of the area. The higher elevations are formed by remnant sections of the platforms. The narrow beaches on the ocean side of the island are composed of limestone platforms, the depressions of which are in-filled by coral fragments and sand. The structure of Fanu Island (Figure 22) differs slightly; this islet is gently inclined northward, and is composed of limestone platforms of medium size and by limestone debris. As on High Island islet the surface of Fanu islet has slightly undulating structures resulting from wave erosion. Tidal bars are about 20 m wide and there is a young beach ridge near the shore. The presence of dead algae on tidal bars 130 m offshore is evidence of tidal action. This islet lies on the reef protruding into the ocean and as a result, the inter-bar depression, characteristic of all motus, is not well expressed on this island. This depression is thought to be that part of the reef which connects Fanu Motu with One Tree Motu. This part of the reef is flooded during the tidal cycle.

Table 12. Number of plant species in atoll formations.

Site No.	Motu	Dominant Species	Number Of Species						% Of Total Number On The Motu
			Trees			Herbs	Lianas	Total	
			Adult	Regrowth	Total				
107	High Island	*Pisonia*	2	3	3	-	-	3	18.5
108	High Island	*Cocos nucifera* *Pisonia*	4	3	5	2	-	7	41.2
109	High Island	*Pandanus*	2	1	2	1	-	3	18.5
110	Fanu	*Pandanus*	4	2	4	2	1	7	50.0
111	Fanu	*Pandanus*	3	2	3	-	-	3	21.4
113	Fanu	*Messerschmidia*	5	2	5	5	-	10	71.4
112	Koe	*Pisonia*	5	6		2	-		28.6
115	Koe	*Pisonia*	1	2	2	2	-	4	20.0

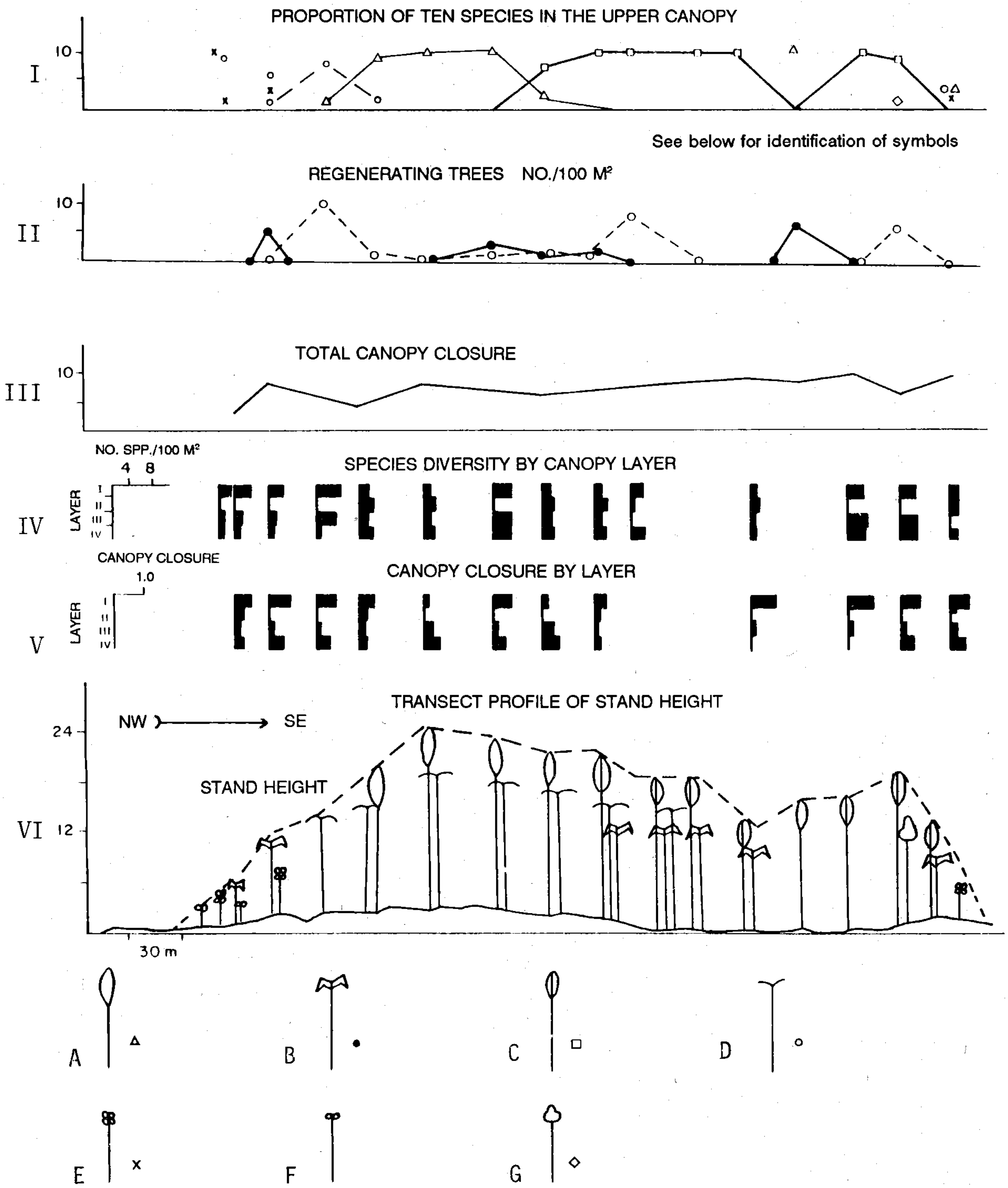

Figure 21. Profile of High Island Motu, Suwarrow Atoll. I. Proportion of 10 species in the upper canopy. II. Abundance of regenerated trees. III. Total canopy closure. IV. Species diversity by layer. V. Canopy closure by layer. VI. Hypsometric profile of stand height. A. *Pisonia*. B. *Pandanus*. C. *Guettarda*. D. Coconut palms. E. *Messerschmidia*. F. *Scaevola*. G. *Morinda*.

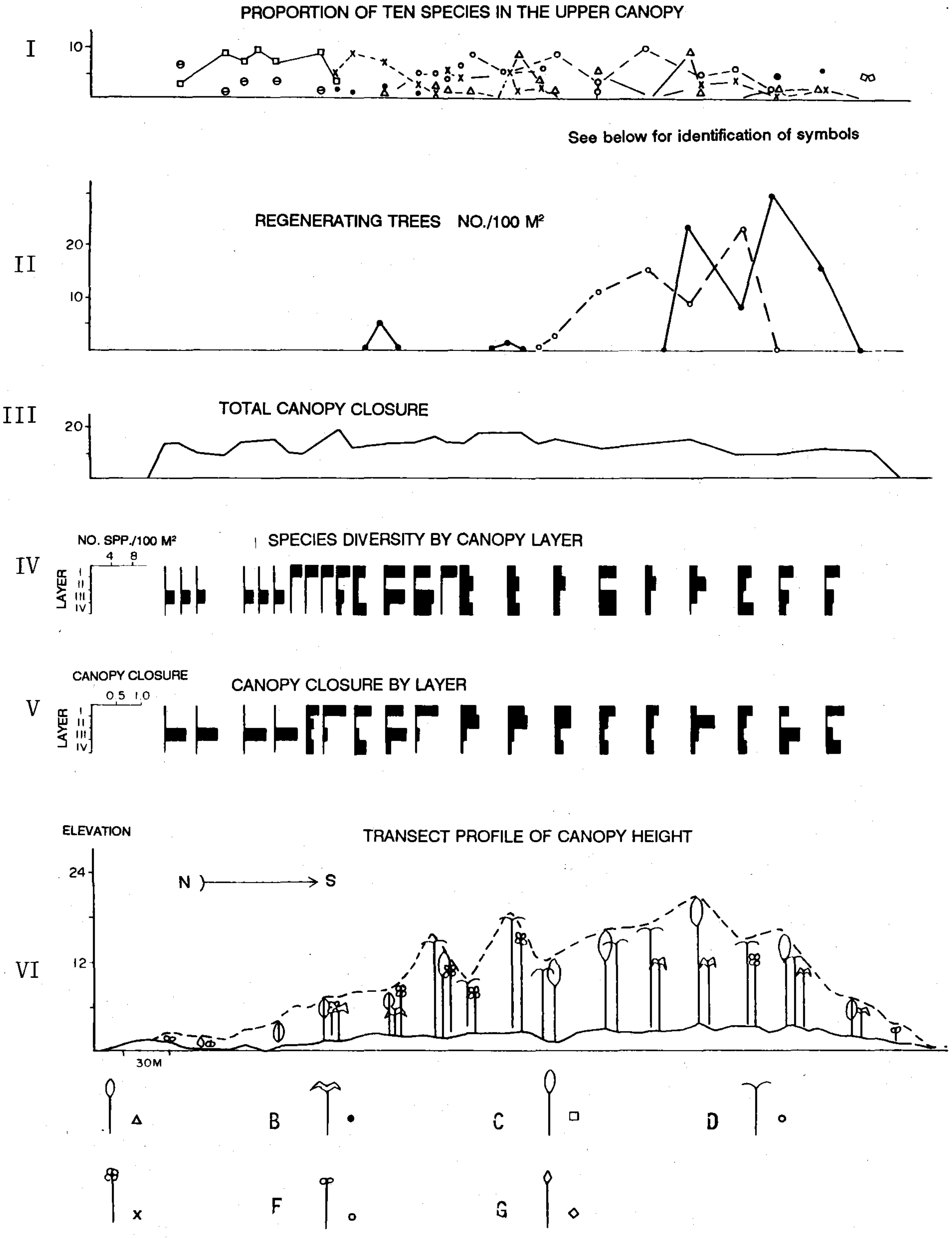

Figure 22. Profile of Fanu Motu, Suwarrow Atoll. I. Proportion of 10 species in the upper canopy. II. Abundance of regenerated trees. III. Total canopy closure. IV. Species diversity by layer. V. Canopy closure by layer. VI. Hypsometric profile of stand height. A. *Pisonia.* B. *Pandanus.* C. *Guettarda.* D. Coconut palms. E. *Messerschmidia.* F. *Scaevola.* G. *Morinda.*

The islet of Motu Koe (Figure 23A) on Pukapuka Atoll is composed of small and medium sized platforms.

The profile begins at the ocean shore of the islet and ends at a large depression occupied by food gardens in the center of the motu. The micro-relief is undulating, and of low relative amplitude.

The profile of Motu Katava (Figure 23B) reveals all the structural elements typical of motus. On the whole, Motu Katava is similar to High Island islet; the part facing the lagoon, is built up of small debris and large platforms are found only towards the motu's central depression, which is composed of small and medium sized debris.

The structural characteristics of the motus are due to their position on the atoll reef, their size and position being related to the prevailing winds.

On the whole, all the profiles show a great similarity in relief; and one can identify the following elements: the ocean facing coast, built of coral fragments and small platforms of limestone; the elevated terrace bars formed by limestone platforms; the central depression usually composed of small coral fragments; the elevated bar near the lagoon composed of small sized debris; and, the narrow lagoon beach composed of coral sand and fragments.

The vegetation on atolls may be zoned into fairly distinct communities. On High Island Motu the vegetation begins some 80 m from the oceanic shore. This community was composed of shrubs (*Scaevola, Messerschmidia*) which were frequently covered by the parasitic plant, *Cassytha filiformis*. As a rule, the crown closure of the shrubs was high (up to 0.9), although the height of this layer seldom exceeded 1.5-2.0 m. This community is characteristic of the peripheries of the motu which are flooded during high tides. The area under these communities depends upon the extent of land 1-2 m above sea level. On very low motus, such as One Tree Motu, which are flooded during hurricanes and during periods of strong wind, this community may be dominant throughout the motu. On High Island Motu, the *Scaevola-Messerschmidia* community occupied a strip only 10 m wide before passing into a two-layer community dominated by *Pandanus* and *Messerschmidia* in the upper canopy, with shrubs such as *Scaevola* and woody trees forming an under storey.

Pandanus with an average closure of about 0.6 usually reached 7-10 m in height and as a rule, the *Messerschmidia-Pandanus* community occupied the coastal strip formed from large fragments of the limestone platform. The highest parts of the motu were occupied by two-layer forests of *Pisonia* in the upper canopy and coconut palm in the lower canopy. Sometimes the upper canopy was absent and the forests were completely dominated by coconut palm. The *Pisonia* trees were from 18 to 22 m high with stem diameters approximately 1 m. Closure of the upper canopy was low, between 0.3 and 0.4. This upper canopy was usually formed by solitary *Pisonia* trees with extensive crowns above the coconut palms which reached 15-18 m in height, and had a closure of about 0.6. Beneath the canopy of *Pisonia* and coconut palms there were solitary specimens of *Morinda, Messerschmidia* and *Pandanus*. However, the community was dominated by regenerating coconut palms, *Pisonia* and the fern *Asplenium*. The regeneration of the palm was especially high when the canopy closure was around 0.6, but with increasing closure (to 0.8), the intensity of regeneration decreased. Under such conditions *Asplenium* dominated the lower layers, which had a projective cover reaching 30% and heights between 0.75 and 1.0 m. This community contained numerous fallen coconut trees and solitary fallen trees of *Pisonia*.

On the slopes facing the central depression *Pisonia* was replaced by *Guettarda*, but other species remained in much the same proportions as the previously described formation. With increasing slope steepness *Pandanus* dominated the community. It was also important as a lower canopy species in the depression. A characteristic feature of the depression was the high closure of the tree canopy which was chiefly composed of *Guettarda*. The high closure is attributed in part to the numerous lianas. The profile of High Island Motu displayed distinct boundaries between the plant communities and transitional communities were of low importance.

On Fanu Motu (Figure 22) which rises gently from the ocean, the vegetation was quite different. The large gently-rising coast is built up of coral fragments and is subject to tidal and hurricane flooding. The coasts of Fanu Motu were occupied by a mangrove community dominated by *Pemphis* which had heights between 1 to 3 m high and a closure of 0.7-0.8. The first beach ridge, rose up to 1 m above the ocean. The community was dominated by *Scaevola* which formed 20-30% of the vegetation. This species was completely absent on areas which were flooded by normal tides. With increasing distance from the ocean and increasing height above the sea level, *Pemphis* and *Scaevola* were found together with *Messerschmidia*, first as shrubs and then as trees. Here the vegetation was between 4 to 6 m high and consisted of two layers. At 2.0 m above sea level, *Pemphis* and *Scaevola* disappeared and *Messerschmidia* was found together with *Pandanus*. *Pisonia* (up to 8 m) high was found further inland. At 2.5 m above sea level, coconuts became dominant, reaching about 16 m in height. There were also some *Pisonia*, *Messerschmidia*, and occasionally *Pandanus*. Unlike High Island Motu, the boundaries between communities on Motu Fanu were not clearly defined. However, the general distribution of species remained the same with *Pisonia* being most important on the highest part of this motu. *Guettarda* was encountered in the interior of this motu although its role on Motu Fanu was never as great as that in the High Island depression. From the profile it can be seen that the forests of Motu Fanu is also of two layers, but of lower heights and canopy closures.

On the whole, the vegetation cover on Motu Fanu seems to be less "organized" compared to High Island. Practically all woody species are present, although in different proportions, and the vegetation on Motu Fanu may reflect the damaging effects of hurricanes since it never exceeded 18 m in height throughout the entire profile. Furthermore, many regenerating trees were present.

The profile of Motu Katava on Pukapuka Atoll, also reveals the same basic patterns described above. However the spatial structure of vegetation on this motu is much simpler than that on High Island. Much of the interior of the Motu Katava is little affected by man and is occupied by a forest community of coconut palm and *Pisonia*. Unlike the coconut and *Pisonia* community on High Island, the trees on Motu Fanu were usually 23 to 24 m high. The stem diameter of *Pisonia* was up to 1.0 m and *Pisonia* which formed the upper canopy had a closure value as high as 0.8. Coconut palms rarely penetrated the upper canopy, but were quite common in the lower canopy. As on the other motus, *Pandanus* was an important component of the more open areas. The herb layer was formed by *Asplenium*.

On Motu Koe the profile began at the islet's ocean shore and passed inland towards the central depression occupied by food gardens. Anthropogenic effects were quite obvious: small trees in the lower layers had been cut and *Asplenium* leaves had been collected as a mulch for the food gardens. The elevated high surface of Motu Koe was very stony. In contrast to the situations described earlier, coconut palms were insignificant here and *Guettarda* was prominent. The coastal vegetation was represented by a narrow strip of *Scaevola*; further inland there was a strip of *Guettarda* - *Pandanus* forest with a shrub layer composed of *Scaevola*. The abundance of *Scaevola* diminished towards the interior of the motu and the herb layer usually contained *Asplenium* and *Phymatodes*.

Most of the profile was occupied by two-layer forests dominated in the upper canopy by *Guettarda*, which reached 14-20 m in height. There were solitary, large *Pisonia* trees up to 22 m with a few coconut palms; the lower canopy was 6 to 14 m high and composed of *Pandanus*. Cleared plots contained *Morinda*, and the species diversity of the herb layer was greater on cleared plots than on natural plots.

Thus, despite certain differences, the structure of the vegetation on all motus has many features in common. *Pemphis acidula* was present on limestone beds; *Scaevola* was found on limestone sand, and *Messerschmidia* was found on both sand and coarse-grained substrates. These species were restricted to coastal locations if the motu was about one or two hundred meters wide. Occasionally *Pandanus* dominated inland locations, giving way to coconut palms, *Pisonia* and *Guettarda*.

However, despite their ecological plasticity, which is especially obvious on motus subject to destructive factors such as hurricanes, under more stable conditions, the spatial differentiation of

See below for identification of symbols

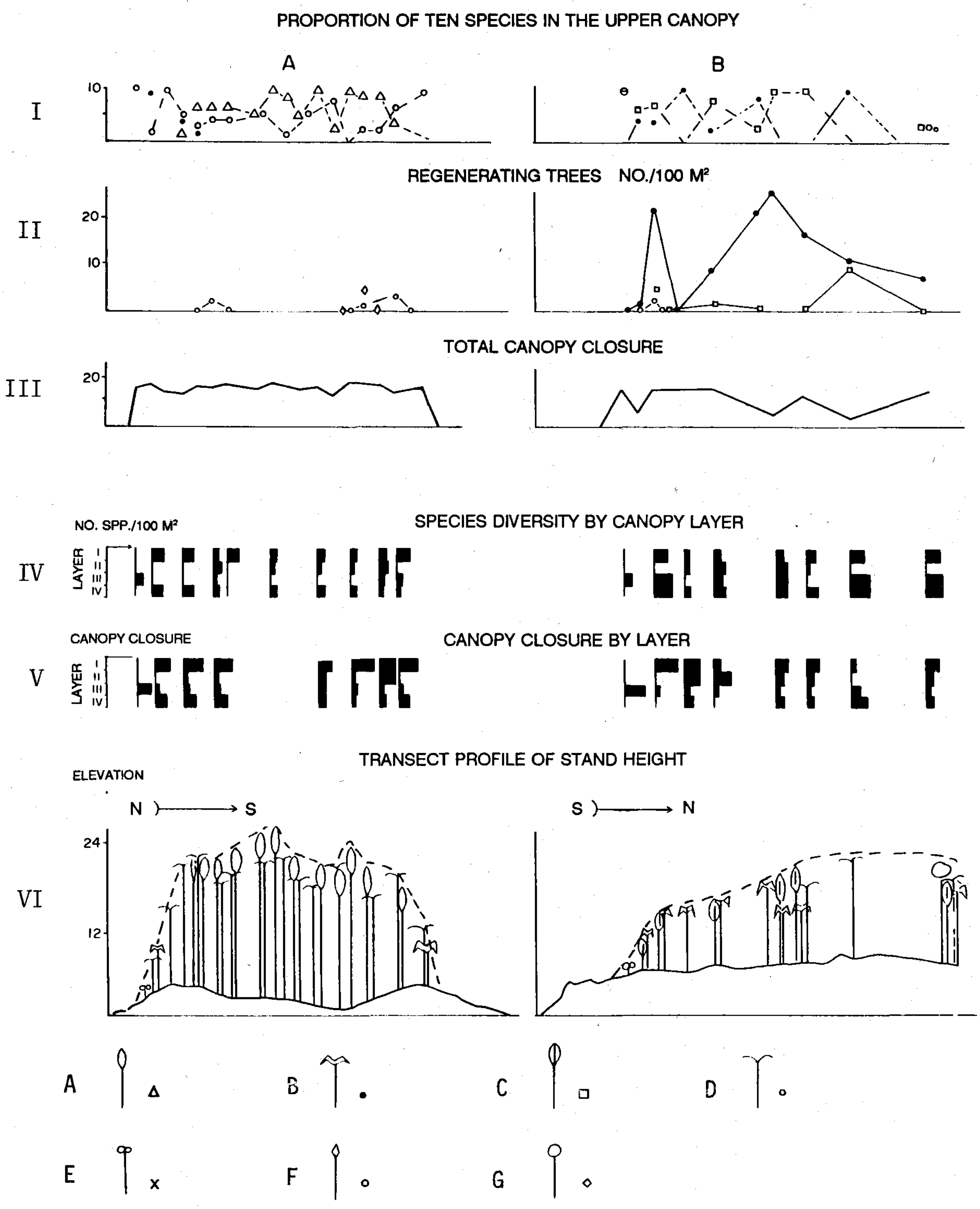

Figure 23 A and B. Profile of Motu Katava (A) and Motu Koe, Pukapuka Atoll. I. Proportion of 10 species in the upper canopy. II. Abundance of regenerated trees. III. Total canopy closure. IV. Species diversity by layer. V. Canopy closure by layer. VI. Hypsometric profile of stand height. A. *Pisonia*. B. *Pandanus*. C. *Guettarda*. D. Coconut palms. E. *Scaevola*. G. *Ficus*.

the species becomes more definite. This differentiation seems to be regulated by the gradients of soil salinity, the extent of soil stoniness, the age of the soil surface, and the light demands of different species.

In general there were no shade-tolerant woody species on atolls. The transparency coefficient of species comprising the lower canopy, namely coconut palms and *Pandanus*, was 0.22 and 0.19, respectively, and testified to their considerable light demands. The average crown transparency on the atolls under study was the greatest (0.31) compared to all other areas examined. These data suggest that much more solar radiation can penetrate beneath the canopy of the woody stand here than in any other tropical and subtropical forests. This may also explain why the grass layer is formed by epiphytic ferns. The intensity of regeneration clearly depends on the closure of the upper layers. When the decay of the wood layer is high, intense regeneration of either *Pandanus*, coconut palms, or *Pisonia* was apparent.

As to their vertical structure, the forests on the atolls resemble those on Raoul Island. The only difference was that the palm, which formed the lower canopy in the forests on Raoul Island, had a higher shade tolerance.

The structure of the natural-territorial complex on the atolls depends on the configuration of the atoll itself, the height of the motu, and the effects of the exogenic factors. As a rule, five types of natural-territorial complexes at the facies rank can be identified for large motus which have been unaffected by hurricanes.

All motus on Suwarrow Atoll can be divided into three groups: small (low), medium and large (high). Small motus are only several hundreds of square meters in area whereas large motus may be of several thousand square meters. All motus are composed of similar natural-territorial complexes but small motus show only one or two complexes, medium ones - 3 and high ones - 2 to 4. A correlation between the types of complexes and the dimensions of the motus, with some complexes developing only on motus which are large enough, can also be found.

The first type of natural-territorial complex is a platform of coral limestone covered by low mangrove bushes growing on primitive soils. It is a part of the rim which is flooded by water only for a short period during high tides. The plants do not exceed 0.5 m in height, and have a projective cover of 5-10%. The second type of complex is the surface of the rim covered by debris and protrusions of the bedrock basement. As a rule, this surface lies some 40-50 cm above the previous complex and is not flooded during high tides. Shrubs (e.g., *Pemphis* sp.) make up heavy standing bushes up to 2.0-2.5 m high.

The third type of complex is formed on ridges of coarse gravel or sandy loam where the vegetation cover, dominated by *Messerschmidia* sp., reaches 2-3 m in height. For this formation to occur the soil surface must be elevated at least 60 cm above sea level and be at least 20 m inland.

The fourth type of complex is characteristic of the middle parts of large motus with surfaces between 2.5 and 4.0 m above sea level and underlain by a lens of fresh or brackish soil-ground water. The local vegetation is represented by coconut palms and other plants described above.

The fifth complex occupies the central depressed part of the motu, having detrital soils and usually fresh ground water close to the surface. On uninhabited motus, such areas are covered by closed vegetation of *Guettarda* and/or *Pisonia*. *Pandanus* and coconut palms are less important. Intermediate regions can be observed between all these complexes and the boundaries between them are regulated by the differences in micro-relief.

The entire set of these complexes is found only on large motus. With decreasing size of motu, the more complex internal communities are the first to disappear. There is a tendency for all complexes to pass through successional stages towards the fourth-fifth complex which appears to be the climax formation. The complexes of the first and second type are usually absent on the windward parts of the motus; hence local differences result from exposure.

Factors such as hurricanes stabilize simple mangrove and shrub communities and destabilize vegetation in the interior of the motu. In general, strong gales completely reconstruct the terrestrial portion of the motus and destroy their vegetation cover (as on Suwarrow Atoll). However, the complexes regenerate rapidly, although their locations and configurations may undergo many fundamental changes.

PIO ISLAND

This island (10° 10′ S, 161° 41′ E) lies within the range of the Solomon Islands, 22 km off the north-eastern coast of the large island of San Cristobal. Pio Island is oval, stretching from northwest to southeast along an axis of 2.65 km and 1.4 km at right angles to the long axis.

The Solomon Islands are part of a typical island arc which is either an intermediate tectonic zone or a recent geosyncline. The archipelago includes 7 large and a great many small islands of which Pio is one. The islands stretch as two almost parallel chains from northwest to southeast and are chiefly composed of volcanic rocks varying in age from Late Mesozoic to Recent. Andesites and basalts are the most common, however, Pio Island is formed completely of Pleistocene reef limestones and is an elevated reef platform based on the summit of a submarine ridge. During the Pleistocene this reef platform was tectonically uplifted. Thus the island is composed of three terraces at heights of 34 m, 13 m, and 2.5 m.

The third terrace, which forms the highest surfaces of the island is almost flat and occupies the bulk of the island area. Radiocarbon data suggest that the age of this terrace is 31930 ± 1300 years. The second and third terraces flank the island along its perimeter. The second terrace is 130-200 m wide and about 23-26 thousand years old. The first terrace is built of unconsolidated coral fragments and sand, and borders the second terrace from the west, north and east as a narrow 20-50 m strip. On the southern coast of the island and facing the small islet of Ugi, the width of the first terrace is 300-400 m. A swampy lagoon, isolated from the sea, lies on the inland side of this terrace. The first terrace is only 2000 to 4000 years old. All three terraces have distinct scarps. The scarp of the second terrace has a cove with a horizontal passage about 5 m long and 1.5-2.5 m high. Beach ridges of consolidated coral fragments can be traced on the surface of the second and first terraces.

In contrast to all the islands considered above, there is no recognizable dry season. The climate is constantly humid with total annual rainfall of 2500-3250 mm. The temperature regime is unrecorded but it can be assumed to be similar to that recorded at the nearby weather station of Bulaga which is located 2 m above sea level. Here the mean annual temperature is 27.5 4C. The mean temperature of the warmest month (December) is 28.1 °C, while that of the coldest month (August) is 27.0 °C (Lebedev, 1973).

The soil cover of the island is a thin ferrallitic soil which is found over the whole island, except on the lower terrace where there are humus-carbonate soils. There are also some slightly transformed sands and bench gravels on coastal plots, mainly within the zone directly affected by the ocean. The thickness of ferrallitic soils on the upper terraces varies considerably. The micro-relief of the terrace surface is formed by limestone fragments and micro-ridge outcrops. Under such conditions there are no soils whatsoever. While the spaces between the micro-ridges are filled with loose soil material, the soil thickness is determined by the depth of the depression.

The flora of this island, like that of the entire Solomon Island archipelago shows affinities with the Malaysian Region (Whitmore, 1969). The vegetation of Pio Island is largely a tropical rainforest with characteristic features such as emergents, which rise above the upper canopy; the development of buttress roots and stilt roots in emergent trees; great numbers of trees with hard, coriaceous leaves (typical of the upper canopy); the abundance of lianas; presence of epiphytic ferns, orchids, and strangler figs; and a poorly defined grass cover.

On this island we encountered more or less typical rain forests of complex vertical and spatial structure and high species diversity. The profile transect crossed the whole island (Figure 24), and displays a number of structural parameters. In terms of their common physiognomic features, the vegetation of the second and third terraces was practically homogeneous.

On the first terrace the vegetation was different. Along the shoreline, especially at the windward northeastern coast, there were communities of *Scaevola, Messershmidia,* and *Pandanus* similar to those described for low atolls. In addition *Calophyllum inophyllum* was present. At some distance from the shore there were solitary coconut palms. A plantation of coconut palms was observed on the first terrace in the southern part of the island. On the leeward shore the typical windward species were not as common and no specific community was observable. The vegetation cover here was characterized by a gradual change in species composition. With increasing distance from the shore, the mangrove communities along the shore gave way to the forest vegetation of the second and third terraces. Close to the shore there were *Pandanus* trees with stilt roots, and numerous specimens of *Hernandia* sp. followed by a strip dominated by *Cerbera* sp. and *Hernandia* sp. It can be said that the floristic composition of these coastal plant communities is typical of the coastal vegetation of islands within the tropical zone of the Pacific (Fosberg, 1960).

The first terrace 30 m inland from the shore supported several gigantic trees standing about 45 m high. The canopy was three layered with heights of 28-30, 20-24 and 6-8 m. The regrowth with 23 species was richer than the adult layers. The crown closure in the stand was 0.9 and the projective cover in the regrowth was 10-20%. Lianas of several species were found on almost all large trees. The lower canopy was dominated by epiphytes, *Piper* sp., representatives of the Araceae, and some ferns. *Asplenium nidus* was encountered among true epiphytic ferns, often growing on fallen trees or on the soil surface.

Table 13 presents some morphometric characteristics of the sample area in the interior of the first terrace, 30-40 m inland from the leeward shore. There were no emergent trees within the sample but the species diversity in this relatively small area was extremely high. The woody tree stand was dominated by one species of *Cerbera*. The overall density of trees, which were mostly between 12-16 cm thick and 18-20 m high, is rather large (1480 per ha).

The regrowth (Table 14) was 1.5 to 10 m high and dominated by one species, which was also rather common in the tree stand. However, *Cerbera* sp. which dominated the forest was not common in the regrowth. The numbers of species in the regrowth were slightly greater than that of the tree stand. Furthermore, the density of small stems in the regrowth was 4 to 5 times as great as that in the tree stand.

The description of vegetation on the third terrace some 450 m inland from the leeward south-western shore (Table 15) gives a general idea of the rain tropical forest of the second and third terraces of Pio Island. Beneath the forest canopy there were solitary large trees (up to 35-40 m high) which did not form a closed canopy (the closure was under 0.2). The upper canopy was around 0.3 in closure and 20-24 m high. The closure in the second layer at a height of 18 m was 0.4. The average closure of the whole stand was 0.9.

Lianas, some which were large were very abundant, and joined the canopy together. In some places it was impossible to distinguish the crown leaves of large trees because they were masked by lianas. The average number of lianas per tree in the second and third layers was three (varying from 0 to 5). In the first layer, there were 7 to 10 lianas on each tree. Among the lianas observed were *Flagellaria,* two species of *Smilax,* and representatives of the family Asclepiadaceae.

Also important were semi-epiphytes and lianas of the family Araceae, as well as epiphytic ferns which also formed the ground cover. The lianas were between 1 to 3 cm thick but some were greater than 37 cm in diameter or more. Among the epiphytes the fern *Asplenium nidus* dominated; it grew on trees at a height of 2-3 to 8 m, on the soil surface or on fallen tree stems. There were also epiphytic orchids and a considerable number of epiphytic cormophytic mosses and liverworts. On large trees, the latter covered from 50% of the lower trunk to 30% in the middle part of the trunk, and up to 60% of the upper trunk surface. Parts of the tree trunks that received more light had a thicker

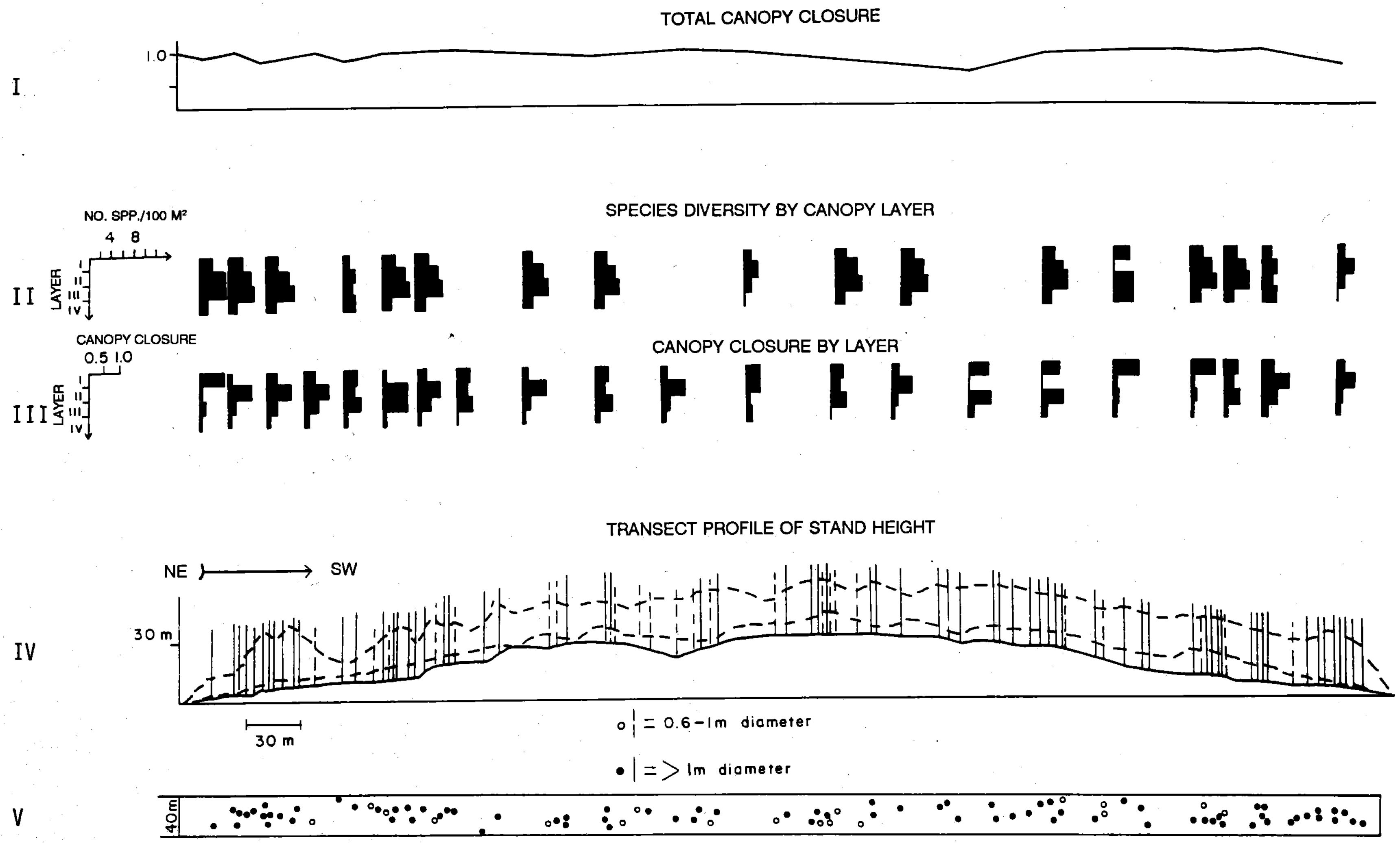

Figure 24. Profile of Pio Island, Solomon Islands. I. Total canopy closure II. Species diversity by layer. III. Canopy closure by layer. VI. Hypsometric profile of upper and lower canopy boundaries and distribution of trees with diameters between 0.6 - 1.0 m, and > 1 m. V. Map of the distribution of trees with diameters between 0.6 - 1.0 m, and > 1 m.

Table 13. Frequency distribution of tree diameters on the first terrace of Pio Island (Number of trees per 250 m^{-2}).

Diameter Class (cm)	Number of Species			Others	Total
	1	2	3	(8 species)	
8-12	1	4	-	5	10
12-16	6	2	-	2	10
16-20	4	-	-	1	5
20-24	5	-	-	-	5
24-28	6	-	-	-	6
28-32	-	-	-	1	1
32-40	-	-	-	-	1
	22	6	-	9	38

cover of liverworts and mosses. This cover was thin and fragmentary on thin tree trunks. An epiphytic fern with linear leaves (*Vittaria*?), and strangler figs composed the upper canopy.

Shrubs and grasses were generally absent; these were replaced by the regrowth and seedlings of woody species. The closure of the regrowth was not uniform; it was 4-6 m high with the stem diameters of 1-2 cm. In proximity to large trees the regrowth was thin. In better-lit places the regrowth was thick and occasionally hard to penetrate. Within the limits of the sample area the quantity of regrowth stems varied from 13 to 20 per 25 m^2.

In the herb layer, there were regenerated trees up to 1.5 m in height; their diameter near the base were < 1 cm. The quantity of regenerated trees and its projective cover, like that in the regrowth at 4-6 m high, greatly depended on the crown closure of the upper layers. Within the sample areas the quantity of seedlings per 25 m^2 varied from 19 to 61. The average number of species was between 6-9 per 25 m^2.

Table 15 shows the distribution of species over the sample area in terms of stem diameters classes: 1 to 8 cm (regrowth); 8 to 30 cm (trees in the second layer); and over 30 cm (trees in the first layer and emergents). Among the latter, five of seven trees had well developed buttresses or stilt roots. These trees varied in height, between 35 to 40 m.

Two species were found to dominate the first and second layers. The number of stems of these two species constituted more than 50 % of all the stems in the plot. The same species dominated the regrowth, and were also present as solitary specimens.

An important factor of vegetation cover in the woody layer was the distribution of large emergent trees which reached 35-40 m in height. The crowns of these trees were 10 m above the main canopy. Their strong buttress roots occupied an area of 12-20 m^2. The lower tree layers near the bases of the emergents and beneath their canopy were usually suppressed. In the absence of emergents the regrowth and the lower layers were well developed. The presence or absence of emergents on a given sample plot was a determining factor in the species composition and the ratio between species (Richards, 1961; Beveridge, 1975). Thus we paid special attention to analyzing the distribution of emergents and the factors affecting their distribution.

Table 14. Frequency distribution of tree diameters for heights between 1.5 to 10 m on the first terrace of Pio (No. of trees per 100 m²).

Diameter (cm)	Number Of Species (Dominants) 1	2	3	Others (11 spp)	Total
< 2	1	22	16	16	55
2 - 3	1	11	-	2	14
3 - 5	1	5	-	-	6
5 - 8	-	-	1	-	1
Totals	3	38	17	18	76

Ignatiev correlated the distribution of emergents using data from sample plots (400 m² each), on thick ferrallitic soils. Table 16 demonstrates the relationship between soil thickness and the presence or absence of emergents.

Large trees were mapped in order to determine the cause of grouping in trees, and whether there was a relationship between size of association and size of trees, and their location. For this purpose, the transect was divided into 10 m long sections and all large trees were counted and grouped according to their size groups: trees with diameters between 0.06 to 1 m, and trees with diameters greater than 1 m. Tree siting was analyzed using nonparametric statistical methods, testing the hypothesis of independent siting (particularly autoconjunction based on a x2 criterion).

Sections were classified according to number of trees present: no trees, one tree, two trees, and more than two trees.

Studies were conducted in order to establish a correlation between the number of trees in section "k" with those at section "k" + l, where l is the log length. With sporadic tree siting, the number of trees at k + 1 is independent of the number at k. Log length varied between l = 1 to l = L/2, where L is the half length of the profile in 10 m units and determines the average length of a tree group or the interval length between groups.

Based on the above, Sozinov (1979) found that:

1. Assumming that there are 100 trees (or 22 individuals per ha) in the profile, the average linear sizes for total number of emergents, trees with diameters greater than 1.0 m at the buttress level, and trees with diameters between 0.6 - 1.0 m, are 10 - 20 m, 50 -60 m, and 140 m respectively.

2. The group dimensions of the largest trees only are 10, 110, 220 - 230, 270 and 540 m. Group dimensions of 220 - 230 m may be regarded as a multiple of 110 m, and 540 m may be regarded as a multiple of 270 m.

These relationships demonstrate that:

1. The distribution of the total (100 trees) number of emergents does not depend greatly on the spatial dimensions of the structural elements of the island's relief. Only groups with the linear dimensions of about 140 m can be correlated with the dimensions of the second terrace and the

relief elements of the third terrace. The best correlations were found in groups which had linear dimensions of 10 - 20 m, which correspond to the interactions between emergents. Groups with linear dimensions of 50 - 60 m correlated well with tree heights, and these in turn, result from the disappearence of emergents.

2. In contrast, the main groups of the largest trees correlated with the linear dimensions of the basic relief elements of the islands. The group with linear dimensions of 540 m correlated with 1/2 the width of the island; the group with dimensions of 220 - 270 m correlated with the linear dimensions of the second terrace and the slope of the third terrace. The emergents were concentrated on the second terraces of the island.

Despite the low numbers, these data illustrate that large emergents are generally found on thicker soils. The profile data indicate greater concentrations of large trees and emergents on the leeward sides of the second and third terraces as compared with the windward side. Furthermore there are fewer large trees on the third terrace than on the second terrace.

The above distribution suggests that the number of emergents is dependent upon the impact of hurricanes, as such impacts will be greater on the windward than on the leeward sides. As a result, community rejuvenation on the windward slopes is more intensive than on the leeward slopes. This conclusion is in good agreement with the heights and thickness of the main canopy as demonstrated in the profile. On the leeward side of the island, where the number of emergents is greater, the height of the main crown canopy and the space occupied by individual crowns are on average, much smaller than on the windward side of the island. In other words, the trees in the lower layers are suppressed by emergents.

The mean total closure of the canopy was very high, between 0.9-1.0, while the lowest value recorded on the profile was 0.6. On the leeward side of the island the canopy closure was found to vary more than on the windward side. The values of crown transparency were very low, 0.06, and in 90% of all cases the values ranged between 0.00 to 0.10 (Figure 17). Such low values of crown transparency are characteristic for almost all vectors (Figure 16).

There seems to be a correlation between the number of emergents and the number of fallen stems. Sample plots (300-400 m^2) with more than two or three large trees, usually contained no fallen trees. In contrast the number of fallen trees was high on plots without emergents. A number of such plots had a few fallen trees and a few emergents.

It would appear that hurricanes are responsible for the various forest formation types with and without large emergent trees and thinned plots. These can be treated as early seral stages of forest regeneration. In addition there were plots which had been cleared for subsistence gardening. In general these were much larger than those formed after a natural tree fall. Such plots were usually cultivated for several years, during which time the forest around them may have started its regeneration. This kind of vegetation structure is typical in that individual microcoenoses and patches related to individual large trees were found to alternate with larger mosaic patches, embracing scores of tree stems of various species.

If we study structure of the vegetation cover of this island in terms of community succession, we can see various stages of cyclic succession. Early stages are indicated when a community consists of thin-stemmed trees and lacks emergents or only has fallen trees. When the number of emergents is high, a later successional stage is indicated.

The relief of Pio Island is more intricate than that of the motus on low atolls. Nevertheless, the spatial structure of vegetation on this island is simple, if considered at the typological level of forests. On a formal landscape basis, three simple land units can be distinguished on this island in geomorphological terms: the land unit of the first terrace with its coastal facies, the facies of interior part and the facies of the mangrove swamp; the land unit of the second terrace with the facies of the scarp and of the slightly inclined surfaces; and the land unit of the third terrace with the facies of the scarp, of the flat surface and the hollow-shaped depression in the center.

Table 15. Distribution of tree diameters on the third terrace of Pio Island.

Diameter Classes (cm):	Under 8 cm (regrowth)					8-30	Over 30
Species ID No.	No. of 25 m² Plots				Total	400 m² Sample Plot	
	1	2	3	4			
203	2				2		
204	6	2		1	9	2	
205						1	
206	1				1		
207	1				1		
208	1				1		
209	1	8	2		11	1	
216	1				1		
220		2	1	9	12	8	1
221		11	18	11	40	8	2
222		2			2		
223		1			1		
225			1		1		
228						4	
230		1			1		
231						2	
234						1	1
235						3	1
227			1		1		
233						1	
AB?						1	
K?							1
?						1	
?						1	
?							1
No. Of Species	7	6	6	3	14	13	6
No. Of Individuals	13	26	24	21	84	34	7

Table 16. Soil thickness on the second and third terraces and distribution of emergent trees.

	Soil Thickness (in cm)			
	0-5	5-15	15-25	Over 25
Total Number Of Plots	17	23	5	6
No. Of Plots With Emergents	0	0	5	5

The facies of the first terrace are well differentiated in terms of vegetation cover. The coastal facies can be additionally subdivided into facies of leeward and windward shores. Within the stow of the first terrace the facies differ not only in their vegetation but also in their soils and thickness of the humus horizon.

The second and third terraces and their geomorphological elements do not differ much in their vegetation. The differences are apparent only in terms of statistical analysis. The different stages may be considered to represent parts of a continuum. It should be noted that in terms of vegetation structure the interior parts of the first terrace are close to that of second and third terraces, although soils on these terraces differed sharply from those on the main part of the island. The vegetation on Pio Island is a poor indicator of the spatial structure of the natural-territorial complex. If the vegetation is used as the basis, it is only possible to distinguish the most evident morphological features, which express only the extreme parameters of the environment.

CHAPTER V. THE FLORA AND VEGETATION OF PACIFIC ISLAND ECOSYSTEMS IN A REGIONAL CONTEXT

Y. G. PUZACHENKO AND L. V. SOZINOV

INTRODUCTION

The lack of agreement in the literature about the floristic classification of the Pacific islands reflects the complexity of their floristic relations and the ambiguity of their position in any system of floristic regions. As an example, in some classifications all islands visited by the Callisto during her sixth voyage belong to the Palaeotropical Region. Kamyshev (1961) included them under the Malesian subregion of the Palaeotropical Region, pointing out that although islands of New Zealand were treated by some authors as a subregion, their flora is Malesian. Alekhin *et al.* (1961) distinguished between the Malesian and New Zealand Subregions of the Palaeotropical Region: the former comprises most of the islands visited by the Callisto; the latter includes, besides New Zealand, the Kermadec Islands. Good (1953) accepts kingdoms to be the largest unit of floristic classification of the earth. He included the Malesian Region, with Aru (among other Provinces of New Guinea), under the Indo-Malesian Subkingdom of the Palaeotropical Kingdom. Some regions of New Caledonia (including Lord Howe and Norfolk Islands), Melanesia (the Solomon Islands), Micronesia and Fiji, the Cook Islands and Tonga belong to the Polynesian Subkingdom.

New Zealand, with the Provinces of Northern New Zealand, Kermadec and some other islands, belongs to the Antarctic Kingdom. The view, that New Zealand and some archipelagos situated relatively near it belong to the Antarctic Kingdom, is also shared by Takhtadjan (1978) in his floristic classification of the earth (Table 17). It includes the following entities, in the diminishing order of area: Kingdom, Province, District; and some intermediate entities; Subkingdom, Subregion, Subprovince. According to Takhtadjan, the Indo-Malesian Subkingdom of the Palaeotropical Kingdom includes the Malesian Region, its Papuan Subregion comprising the islands of New Guinea and the Louisiades (the Papuan Province), the Solomon Islands (the Bismarck Province), and also the Fiji Region, with its Fiji Province comprising the islands of Fiji, Tonga and Niue. The Polynesian Subkingdom includes the Polynesian Region, with the Polynesian Province including the Cook Islands.

The New Zealand Region consisting of the Norfolk, Kermadec, Northern New Zealand and some other Provinces are included under the Holantarctic Kingdom.

Describing individual chorions (or floristic regions), Takhtadjan indicated that the Indo-Malesian Subkingdom is characterized by extremely high endemism, with 11 endemic families of vascular plants and a vast number of endemic genera and species. There is no other chorion in which so many primitive, ancient forms of flowering plants have survived. In the Malesian Region there are 2 endemic families and about 500 endemic genera. On New Guinea and the Solomon Islands, the numbers of endemic genera are at least 140 and 6 respectively. There are over 25,000 endemic species, including a great number of ancient primitive forms of flowering plants. In the Papuan Province of this Region (New Guinea, Louisiades) there are 1400 genera with 140 endemics among them and over 9000 species with about 8500 endemics. According to Pavlov (1965), the proportion of endemic genera and species on New Guinea is 10 and 84.7% respectively. Despite its proximity to Australia, the Guinea flora is distinctly Malesian. Thus, of the 1400 genera on New Guinea about 60 and 495 have affinities with Australian and Indo-Malayan taxa, respectively. It is the richest Province of the Indo-Malesian Kingdom. The Bismarck Province comprising the Solomon Islands has an impoverished Papuan flora. The Solomon Islands, which have 6 (or 3 according to another source) endemic genera must be regarded as a Subprovince.

The Fiji Province of the Fiji Region (Fiji, Tonga and the Niue Islands) has one endemic family, Degeneriaceae, and 11 endemic genera. The largest numbers of endemic genera and species occur on the islands of Fiji which have a flora (especially that of Fiji), considerably richer and more ancient than that of the New Hebrides Province, and also a higher specific endemism (70%).

The Polynesian Subkingdom of the Indo-Malesian Kingdom has purely insular floras of the post-Pliocene and even post-Pleistocene which are characterized by high specific and generic endemism but a lack of any endemic families. These floras are primarily Indo-Malesian in origin but also contain Australian elements, and some American derivatives in the east.

The Holantarctic Kingdom embraces, in addition to the cold and temperate areas, parts of subtropical zones of the Southern Hemisphere. It is characterized by 10 small mono- or oligospecific endemic families and a large number of endemic genera. Some genera and even species are common to subantarctic America and New Zealand, or to their adjacent islands. Some genera and species of the Holantarctic Kingdom have reached eastern Australia, Malesia, Central America and the Hawaiian Islands.

In the Palaeocene, a center of temperate flora existed in the Southern Hemisphere. Other forms were dispersed to the Region from the Holarctic, forming endemic species and even superspecific taxa.

The New Zealand Region has a single endemic family (not unanimously admitted to be endemic), the Phormiaceae, and about 45 endemic genera. The proportion of specific endemism is very high: 40% among ferns and about 75% for the two genera of woody ferns, *Cyathea* and *Dicksonia.* Among coniferous and flowering plants, endemism reaches around 100% and over 80% respectively. The elements of the flora in order of dominance are: Holantarctic (in the broad sense) Palaeo-New Zealand, Palaeotropical (including Indo-Malesian, Polynesian and New Caledonian), Australian, Holarctic and cosmopolitan entities. The Palaeotropical element came here via the ridges of Lord Howe and Norfolk Islands, which are now almost submerged. A second spread of the Holantarctic element occurred in the Pliocene and especially in the Pleistocene, when some Holarctic species also arrived. New Zealand and Australia share many more Holantarctic elements than Australian elements.

The Norfolk Province consists of Norfolk and Philip Islands, which together have 174 native species of vascular plants. There are 14 endemics among 45 fern species and related plants and 35 endemics out of 128 flowering plants. The only Norfolk conifer, *Araucaria,* is endemic; and this Province also shares 4 endemic species with New Zealand. A considerable number of vicarious species and subspecies are common to Norfolk and Northern New Zealand or Kermadec Provinces. The total number of endemic species is 50. Three endemic species occur only on Philip Island, although one of them may be extinct or very scarce. Approximately 244 species have been introduced to Philip Island since its discovery by Cook: these include weeds, horticultural and agricultural crops and about 30 herb species (Turner *et al.* 1975).

The flora of the Kermadec Province comprises about 120 species of vascular plants (Takhtadjan, 1978) or 113 species (Sykes, 1977). Among these are 16 endemics (Takhtadjan, 1978) or 23 endemic species and subspecies, of which 2 are as yet undescribed (Sykes, 1977). Also, 152 species are recorded as being more or less adventive and 30 species are persistent relics of cultivation.

According to Sykes (1977) the Kermadecs have a much higher proportion of either indigenous or New Zealand-derived species than do Norfolk and Lord Howe Islands. The frequent southwest winds in the Kermadecs during winter, and the strong winter currents that flow northeast from northern New Zealand, are suggested as features promoting New Zealand species in the Kermadec Islands. The tropical or Polynesian element of the flora is represented by a few coastal, strand species confined exclusively to Raoul and the nearest Herald Islets. Two endemic taxa of this type, *Boehmeria australis* var. *dealbata,* and *Homalanthus polyandrus,* are extremely rare. The lower proportion of endemics on these islands may be explained by their younger age compared to that of Norfolk and Lord Howe Islands.

We shall also consider the biotic distribution patterns in the tropical Pacific proposed by Thorne (1963) to the 10th Pacific Science Congress (Table 18). This differs significantly from Takhtadjan's classification in structural terms but not at the lower level subordination (Table 16). As for the region under study, Thorne includes the Fiji district with the Fiji, Tonga and Samoa archipelagos under the Polynesian Subregion, with Micronesia instead of Papua, as Takhtadjan does; Niue Island is placed within the Polynesian district. There are practically no other differences.

Thus, among the islands visited by the Callisto during her sixth voyage, Norfolk and the Kermadecs proved to be most isolated, not only by the their geographical positions (in the subtropics), but also their floral origins from New Zealand or Holantarctic elements. The Cook Islands have a flora derived from Indo-Malesian and Australian forms, as do most of the other Polynesian islands. The rest of the islands are included in the Indo-Malesian Kingdom, its Subkingdoms and Regions.

We shall consider (at length) the relationships between the geographical elements of phanaerogamic floras and sizes of archipelagos, the distances between them and present-day climatic conditions. Data on regional floral origins derived from Chew (1975) and Braithwaite (1975), are presented in Table 19. The number of widespread and Palaeo-Oriental genera is almost a direct function of the archipelago size (Table 20); widely-distributed genera being less sensitive to the size changes than are the others. The maximum and minimum numbers of widespread species are 196 (Bismarck Islands) and 118 (Tonga; Samoa). The maximum and minimum numbers of Palaeo-Oriental genera are 338 (Solomon Islands) and 115 (Tonga).

For the distribution of genera allied to Papua, the distance from the centre seems to be of a greater importance. Islands and archipelagos close to Papua New Guinea (Bismarck, Solomons and New Caledonia) share 35-37 Papuan genera; Fiji and the New Hebrides share 20-21 genera; and the most distant islands have only 9-12 Papuan genera.

The distribution patterns of the Australian element are similar: a maximum number of genera occurs on New Caledonia, considerably fewer on the New Hebrides, fewer still on Fiji and the Solomon Islands and very few on Tonga and Samoa which are most distant from Australia. In this case, however, the differences between New Caledonia and the New Hebrides (which are located relatively near to each other), are considerably greater than those demonstrated by distributions of the Papuan elements. Thus, other factors, in addition to distance, may be involved.

The distribution pattern for Pacific genera is quite specific: the records are the highest for New Caledonia, the New Hebrides and Fiji. Pacific genera occur rather commonly on the Solomon Islands, Samoa and Tonga, and very rarely on the Bismarck Islands. In contrast to the Australian genera, the Pacific genera occur more regularly, and are as prominent as the Papuan genera in the floras of Tonga and Samoa, the most distant islands. Such a pattern indicates that the Pacific element has a center of origin in New Caledonia, the New Hebrides and Fiji.

Thus, different geographical elements are distributed non-uniformly. On the whole, the widespread and Palaeo-Oriental genera make up 60-90% of the floras, the percent depending to a greater or lesser degree upon the area of lamd. This suggests indirectly, that distances and climatic differences are factors of minor importance for Pacific elements.

Distance seems to be of primary importance in the distribution of the Papuan element. Climatic conditions are seemingly of no importance, since Papuan species are equally distributed on the permanently very humid Bismarck Islands and in moderately humid (to occasionally arid) conditions on New Caledonia.

Climate exerts the most conspicuous influence on the Australian element. The precipitation pattern of New Caledonia is almost identical to that of northeastern Australia, in that three regimes occur (Brookfield and Hart, 1966):

1. Occasionally very humid, but dominated by arid conditions.

2. Moderately humid with seasonal variations from moderate to arid conditions.

3. Permanently arid.

The rest of the islands have a predominantly more humid climate and only small areas have the regime described under 1, above.

Climate characteristics seem also to be important to the distribution of the Pacific element. Accepting that the greatest number of Pacific genera on New Caledonia, the New Hebrides and Fiji may reflect to some extent the optimal regional climatic conditions, and this area as the center of origin for the Pacific element, one may expect the Pacific genera to occur most frequently under a climate which is moderately humid and arid with a prevailing rainy period (or occasionally rainy with a prevailing dry period). Plants of the Pacific element are probably distributed only to places with a permanently humid climate.

Finally, endemics in the floras of different archipelagos vary greatly. The numbers of endemic genera on the very large New Guinea and the relatively small New Caledonia are approximately equal; there are slightly more on Fiji and slightly fewer on the Solomon Islands; and there are very few, if any endemic genera on the other archipelagos.

New Guinea, New Caledonia and apparently Fiji are ancient areas, and this factor in itself suggests the possibility of their being centers of origin and endemism. However, the equal number of endemic genera on New Caledonia and New Guinea, in view of the large differences in size and complexity of areas is at variance with this suggestion. The extremely high proportion of endemic genera on the relatively small area of New Caledonia may result from its insularity and above all the highly specific climatic pattern, which differs from almost all other islands. Similarly, the relict endemic genera which persist on Fiji may be correlated with the varying precipitation pattern on that archipelago.

Thus against the Palaeo-Oriental background of the Region, it is likely there were other, smaller, independent sources and dispersal centers for flowering plants. A similar conclusion would result from the analysis of ferns (at the generic level; Braithwaite 1975). The similarity coefficient (Table 21) reflects the extent to which a richer flora may influence a poorer one and presupposes the existence of a certain main center of origin. In the island systems under study, this main center is New Guinea. The Solomon Islands flora is derived directly from New Guinea but comprises considerably fewer genera. The situation on the New Hebrides and Fiji is very similar to New Guinea, although their fern floras differ significantly from that of the Solomon Islands. This situation could only arise if some genera from New Guinea had dispersed only to the Solomon Islands while others had moved only to Fiji and the New Hebrides. Because the proportion of New Guinea genera on New Caledonia is very high, it is unlikely that New Caledonia acted as a primary dispersal center. The fern floras at the generic level become less similar from those of New Guinea as one moves east through the New Hebrides to Fiji, reflecting the effects of distance. However, although the New Hebrides are much closer to New Caledonia than to Fiji, there are greater similarities between the Fijian and New Caledonian fern floras. Both classifications, Takhtadjan's floristic and Thorne's biotic distribution patterns, correlate well with the regional precipitation and temperature patterns of the island system under study. For example, New Caledonia which has the most distinct temperature and precipitation patterns in the whole region, is also floristically very distinct at the subregional level (Thorne, 1963).

The Bismarck and Solomon Islands, which have the most humid climate (with well-defined arid periods over very small areas) also have peculiar patterns of floristic and biotic distribution compared with those of the New Hebrides, Samoa and Tonga. Also, the New Hebrides with a more humid climate and a less defined arid period than Fiji, Tonga and Samoa, are treated by Thorne as a Region.

It follows from the foregoing that the only distinct floristic boundaries (at the generic level) serve to separate New Caledonia from all the other tropical islands of the southwestern Pacific. Other boundaries are indistinct and result from gradual clinal changes, primarily in precipitation. At the generic level the distances from the source of origin are definitely of little effect. In the course of time the spatial barriers have largely disappeared, and the present ecological situation is of primary importance in explaining biogeographical distribution.

As noted, the present flora is composed primarily of common and Palaeo-Oriental genera, the number of which is directly related to the area of the archipelago and consequently to the complexity of ecological space. Some deviations from the 'area-generic number' correlation may result from the fact that the ecological space area relationship is not a simple one. For example, the Tonga archipelago (with an area almost twice that of Samoa) consists of very small but numerous islands and is very simple structurally. Samoa consists of three large islands which are complex structurally. New Caledonia is smaller than the New Hebrides, but has more variable climatic conditions which might permit the higher proportion of widespread genera, but have no effect on the Palaeo-Oriental genera.

Thus, for most of the flora at the generic level there is an equilibrium between the number of genera and present habitat complexity; insularity is definitely of little importance.

In view of the minimal age of the archipelagos under study, one may suggest that having an origin in the Pleistocene may permit sufficient time for the insular flora to reach an equilibrium at the generic level, because a generalized ecological situation can be established over a vast area.

This conclusion is valid probably only at the generic level and for general characteristics of whole island systems and is not applicable to species or individual organisms, or to specific habitats or islands, especially small and geologically young islands.

Table 17. Biotic distribution patterns in the Pacific. Numbers refer to endemic families, genera and species (After Takhtadjan, 1978).

Kingdom	Subkingdom	Region	Subregion	Province	Subprovince	District
Palaeotropical			Papua	Papua, 140 genera 10% of Louisiade total (Paulov, 1965) 9500 spp. 85% of total (Pavlov, 1965)		New Guinea
	IndoMalesian 11 Families			Bismarck		Solomon Island
		Malesian 2 Families 500 Genera 25000 Spp.				
		Fiji	Fiji 1 Family 11 Genera Species (70%)			Fiji Tonga Niue Island
Polynesian No Endemic Families Many Genera & Spp.		Polynesian			Cook Island	
Holantarctic 10 Endemic Families Many Genera	New Zealand 1 Family 45 Genera Many species	Norfolk Kermadec Northern New Zealand				Norfolk Island Philip Island

Table 18. Plant regional and subregional groupings of Pacific Islands (Thorne, 1963)

Region	Subregion	Province	District	Indo-Pacific islands
Oriental	Indo-Chinese	South-Chinese	Taiwanian	Taiwan, Ryukyu
		Indo-chinese		Hainan
	Indo-malayan	Malayan	Malayan	Malay Archipelago
			Sumatran	Sumatra
			Javan	Java, Bali
			Bornean	Kalimantan, Balabac, Palawan Calamianes
		Lesser Sundan		Sunda (Lomboc to Timor and Babar)
		Philippines		Philippines to Botel-Tobago
		Celebesian		Sulawesi
	Papuan	Moluccan		Moluccas, Banda, Kei, Timor Laut
		Papuan		Aru, Misol, Salawati, Waigeo, New Guinea Trobriands, Woodlark, D'Entrecasteaux, Louisiade
		Torresian		Torres Strait, coastal Queensland, NE New South Wales
		Bismarckian	Bismarckian	Bismarck, Admiralty
			Solomonian	Solomon
	Polynesian	Fijian	New Hebridean	Santa Cruz, Banks, New Hebrides
			Fijian	Fiji, Tonga, Samoa
			Micronesian	Bonin, Volcano, Mariana, Palau, Caroline, Wake, Marcus, Marshall, Nauru, Ocean, Kiribati, Ellice, Wallis, Horn, Howland, Baker, Phoenix, Tokelau
		Polynesian	Polynesian	Line, Niue, Cook, Society, Gambier, Tuamotu, Rapa, Marquesas, Pitcairn, Henderson, Easter, Sala-y-Gomez, Mangareva, Tubai
		Hawaiian		Hawaii to Midway, Johnston
		New Caledonian	New Caledonian	New Caledonia, Loyalty

Table 18 (continued). Plant regional and subregional groupings of Pacific Islands (Thorne, 1963)

Australian	Australian	Australian		Australia, except for coastal Queensland and NE New South Wales, Tasmania
	New Zealandic	Kermadecian	Lord Howean	Lord Howe
			Norfolkian	Norfolk
			Kermadecian	Kermadec
		New Zealandic	New Zealandic	New Zealand, Stewart
			Chathamian	Chatham
			Antipodean	Antipodes, Bounty, Auckland, Campbell, Snares
Antarctic	Subantarctic	Kerguelenian	Macquarian	Macquarie
		Magellanian	Fuegian	Fuegian and other S Chilean coastal islands towards Penas Bay
	Antarctic	Antarctic		Antarctica and adjacent islands
Neotropical	Chilean	Fernandezian		Juan Fernandez, Desventuradas
	Peruvian	Galapagean		Galapagos, Cocos
Holarctic	Nearctic	Caribbean	Mexico	Revilia Gigedo, Las Tres Marias, Clipperton
		Sonoran	Sinaloan	Cedros
		Californian	Californian	Coastal islands of California, San Benito, Guadeloupe
			Vancouverian	Southern Alaska, Vancouver, Queen Charlotte,
		Aleutian		Commander, Aleutian
	Palearctic	Siberian	Kurilean	Sakhalin, Kuril
		Manchurian	Japanese	Japan

Table 19. Geographic origin of the Phanerogam (Chew, 1975) and Pteriodophyte (Braithwaite, 1975) genera of some southwestern Pacific Islands. (Numerator is the total number of genera originating from each region, the dominator the percentage of the total genera found in each island group.)

	New Guinea	Bismarck	Solomon	Fiji	Tonga	Samoa	Vanuatu	New Caledonia
PHANEROGAMS								
Widespread	-	196	189	167	118	118	162	186
		31.0	28.9	35.1	44.9	39.3	35.9	28.3
Palaeooriental	-	379	388	232	115	152	218	206
		60.0	59.4	48.7	43.7	50.0	48.3	31.4
Papuan	-	35	37	20	12	9	21	36
		5.5	5.7	4.2	4.7	3.0	4.6	5.5
Australian	-	4	6	7	3	2	13	51
		0.6	0.9	1.4	1.1	0.7	2.7	7.8
Pacific	-	3	17	26	9	14	24	31
		0.5	2.6	5.5	3.4	4.6	5.3	4.7
Endemic	140	1	26	9	14	24	31	130
	10	0.1	5.5	3.4	4.6	5.3	4.7	19.7
Unknown	-	14	11	13	6	6	12	15
		2.2	1.7	2.7	2.3	2.0	2.6	22.9
Total Genera	1400	632	654	476	263	302	451	655
PTERIDOPHYTES								
Number Of Genera	156	-	98	88	-	83	83	83
No. Endemic Genera	6	-	0	0	-	0	0	3

Table 20. Characteristics of some islands of the Southwest Pacific.

	Bismarck	Solomon	Fiji	Tonga	Samoa	Vanuatu	N. Caledonia
Area (km² x 100)	50	42	18	7	3	12	9
Highest elevation (m)	2300	2439	1324	1029	1858	1879	1650
Mean annual temp (°C)	27.3	27.5	24.8	25.1	26.1	25.0	22.8
Annual temperature range (°C)	0.7	0.6	3.4	4.5	3.6	4.3	6.1
Mean minimum temperature (°C)	26.9	26.2	22.9	21.4	25.5	22.4	19.4
Annual rainfall (mm)	2500	2500	2000-2500	1750-2000	2250-2500	2250-2750	1500-1750

Note. Temperature characteristics are for capitals of the archipelagos, after Lebedev (1973). Rainfall data after Wiens (1961).

Table 21. Numbers of genera and Similarity Coefficient (K) for fern floras at the generic level for some southwestern Pacific Islands (K = 1 a/c, where a = Number of genera in common; c = smallest number recorded in one of the two areas). Data derived from Braithwaite (1975).

	New Guinea	Solomons Islands	Fiji	New Hebrides	New Caledonia	Total No. Of Genera
New Guinea		0.00	0.02	10.01	0.13	156
Solomon Islands	98		0.15	10.16	0.26	98
Fiji	87	75		10.06	0.15	88
New Herbrides	82	74	78		0.20	83
New Caledonia	73	62	71	67		83

CHAPTER VI. VEGETATION STRUCTURE AND PLANT SUCCESSION

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INTRODUCTION

The structure of the vegetation is an important factor in determining productivity and stability of ecosystems and an important area of investigation in plant ecology. Whittaker (1965), Webb *et al.* (1970), Mazing (1972), Korchagin (1977), and in particular Odum (1971) have emphasized that the structural characteristics of vegetation reflect locally specific, abiotic conditions and the nature of succession on both ecological and evolutionary time scales. The structure of climax vegetation, which has developed over a long time under relatively constant climatic-edaphic conditions, is of particular interest. The vertical stratification and composition of a plant community may affect its stability, direction of succession, and rate of primary production (Sukachev, 1974). Studies of the structure of plant communities may provide an understanding of the nature of the plant association and changes which occur in them (Korchagin, 1976). The vertical stratification of a plant community reflects the growth and developmental characteristics of the species found within it. Thus, climax community structure represents a complex interaction of many different processes.

Sukachev's concepts of vegetation dynamics and spatiotemporal relationships of tropical ecosystems (UNESCO/UNEP/FAO, 1978) are used in this chapter. The following processes determine the structure of plant communities: species interactions, syn- and endoecogenesis, and intracenotic changes.

SPECIES INTERACTIONS

Species interactions and associations are usually concerned with the co-evolution of populations (Yablokov and Usupov, 1966). Through an understanding of the relationships between evolutionary rates in groups of organisms and communities and by determining the interactions between biological components and environmental change (Timofeeff-Resovsky *et al.*, 1969), one can forecast evolutionary changes in the plant communities of tropical islands, which represent isolated habitats of differing age. Mature tropical ecosystems display increased predictability of the physical structure of habitats which is associated with the increased importance of co-evolution, and the decreased importance of abiotic limiting factors as selective forces during evolution. By providing a theoretically limitless range of evolutionary opportunities, biotic interactions may partially explain the high species diversity of humid tropical ecosystems (Letouzey, 1978).

In Odum's opinion, coadapted communities in mature ecosystems are characterized by high species diversity, high accumulation of biomass and an energy assimilation-respiration balance approaching unity. Letouzey (1978), suggests that mature ecosystems are also characterized by an overall spatial homogeneity. In discussing the equilibrium of species numbers on islands Simberloff (1974) distinguished two processes associated with species interactions:

1. The long term equilibrium in numbers of large taxa determined by immigration of new species which are expanding their ranges and the extinction of native species usually with a restricted distributional range.

2. The short term equilibrium associated with increased adaptation to the physical habitat and the co-adaptation of species resulting in forms better adapted to specific island conditions and extinction of less well-adapted species.

COMMUNITY PROCESSES

Self-regulating processes may greatly influence the structure and functioning of a tropical community by bringing about complex and sometimes opposing adaptations of species to habitat and to each other. It may be possible to distinguish two or three groups of species, which form seral stages which differ dramatically in their overall morphological and physiological characteristics (Ashton *et al.*, 1978; Fontaine *et al.*, 1978). Stable ecosystems may develop as a result of transformations within the community under conditions of co-adaptation of a large number of species with finely-differentiated requirements for light, relative humidity, and temperature. Such species may be differentiated by the timing and intensity of flowering; specificity of leaf flush; canopy spreading, conditions for fruiting and seed germination, amongst others. At the same time a particular species may exert a powerful influence on the habitat via soil pH changes or liberation of toxic substances which can affect the growth of other species. Since the life-spans of individual species from the same or different seral stages may differ by a factor of 2, succession and species replacement do not conform to a single pattern. Mean life-spans for individuals of different species were estimated to be 20-40, 50-100, 100-300, 300-500 and even over 1000 years (Ashton *et al.*, 1978). In general, pioneer species of early seral stages characteristically have short life spans. Species of later stages and the climax vegetation such as emergents, have long but widely differing life-spans.

Thus, for any ecosystem one can predict that species interactions and successional processes will be different in different sets of species. For example, while the emergent layer may remain practically unchanged, some species in the lower layers may undergo significant, and sometimes irreversible changes.

All investigators of tropical forests, beginning with Richards (1952), have emphasized the role of tropical forest species in altering micro-climatic variables, thus favoring climax species. As a result of regional macroclimatic variations which may include a more or less arid period, communities of grasslands, maquis, and savannah which have a low probability of reaching a tropical forest climax may develop during succession.

Secondary Succession

The complexity of short term alterations due to high species diversity has been the subject of many studies which have predicted different outcomes under different environmental conditions. Secondary succession following the death of an emergent tree results in a 20 m gap appearing in the forest canopy. The understorey may or may not survive; however, increased light penetration may induce a rapid growth of seedlings from the soil seed bank. Such gaps in the canopy have different abiotic conditions, resulting in the unequal development of different species, further increasing the complexity of the community. During later successional stages, the gap may be due to the death of an emergent and some trees of the lower storeys, resulting in a different set of abiotic conditions. The impacts of fallen trees on the lower layers are unpredictable; hence the variation in the patterns of secondary succession and the difficulty of compiling a single typology.

According to Ashton *et al.* (1978), a biomass equivalent to that of the whole forest dies and is renewed every 40-100 years. They further assert that the pattern of change is brought about by different processes operating on different scales; some of which affect individual trees, others whole species populations. The scale of these processes may also vary between species; some may affect part or all of a forest, and yet others, the forests of a whole region. Phenological changes such as flowering, bud-burst and other life processes may be determined by seasonal periodicity, with two to three year climatic periodicity determining population changes in species with short life-spans. In the tropics climatic fluctuations of a 40-100 year periodicity may potentially interact with the main secondary successional processes, while those of a millenium or longer periodicity may interact with the process of primary succession. Long-term climatic fluctuations do not affect phenological processes, but present a stable background to the relatively shorter-term processes, and affecting only the relevant structural and functional characteristics of the whole community.

Long-term Climatic Change And Vegetation

Quite clearly, external factors operating on different time scales differ in different biomes. There are some data, suggesting that the tropical vegetation underwent radical, reversible changes in the Late Pleistocene and Holocene. According to Livingstone and Hammen (1978), over the last 30,000 years significant changes have occurred in the altitudinal zonation of vegetation of New Guinea. Around 30,000 BP the altitudinal limit to tree growth may have been as low as 1,500 m. Between 15,000 and 6,000 BP, during the main period of deglaciation, active vegetation change occurred; the forest limit rose to around 4,000 m by 4,000 BP and subsequently fell to about its present level. Long-term fluctuations in precipitation and temperature caused changes in the distribution of sclerophyll and rain forest in Australia (Lake Euromoo and Quincan). Pollen diagrams show that dry sclerophyll forest dominated from around 10,000 BP to ca 7,500 B.P. when it was replaced during the next 1,000 years by warm temperate rain forest. This rain forest climax remained at maximum extent for 3,000-4,000 years, subsequently changing to subtropical rain forest. At around 2,000 B.P. the subtropical rain forest became drier and partially regressed to a sclerophyll forest. Data from studies of the Hawaiian vegetation of the last 10,000-12,000 years show three main stages:

1. During the late Glacial or early Postglacial the extent of rain forest was restricted. The summits of high mountains were covered by subalpine forests, which were replaced by more humid types of vegetation towards the very end of the period.

2. During the Postglacial warm period, the rain forest expanded and the dry subalpine forests retreated (a succession of *Chirodendron, Myrsine,* and *Metrosideros* occurred).

3. During the last 3,000 years, the boundary of the humid vegetation moved lower again, while towards the end of this period the humid forest limit rose again. Thus, in the tropical forest region of the Pacific significant, long-term cyclic, reversible changes of vegetation distribution have occurred.

Short-term Climatic Impacts

Although data concerning the impact of short-term climatic fluctuations are not available, such fluctuations may have operated as a trigger mechanism causing savannah formation under conditions which favored the occurrence and spread of fires. While fires, hurricanes, landslips caused by heavy rainfall and erosion, which stimulate secondary succession are all short-term processes, the frequency of their occurrence is a function of longer-term processes. Some factors may act synergistically, such as slash and burn agriculture and droughts, causing anthropogenic grasslands formation; the condition of vegetation on a slope, or degree of slope and rainfall intensity causing erosion; the presence of emergents and hurricanes causing increased tree fall.

Vulcanism And Seismic Impacts

Volcanism and seismic activity may be considered in a similar manner. Long periods of exposure to volcanic activity have resulted in the development of unique plant species and communities which are well adapted to lava and ash surfaces with their highly distinctive edaphic conditions. The impact of aperiodic volcanic disturbances may be distinguished from that of more regularly occurring fluctuations by its discrete spatial and temporal distribution. While more gradual fluctuations may cause changes in ecosystem equilibrium, volcanic disturbances bring about abrupt changes resulting in seral succession.

Other Episodic Events

The area and extent of successional changes depends upon the magnitude and extent of the factor initiating the process. Hurricanes for example, rarely destroy the vegetation completely, but result in a thinning of the emergent layer, causing mosaic patches of secondary succession dominated by the surrounding surviving vegetation. In a volcanic situation, however, the existing vegetation may be totally or partially destroyed depending upon the magnitude and extent of ashfall. It is essential that the time scale for these processes be considered in relation to short-term cyclic processes since they may exert a direct influence on them, and together these two sets of factors influence the course of succession.

Extensive anthropogenic impacts on vegetation during the last 2- 3,000 years, at altitudes of about 1,500 m in New Guinea have been traced by pollen diagrams which also indicate a somewhat less active human influence during the preceding 5,000 years. At altitudes of 2,500 m near the present-day limit of agriculture, anthropogenic impacts occurred much later (Livingstone and Hammen, 1978). These changes correspond to relatively long-term influences and affect large areas. In contrast, the mode of agriculture causes short-term effects in small patches (0.2 ha) with gardening lasting several years with intervening decades of fallowing.

Similar periodicity characterises both the present and future exploitation of forest resources. More active research concerned with identifying the optimum mode of exploitation which will ensure minimal disturbance of natural forest regeneration and hence species composition is needed.

Among the external factors affecting succession is the invasion of plants and animals. As a consequence, one or several new species may become established in a community and replace some native species, and thereby change the whole 'biogeocenosis' (Sukachev, 1972).

Succession operates on different time scales and reflects spatial interactions at the levels of the species, the community, and the biogeographical region. Succession may be a factor of a particular importance in the development of insular ecosystems which have relatively limited possibilities for the exchange of species. On a geologically old island, the effects of species associations/interactions may be indistinguishable from the effects of co-adaptation, whereas at relatively short time scales, it may be a determining factor in the compositions of insular communities. According to Simberloff (1974), a non-interactive equilibrium number of species is established over a few millenia by the flow of immigrants, on the one hand, and the extinction of native species, on the other. In this case the biota of the island is postulated to have a random structure. Over several millenia a sortative process results in an interactive equilibrium number of species as a result of selection for co-adapted species from successive colonizing groups which contribute to the diversity of the biota, and increased extinction rates caused by a narrowing of ecological niches. Quite obviously, the immigration rate must be a determining factor in the time taken to reach equilibrium species diversity and in determining the structural characteristics of formations and ecosystems.

As an initial starting point, external factors, according to the nature of their effects on communities, may be divided into continuous factors with differing periodicity and, those that are spatially and/or temporally discrete. They may be further classified as to the magnitude of effect and their basis, whether climatic, orogenic, geomorphological, or anthropogenic. While analyzing their effects on ecosystems, external factors must be examined in combination with intra-community factors operating on the same spatial and temporal scales. Hence long-term interactions expressed within broadly defined areas are logically treated as a background for short-term processes operating over more limited areas. During the research program of the 'Callisto,' interactions over relatively short evolutionary time, and at the level of short-term successional change were examined.

METHODS

The vertical changes in structure and vegetation cover were analyzed in terms of density and the species composition of each layer. The density of each layer indicates the extent to which a community is actually filled by plants, and species diversity, the manner in which this density is achieved. Species diversity is by itself, an important structural characteristic which changes with ecosystem succession over time.

The characteristics of tree crown shape were obtained from an analysis of wide-angle photographs of the canopy (Anderson, 1966). Following Webb *et al.* (1970), the canopy layer was defined as the more or less continuous layer of tree crowns, excluding emergents.

The definition and description of the vertical structure of tropical rain forests poses difficulties. Some researchers distinguish one or two canopy layers (Clements, 1916; Odum, 1971), while others consider it to be a diffuse continuous layer (Richards, 1952). Richards (1952) indicates that it is possible to define layers in the canopy of edaphic climax communities, such as mangroves, tropical rain forests on rendzinas, pioneer variants and secondary successional communities. Thus, within the forests of the tropical zone, all possible variations of vertical stratification seem to be present.

The main criterion for distinguishing canopy/vegetation layers in temperate zone forests (Korchagin, 1976) is the presence of morphologically similar plant types (trees, shrubs, and grasses), which have maximum limits to their vertical growth. However, morphological criteria are not always reliable when defining the primary and secondary canopy layers of trees, or when dividing the herb layer into sub-layers. Similar problems are also encountered in tropical rain forests.

The aim of developing a generalized typology was to detect typical combinations and patterns with a reasonable level of precision. In the tropics the use of lifeforms in characterizing layers varies in its effectiveness. In a typical tropical rain forest, three main life forms are commonly encountered: trees, lianas and epiphytes, which on the basis of the location of their leaves, may belong to the same vertical zone or canopy layer.

When the foliage is concentrated into a single narrow storey it is visually different from a community in which the foliage covers a greater vertical range, no matter how the individual canopy layers are defined. Figure 25 shows a typical profile diagram of a tropical rain forest a hundred miles to the northeast of Port Moresby, Papua New Guinea (Paijmans, 1970). The diagram has been drawn on the basis of a detailed examination of a 0.8 ha sample area with a complete inventory of trees over 30 cm in diameter. Figure 26 shows the distribution of trees by height classes with an interval of 3 m. According to Paijmans' estimation, the species diversity of this forest is high, and equalled or exceeded only on Borneo and in the Malay peninsula. This profile diagram gives a detailed and objectively defined vertical structure: one can distinguish a layer of emergents of between 30 and 50 m; an upper canopy with height between 16 and 30 m; a lower canopy with heights from 7 to 16 m. Finally, between 3 and 6 m, there is a layer of small trees, which was not studied by the authors. We describe a similar vertical structure for sample areas on Pio, and simplified variations were noted on Niuafo'ou and Bagaman Islands.

Given the above complexities, a unified approach in distinguishing canopy layers in tropical forests was used. When particular lifeforms were prominent, they were used in defining canopy layers. When a community was composed of a single lifeform, the division was based on height classes defined with reference to the indicator lifeforms: herb, shrub and trees. In fact, each layer may be formed only of tree species, a situation which occurs in early seral stages or in coastal strand vegetation where trees may be present in both the shrub and the herb layers. Thus, through a combination of lifeform and height criteria one may distinguish the layers as sub-communities and evaluate the characteristics of the plant associations.

The age of tropical forests is impossible to determine precisely although the basal diameter and degree of development of buttress roots may serve as a relative indicator of age, and are particularly useful in recognizing old forests.

In tropical forests, growth rate varies with tree diameter and is affected both by tree location in the canopy and by the successional stage of the forest. In the earliest stages of succession, the growth rate is generally high. However with increased age, the rate of growth seems to decrease considerably. According to Neindzic (cited in Ashton *et al.*, 1978), in the tropical rain forests of Amazonia the annual growth for trees with diameters between 25 and 35 cm was 8 mm; for trees with diameters between 145 and 155 cm, it was 3.7 mm. For the rain forests of Puerto Rico Odum *et al.* (1978) estimated that annual growth rates were between 6.35 and 2.03 mm in diameter (average 3.55 mm). Trees as a lifeform were represented by abundant seedlings and low small undergrowth species in the shrub layer, by a taller undergrowth, and in the tree layer proper by trees of different sizes. The seedling and small undergrowth trees are usually morphologically different from the tall undergrowth trees. Seedlings in the herb layer are usually without branches having only terminal leaves; in the taller undergrowth, the crown is not yet formed and branches are few.

The tree horizons proper are subdivided into canopy layers having distinguishable morphological characteristics of leaves, crown and trunks. Most emergent trees have large buttress roots. The crowns of the upper canopy trees are usually umbellate, flat or spherical, while those of the lower layer are conical and cylindrical. The trees of the upper canopy have feather leaves and leaves with relatively small-sized blades. Thus, one may define the layers as follows: the lowest, corresponding to the herb layer has leaves at heights between 0 and 1.0 m; the shrub layer is found from 1 to between 4 and 6 m; the lower canopy, from between 4 and 6 m to between 16 and 20 m.; the upper canopy, between 16 and 20 m, and finally a layer of emergents which do not form a closed canopy. The tree layer of early successional stages is formed by pioneer species which may grow in height at a rate between 1 and 4 m per year and between 2 and 4 cm in diameter. Although such estimates are rather variable, diameter is a good age criterion if the successional stage and lifeform of the trees are taken into account. The vertical distribution of trees in shown in Figure 26.

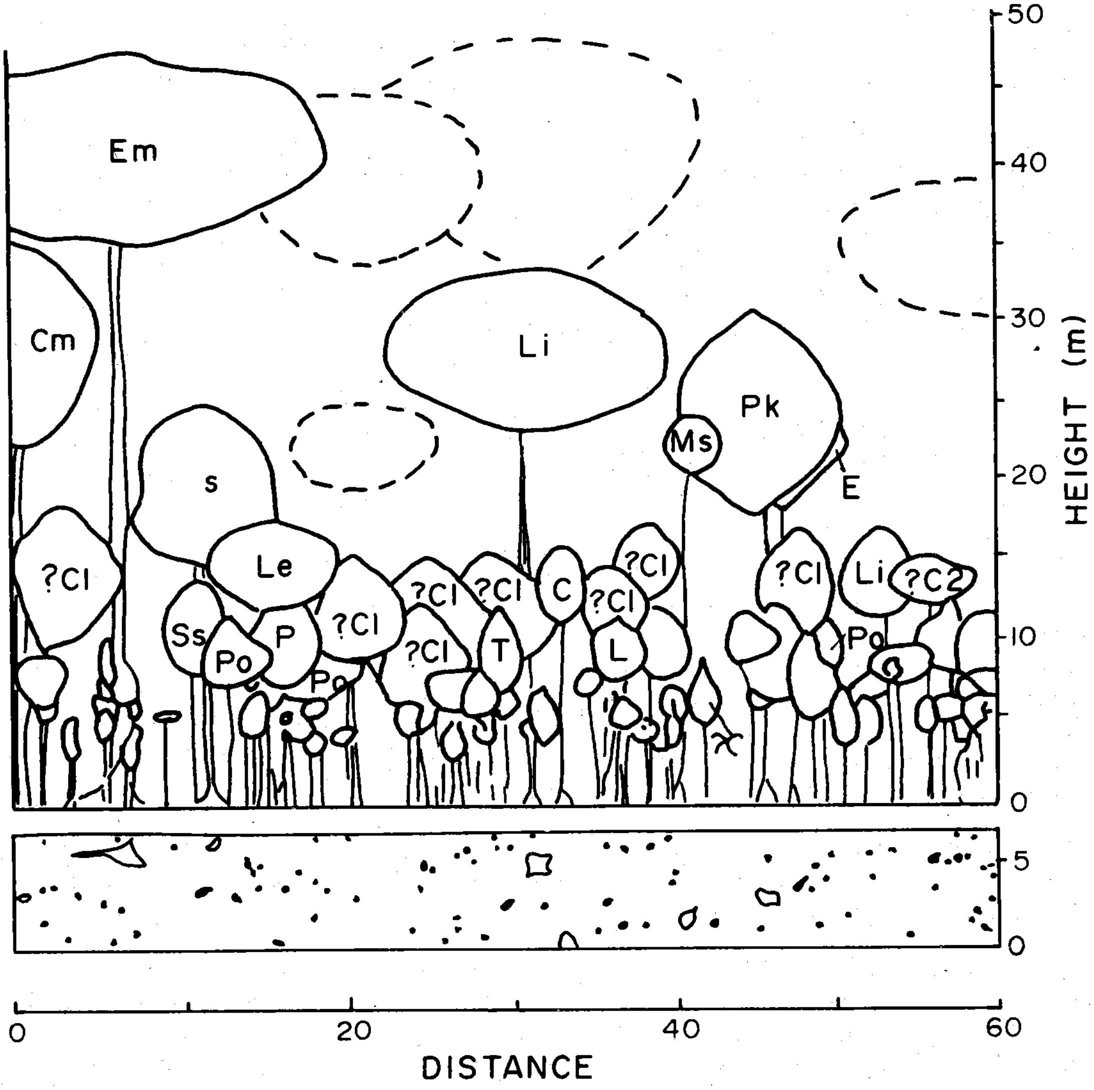


Figure 25. Profile diagramme of the tropical rainforest in Papua New Guinea (after Paijmans, 1970). Trunks with diameters >30 cm are shown by double lines. Key to symbols: C. *Cryptocarya* sp.; Cm. *Cryptocarya multinervis*; ?C1-2. *Cryptocarya*? spp.; E. *Euodia* sp.; Em. *Endospermum medullosum*; G. *Garcinia* sp.; L. Lauraceae; Le. *Levieria* sp.; Li. *Lithocarpus* sp.; Ms. *Myristica subulata*; P. *Planchonella* sp.; Pk. *Planchonella kaernbachiana*; Po. *Polyosma* sp.; S. *Sloanea* sp.; Ss. *Saurauia schumanniana*; T. *Terminalia* sp.

Quantitative methods of classification, were undertaken to form the basis for evaluating the similarities and differences between communities. According to the general aim of the study we were interested in combining into one category those communities which had similar canopy distributions. Similarity was more appropriate in this regard since such measures remove insignificant differences in values and reflect overall similarity in vertical distribution of the quantitative measures of each related characteristic. An index of similarity, (Vasilevich, 1969) was used to compare species composition while density was expressed in terms of a scale from 0 to 1. In addition a distance statistic based on the composition of different communities using an integrational classification procedure without threshold values as described by Puzachenko and Skulkin (1981) was included. A sequential, dichotomous division of the whole matrix into classes and subclasses was accomplished for each class at each level.

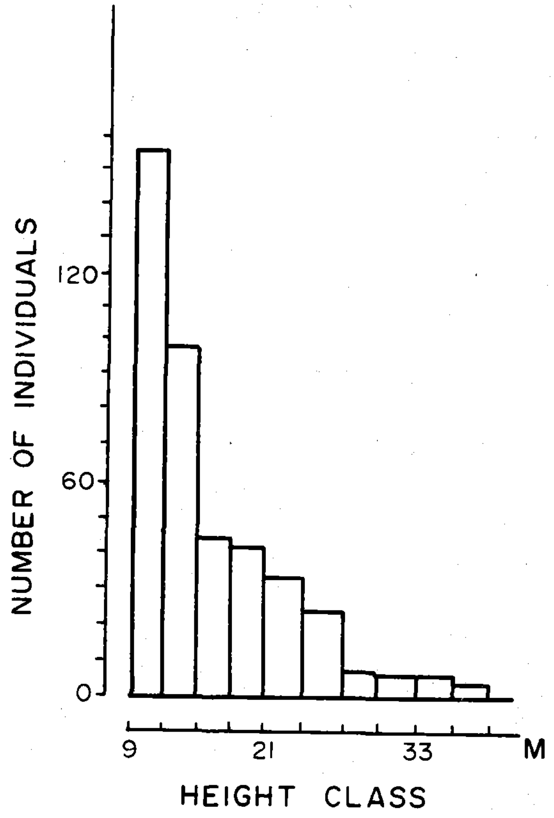


Figure 26. Distribution of tree trunks by mean height class in a tropical rainforest of Papua New Guinea (after Paijmans, 1970).

RESULTS

CLASSIFICATION OF VEGETATION TYPES

Due to the heterogeneity of vegetation cover 16 classes of communities were distinguished by the distribution of the densities for four canopy layers, and 13 classes were distinguished in terms of the distribution of species abundance. Figure 27 shows a dendrogram reflecting the results of an iterative procedure for classifying the 176 community descriptions on the basis of canopy layers and species density.

In the following community descriptions "complex stratification"refers to communities in which not less than three canopy layers have density over 0.3; "simplified stratification" refers to communities with not less than two such layers, and simple communities have only 1 such layer. "High density variants" are defined as those in which two canopy layers have density > 0.6; "median-density variants" are those in which there is only one such canopy layer. High-density canopy layers would be those in which the density of the canopy is > 0.8; "median" and "low" density canopy layers have, values between 0.6 and 0.8; and between 0.3 and 0.6, respectively.

Thus, using our classification the following plant communities were distinguished:

I. Simple stratification with high-density in the third (shrub) layer.

II. Complex stratification with median density, lower tree canopy absent.

III. Simple stratification with a high-density in the herb layer.

IV. Simplified stratification and low density of the shrub and herb layers.

V. Simple stratification with high-density in the lower canopy.

VI. Simplified stratification with high-density in the upper canopy and shrub layers.

VII. Simplified stratification with medium density in the upper canopy and herb layers.

VIII. Simple stratification and low densities in the upper canopy layer.

IX. Simplified stratification with low density of tree canopy layers.

X. Simplified stratification with medium density of both tree canopy layers.

XI. Simple stratification with median density in the lower tree layer.

XII. Simple stratification with high density in the lower tree layer.

XIII. Simplified stratification and high density in the lower tree and herb layers.

XIV. Complex stratification with high density in the lower tree layer and no herb layer.

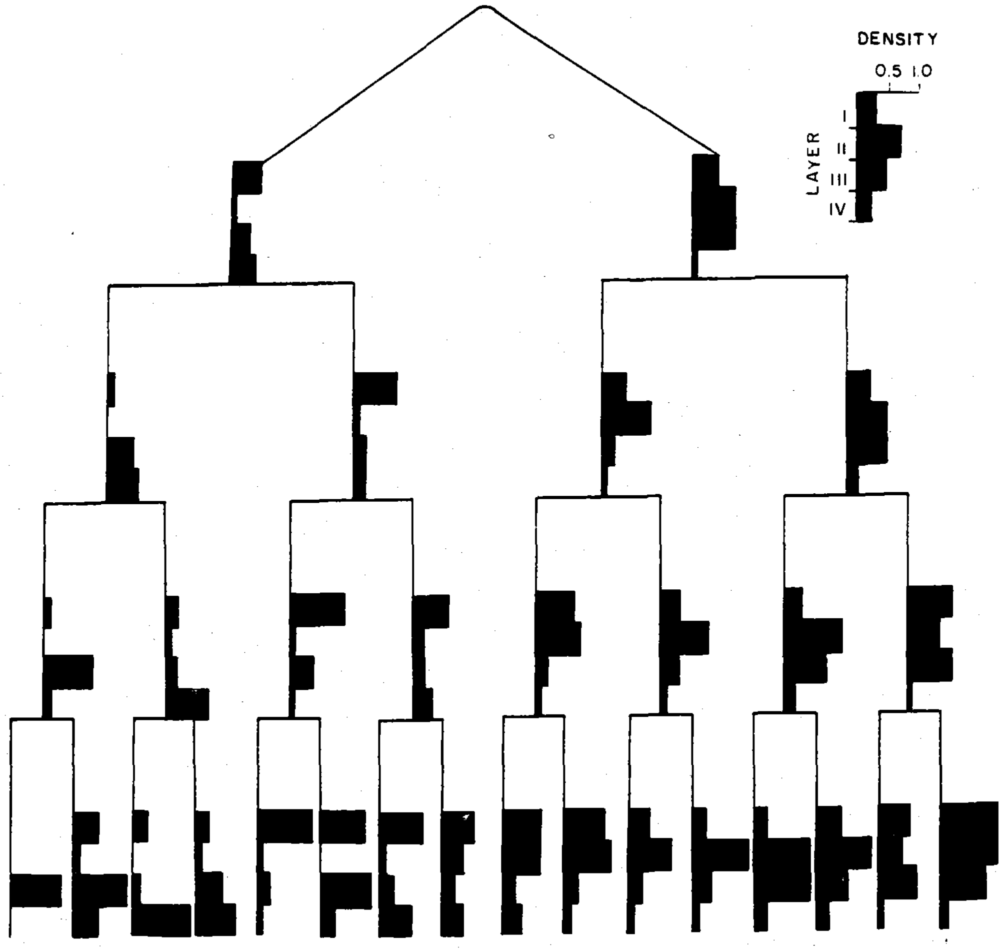
XV. Complex stratification of median density and no herb layer.

XVI. Complex stratification of high density with no herb layer.

SPECIES DIVERSITY AND CANOPY TYPES

In later descriptions of the complex and simplified variants we indicate which layer(s) has (have) a density below 0.2 or 0.3. In the case of simple stratification, the main canopy layer is indicated. As the same complexity of stratification may be seen under different densities, an additional qualifier of this parameter has been introduced. In the case of complex stratification, where two or more layers have density over 0.6, the community was classified as very dense. When only one layer has a density over 0.6 or has three layers with densities ranging between 0.3 and 0.6, these communities are referred to as being of mean density.

The terms "shrub" and "herb" are used only when these lifeforms are present in the corresponding layers. In all other instances they will be referred to as the "third" and "fourth" layers respectively.



I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	STRATIFICATION TYPE
2	17	8	14	17	18	16	14	23	23	22	23	16	28	24	19	MEAN HEIGHT OF THE UPPER CANOPY
0.31		0.43	0.48	0.22	0.13	0.26	0.35	0.28	0.11	0.21	0.12	0.04	0.06	0.07		
8	2	10	13	23	6	17	19	8	17	17	11	6	6	8	4	NUMBERS OF DESCRIPTIONS

Figure 27. Classification of plant communities by similarity of layer density.

Figure 28 primarily reflects the nature of changes in species diversity by layers. At the highest level the typology combines descriptions of two types; the first characterized by relatively high species abundance in the lower canopy and in the third or shrub layers; the second by high species diversity either in the first tree or in the fourth herb layer, or in both. The most characteristic feature of the second type is a low diversity of the second tree layer. Thus, shade tolerant-tree species are apparently not characteristic of the second description type, while the first type is distinguished by shade-tolerant species.

In accordance with the above scheme, the complexity of individual layers is classified as follows: very complex, if there is more than one species in each layer; complex, if there is more than one species in each of three layers; simplified, if there is more than one species in two layers; and simple, if there is only one multi-species layer.

Species abundance is considered to be low, if a layer has less than two species; medium, between 2 and 4 species; and high, if there are over 4 species in a layer, based on the mean for several visual descriptions within an area of about 300 or 400 sq m.

We have classified the species diversity of layers as follows:

I. Simple layering, shrubs with low species abundance.

II. Complex layering, with high species abundance in the herb layer.

III. Complex layering, with medium species abundance in three layers.

IV. Complex layering, with medium species abundance in the first tree and fourth (herb) layers.

V. Complex layering, with low species abundance.

VI. Simplified layering, with high species abundance in the first tree layer.

VII. Simplified layering, with medium species abundance in the first tree layer.

VIII. Simple layering, with medium species abundance in the first tree layer.

IX. Simplified layering, with medium species abundance in the first tree and the fourth (herb) layers.

X. Complex layering, with low species abundance.

XI. Complex layering, with medium species abundance in the second tree layer.

XII. Very complex layering, with medium species diversity.

XIII. Very complex layering, with high species diversity.

ISLAND AGE AND STRATIFICATION OF PLANT COMMUNITIES

Table 22 presents the distribution of stratification type by species diversity for each island. The representative types of stratification are denoted by a "+". On the whole, species diversity of communities on ancient islands is greater than on young islands. Furthermore, a greater number of species will be found within the different layers on an older island.

Comparison of young, atoll motus with Pio, an uplifted reef platform supports the above hypothesis. The old islands are characterized by complex communities with a medium and high species abundance, with the greatest number of species found in the second and the third layers. Raoul is

Figure 28. Classification of plant communities by similarity of species diversity according to layers.

distinguished by communities with complex stratification, but with low or medium species abundance. Like those of the atoll motus these are simplified communities with a medium species abundance, usually concentrated in one layer. On Raoul there are very few shade-tolerant species, which are also absent on the motu atolls. Generally, old islands support approximately twice the number of total species in each community compared to young islands.

It should be noted that the species diversity of a particular community may not correspond to the species diversity for the island as a whole. For instance, a comparison of the islands of Raoul and Norfolk shows that differences in species abundance at the community level within an area of about 400 sq. m are much greater than those obtained when comparing the total number of native species. That is, "old" communities of Norfolk, as a rule, have a greater share of the island's total species than "young" communities of Raoul. Such a relationship may reflect different trends of species adaptability and the formation of more complex and diverse spatial recombinations of species with increasing island age. The distribution of formation types and their species abundance for the two tropical high islands of Bagaman and Niuafo'ou are practically the same. Niuafo'ou, which is of Pleistocene age with its surface being constantly rejuvenated by vulcanism, and the geologically very old Bagaman island, are characterized by two different types of communities:

1. Bagaman is very complex, with a high species abundance.

2. Niuafo'ou is complex, with high or medium species abundance in the third and fourth layers.

Forest formations make up communities of the first type while the second type is characterized by initial seral stages of secondary succession. The lower layers are often formed by herb and shrub lifeforms. Thus, the age of the island ecosystem does not apparently influence species abundance on these island ecosystems as a whole.

On Niuafo'ou, only 23 species of trees were identified in six sample plots both on the crater slopes and in the caldera. Of these, only two species were found in all plots. A further two species were found in five plots; another two in four plots; one in three plots, and the rest in only one or two plots. On average, each plot contained 8.5 species. By contrast, six sample sites of the same size in the typical tropical rain forests of Papua New Guinea contained between 50 and 70 species of trees with trunk diameter over 30 cm. The mean number of species per sample site was between 10 and 20. The similarity in species abundance and vertical stratification of species on Bagaman and Niuafo'ou suggests that Niuafo'ou island is sufficiently old to have accumulated species of a wide ecological range. Niuafo'ou is an oceanic, isolated island, and vulcanism on the island during the whole of the Pleistocene and Holocene did not apparently lead to complete extinction of vegetation; community evolution proceeded independently of vulcanism. This assumption, although it needs examination suggests that in the tropical Southwest Pacific, isolation does not greatly influence the floristic complexity at a generic level. The set of species found on a comparatively young island is, to all appearances, sufficient for the formation of complex stratified plant communities.

Thus, on the basis of species abundance, ecosystems on the islands of Norfolk, Pio, Bagaman, and Niuafo'ou may be classified, from the viewpoint of primary succession, as relatively mature while those of Raoul are undoubtedly young. This conclusion cannot be extended to the motu atolls, as the limited species diversity and the simplicity of communities may be considered a result of unfavorable edaphic conditions, the small size of area, and isolation. Rather, high community complexity on the lower terrace of Pio and on Bagaman, which have similar edaphic conditions, indicate that this factor in itself does not impose great limitations on species diversity.

On the raised coral islands, whose age is several tens of thousands of years, thin soils are quite common. These soils may be considered to result from a long evolution of the whole ecosystem, and support the existence of species under the unfavorable edaphic conditions of young terraces. On the motu atolls, one finds conditions potentially favorable for quite a wide spectrum of species within rather small areas. In any case, edaphic conditions alone cannot account for the simplicity of plant communities on these atolls. The small extent of the area cannot limit the growth of shade-tolerant species and cannot account for their absence on the atolls. For the motus, low species diversity may be a function of their youth, possibly enhanced by their small area size and by unfavorable edaphic conditions.

Thus, successional maturity leads to an increase of the number of species in the second and third layers of the plant community, particularly that of shade-tolerant species. Correspondingly, one may expect that mature communities reaching the climax vegetation type will also be characterized by a more complex vertical distribution of the foliage and, hence, vertical stratification.

Table 23 illustrates distributions of stratification types by density with a fixed type of distribution of the number of species by layers. Communities which have low species diversity or those in which species are concentrated into one or two layers, correspond to simple or simplified stratification by density. Conditions of high species diversity with many species found in different layers, particularly in the tree layers, are normally characteristic of very dense or extremely dense forests. There are also many variants with simple and simplified one or two-layer forests having quite a wide range of density.

When species diversity is low and species stratification simplified or complex, such as in the plant communities of Raoul, then we usually have a double canopy forest with a high or medium density. Communities on motus which have medium species diversity in two layers are single canopy forests with a high or medium density. Finally, communities whose species diversity is usually concentrated in the lower layers are characterized by quite a wide range of different stratification types, including transitional stages ranging from communities with developed herb and shrub layers, to communities with one tree layer and well developed third or fourth horizons.

Thus, species abundance and its distribution by layer quite clearly affects the density of each layer. In all cases, multi-species communities have a greater diversity of vertical leaf canopy structure, while monospecific communities have a structure with limited variation. Indirectly, such relationships suggest that multi-species communities, under the influence of internal and external factors causing succession, may form different vertical stratifications of the canopy. For low- diversity communities, succession is simpler and, other things being equal, takes a shorter time to reach its climax. Consequently, mature climax communities have a much more complex series of secondary successional stages than the young ones. The most typical plant communities of Raoul and of the atoll motu display fewer types of stratification. The typical communities of Raoul are characterized by three of the eight possible types of vertical stratification of the canopy, while the motus are characterized by two of seven possible types. In mature climax communities, five of a possible thirteen types of vertical stratification were found.

The above relationships hold for the typical communities of each island. On each island there was a wide range of vertical structures, reflecting the complex processes of association and interaction not only of the vegetation, but also of the whole biotic community (Table 24). Complex multi-layer, very dense and extremely dense forests are characteristic only of tropical mature climax ecosystems which are independent of the island type. In mature subtropical forests, even in those of high species abundance, there are simple or simplified vertical structures with a very high or high density of the second tree layer. The other three layers are present, but their density is not usually greater than that of the second layer.

INTRA-ISLAND VARIATIONS IN VEGETATION

As may be seen from Table 22, the diversity of canopy vertical stratification is a function of island heterogeneity. This heterogeneity allows us to study the response of the vegetation cover to a wide range of extrinsic and intrinsic factors.

Raoul

Most variations in stratification described for Raoul may be accounted for by a single series of secondary successional stages and cyclic alterations. Only the communities with a high density in

Table 22. Distribution of species abundance by community layer on islands in the Southwest Pacific.

	I	II-III	IV-V	VI-VII	VIII-IX	X-XI	XII-XIII	N_i
Raoul		7 0.17	3 0.07	2 0.05		+24 0.57	6 0.14	42
Norfolk						+1 0.33	+2 0.67	3
Niuafo'ou		+19 0.47	1 0.02				+21 0.51	41
Bagaman		+3 0.30	3 0.30				+4 0.40	10
Motus	+8 0.12	10 0.16	+11 0.29	+8 0.15	+10 0.18	7 0.11	8 0.13	62
Suwarrow & Pukapuka		1 0.06				2 0.12	+17 0.83	20
Philip		+3 1.00						3
N_j	8	43	18	8	12	34	55	178
P (a_i)	0.04	0.24	0.10	0.04	0.07	0.19	0.31	

+ = representative types of stratificatiion

Table 23. Correspondence of the type of species diversity distribution by layers (A) to the type of stratification by layer density (B) of Southwest Pacific Islands.

B A																
	+ 8 1.00															
		+ 1 0.08	+ 4 0.33	+ 2 0.17	1 0.08	+ 2 0 17	+ 2 0.17									
			+ 5 0.17	+ 6 0.21	+ 8 0.28	1 0.03	+ 4 0.14	3 0.10			1 0.03		+ 1 0.03			
 		+ 1 0.07			+ 5 0.36	+ 2 0.14	+ 5 0.36	+ 1 0.07								
 					+ 1 0.20		+ 2 0.40	+ 2 0.40								
 					1 0.10		+ 2 0.22	+ 4 0.47	+ 1 0.10	+ 1 0.10						
			+ 1 0.07		1 0.07		1 0.07	1 0.07	+ 3 0.21	+ 3 0.21	+ 3 0.21	+ 1 0.07				
										+ 8 0.47	+ 4 0.23	+ 5 0.29				
				+ 2 0.13			1 0.07	+ 3 0.20	+ 2 0.13	+ 2 0.13	+ 2 0.13			+ 1 0.07	+ 1 0.07	+ 1 0.07
				1 0.03	+ 6 0.17	+ 1 0.03		3 0.09	1 0.03	2 0.06	+ 6 0.17	+ 3 0.09	+ 1 0.03	+ 4 0.11	+ 6 0.17	+ 1 0.03
No. of Descriptions	8	2	10	11	23	6	17	17	7	16	16	9	2	5	7	2
Proportion	0.05	0.01	0.06	0.07	0.15	0.04	0.11	0.14	0.04	0.10	0.10	0.06	0.01	0.03	0.04	0.01

the herb and shrub layers reflect the influence of extrinsic factors such as intensive erosion and slope denudation or vertical zonation. Most typical was a stratification pattern with medium density in the upper canopy, a high density in the lower canopy, and low density in the third and fourth layers. Such stratification corresponded to the variation in *Metrosideros kermadecensis* and a hay-scented fern in the upper canopy, and coconut palm in the lower canopy and the third and fourth layers.

The process of species interactions may be described as follows: *Metrosideros kermadecensis* occupies ash surfaces and forms dense young monospecific stands and the simplest single storey communities on the island. With continued growth, some *Metrosideros kermadecensis* die back, such that during the mature stage the species forms stands with a comparatively low density 0.6/ha. During the course of further die-off, a second layer of understorey forms, which at lower altitudes is composed of Myrsinaceae. The seral stage length of low to medium density *Metrosideros kermadecensis* is probably quite long, and several generations may succeed each other under their own canopy. As the density is relatively high, the succession of palm generations may occur only when there is a mass falling of trees from the second layer. With age, the upper canopy of *Metrosideros kermadecensis* gradually dies and is replaced by palm trees. Potentially, this process leads to the formation of a pure palm forest. Thus, in this case we have at one and the same time succession involving species replacement as evidenced by the development of coconut palms. The life expectancy of *Metrosideros kermadecensis* is, however, far greater than that of the palms, so that these two different types of succession go on practically independently of each other. The general sequence of changes within the typological classification may be presented in the following way:

VII → IV → IX → VII → VI → IX → X → XI → XII → IX → XII.

Depending on conditions, the dominant species may be co-dominant with other species: for example, *Metrosideros* with hay-scented fern, palm, *Miliceus* and *Casuarina*. On Raoul there is no climax community. An equilibrium is maintained by periodic volcanic ashfall, partial destruction of vegetation, and creation of conditions suitable for a natural renewal of *Metrosideros kermadecensis*. The ashfalls are an indispensable condition of the ecosystem's dynamic stability.

Pukapuka and Suwarrow Atolls

A wide range of vertical stratification types is found on the motu islands, the distribution of which is determined by external factors. Their recent surfaces, periodically subjected to surf and tidal activity, are occupied by one-layer shrub communities, whose species composition changes according with distance from the shore. The center and most stable parts of the motu contain two-layer simplified communities formed by *Pisonia* in the upper canopy and by *Cocos nucifera* in the lower canopy. The density of the first layer may fluctuate from medium to low. The trunks of fallen trees are numerous and evidence of a recent downfall. Seedling palms are usually very abundant in the third and in the fourth layers.

On Pukapuka and Suwarrow atolls, which are subject to hurricane destruction, a similar vertical structure is found. The vegetation formed medium-density, one-layer forests with a predominance in the upper layer of *Pisonia* or *Guettarda*, and a low density second layer of coconut palms or *Pandanus*. There is little difference in the heights of *Pisonia, Guettarda*, coconut palm, and *Pandanus*, so that the tree stand is essentially one-layered. *Pisonia* usually occupies uplifted areas facing the oceanic side of the atoll, while *Guettarda* can be found in depressed areas towards the inner part of the motu. Under the canopy, the regeneration of coconuts or *Pandanus* is quite common. Depending on the density of the upper layer, the regeneration enters the third layer or stops in the fourth one. A ground cover of large epiphytic ferns is also quite common.

Forests with two well developed layers, the first of *Pisonia* and the second of coconut palm, represent the next stage of atoll vegetation development. Usually these are communities with a medium density in both layers. *Pisonia* never has a very high density, and under the canopy of such forests there is usually an insignificant, but continuous regeneration of coconut palms. The next sere in this community shows increasing density of the second tree layer of coconut palm with an unchanging density of *Pisonia*. Cyclic change in this community will be due to the death or felling of individual palms of the second layer and a corresponding regrowth of younger palms. Such alterations may take place against a background of a permanent upper canopy of *Pisonia*. The life span of *Pisonia* is apparently, much greater than that of coconut palm, and the cyclic transformations associated with the breaking up of its canopy are much more prolonged and may possibly be initiated by hurricanes. In the central parts of the motus, one may find areas where the upper layer of *Pisonia* is sparse. In such instances, the density of the second layer of coconut palms is higher.

Guettarda does not usually form such tall plantations or groves as *Pisonia* does; its last stages are characterized by variants of one-layer stands of two or three species. Sometimes communities with a very high single canopy forest of *Guettarda* and *Pandanus* are found in depressions.

Thus, in the central parts of motu atolls we may distinguish the following sequence of transformations in the vertical structure of vegetation initiated by hurricanes:

IV → VII, VIII → V → IX → X → ... IX → X → ... IX ..., etc.

Communities formed by shrubs and small trees (typically *Scaevola, Messerschmidia* and *Pandanus*) occupy the area between the beach and the interior of the motu. The coconut palm is sometimes a significant component. These communities are influenced by external factors, such as hurricanes, strong winds and salt spray and their persistence is probably due to the influence of these factors, as these species are predominant in the most windward parts of the motu. On the whole, they are one-layer formations with a very high density in the first layer. Sometimes along with a well developed first layer is a dense third layer, composed of *Pandanus*. These communities, generally of small height, are sometimes characterized by a medium density upper layer composed of *Messerschmidia* or *Pandanus* and a lower layer of *Scaevola*. While cyclic alterations in community structure are apparent, their rates are not great.

Both alterations due to external factors and cyclic transformations may be identified in the main part of the motus. It is significant that the vertical structure of vegetation in the central part of these islets approaches the vertical structure of the vegetation of Raoul. It is possible that such simplified relationships which provide for a high density with a minimal complexity of the canopy are typical of early seral stages of communities.

Niuafo'ou

On Niuafo'ou the vegetation is characterized by high species diversity, and suggests maturity. In terms of stratification, however, they are like the younger communities of the motus. An apparent reason for this similarity is the early successional stage and relative youth of the predominant vegetation, which is determined by the influence of vulcanism and anthropogenic factors. The great diversity of vegetation formations on this island is the direct consequence of the different quality and magnitude of environmental factors. This heterogeneity of habitats results in part from the following edaphic variations: lava surfaces, lava-slag surfaces covered by a thin layer of ash, lava-slag surfaces covered by a medium-depth layer of ash and ash soils proper, which are repeatedly covered by ash falls. These edaphic variations are the different results of vulcanism and are important in determining the differences in the rates and trends of regeneration.

On lava surfaces, the colonization of vegetation is sporadic and does not greatly depend on the age of lavas, but seems more dependent on the types of lava bedding materials. The patches of renewed vegetation may be classified as an open forest with more or less well developed shrub and herb layers. In those cases where the lava is covered with a thin continuous layer of ash, the vegetation is an open forest type with *Casuarina* predominant in the upper canopy. A medium-density shrub layer, and a well-developed herb layer are also present. The density of the tree canopy varies with the thickness of the ash layer, and possibly the age of the surface. In any case, succession proceeds from a shrub-herb vegetation with single layer of drought-resistant tree species. In depressed low-lying areas communities of a maquis type, formed almost completely by shrubs and small trees (*Scaevola, Messerschmidia,* and *Morinda*), were encountered. In a small crater, succession had proceeded directly to a one-layer, high density forest consisting of four to five species, which is typical of the initial seral stages of tropical rain forest succession. The inner slopes of the crater were covered by a thin layer of ash, while the crater floor was filled by a lake.

The formation described above suggests that the structure of the communities and the role of individual lifeforms in the early stages of succession are determined by moisture availability. Where the thickness of ash is considerable or where moisture can accumulate because of relief, the vegetation is dominated by trees.

In areas with a medium soil water regime, shrub lifeforms and small trees predominate; these are analogs to the communities of the motu. The shrub and herb vegetation of more arid areas seems to be characterized by a long-term stability, and their succession to tropical rain forests proper is unlikely. The succession of the old *Casuarina* forests consisting of a sparse upper canopy of very large *Casuarina* trees, and dense lower layer of typically tropical rain forest species, suggests this as a possible successional sub-climax stage in these communities.

The change from a xeromorphic community to a tropical rain forest, proceeds as follows:

$$\left.\begin{array}{l} \text{I, II} \\ \text{III} \\ \text{IV} \end{array}\right\} \rightarrow \text{V, VI} \rightarrow \text{VII, VIII} \rightarrow \text{IX, X} \rightarrow \text{XI, XII.}$$

When the thickness of the ash layer is greater, as in the crater, the first stage of succession proceeds directly to a tree community, a process also seen in the secondary succession abandoned gardens. A short time is required to form these simple, one-layer forests of pioneer, light-requiring, tree species, which are distinguished by high numbers of individuals, in the first, third, and fourth layers. With increased tree heights, these forests become differentiated into a two-layered forest. The density of species in the fourth layer is then low. At this stage, coconut palms are common in the lower canopy, but also are present in the first layer. Further growth of the coconut palm depends on gaps produced in the upper canopy and the density of the undergrowth. Thus, all of the variations of vertical stratification, simple or simplified, may be considered as transitional seral stages.

Judging by the diameter of the trees and the degree of buttress root development, these changes in species composition can occur rather rapidly, but anthropogenic pressure does not permit the formation of a complex tropical forest. Selective felling of trees occurs in woodland. The other three medium and low-density layers are formed by shoots, undergrowth, and small trees. With less economic pressure on terrestrial vegetation, these communities develop into two-layer forests of medium and high densities. Thus, the initial stages of succession can be described by the following alteration of stratification types:

$$\left.\begin{array}{c} \text{V} \\ \text{VII} \\ \text{VIII} \end{array}\right\} \rightarrow \text{IX, X} \rightarrow \text{XI, XII.}$$

On Niuafo'ou, forests which are untouched by human activity or not subjected to intensive volcanic influence are rare. Descriptions of vegetation in the caldera and on its slopes indicate that there is a succession from the initial seral stages of a simple or simplified structure to more complex high density tropical forests of considerable height and with emergent trees.

Bagaman

The forest vegetation on Bagaman may be considered a continuation of the successional processes taking place on Niuafo'ou. The descriptions of the vegetation were made in old secondary forest, with no emergent-trees. The first layer was formed by pioneer species, such as the silk-tree and on the steepest parts of the slope, the *Casuarina*. On Bagaman, we encountered variations of a simple stratification, with a high density of the upper canopy layer and a low density of the lower one. We considered this forest to be the last seral stage present on Niuafo'ou. Such communities were localized to one area in the upper part of the slope. Close to this community was a simplified one which had a medium density lower canopy and a high density upper one. These communities are similar to those of Niuafo'ou, and are characterized by tree heights of between 25 and 30 m and by mean tree diameters between 30 and 40 cm. All the other communities on Bagaman have smaller trunk diameters, usually smaller heights, and are similar to the pioneer, simply stratified communities of Niuafo'ou.

The youngest types of communities have tree diameters less than 20 cm, and are characterized by a very complex stratification, with a medium to high density of the three upper layers, although their heights are not over 20 m. These forests appear to have formed after the collapse of the first layer, and by the disruption of an earlier successional stage of the second layer. This assumption is supported by the presence of single trees rising above the canopy. In the course of succession one might expect some simplification of vegetation structure due to the penetration to the upper layer of the most rapidly growing species and the dying off of some trees in the lower layer. We have not seen such forests on Bagaman. Thus, the theoretical changes to the forests at the interface between pioneer stages and the basic forest types could be expected to follow these changes of stratification type:

XI, IXX → XV, XIV → XIII, XIV → ...XI, XII.

On Bagaman, there are also stable grassland and savanna communities with a vertical stratification similar to the one described for the ash-slag plains of Niuafo'ou. Although these grasslands are composed of different species, they are physiognomically alike. The secondary communities of savannah and grassland may be assumed to be climatically determined and as on Niuafo'ou, their replacement by native forest is unlikely. In addition, there are also communities of mangroves with a typical one-layer vertical stratification. The mangrove communities are probably an edaphic climax and stable, if the conditions of sedimentation in the lagoon do not change. Successional changes are possible only with a change in external environmental conditions.

Pio

The types of vertical stratification represented on Pio are most similar to those of Bagaman. However, the vegetation displays different physiognomic features. The communities of Pio are characterized by the presence of emergents; a greater height of the tree canopy, and correspondingly, trees with greater diameters. These variations in stratification probably represent the final stages of succession prior to achieving a climax community. The course of succession is modified by hurricanes but these are of minor importance. The mean height and mean diameter of the stand, the number of emergents, and the abundance of wind-fallen vegetation serve as criteria for correlating the stratifications within a cycle (Table 25).

In the case of cyclic transformations, the starting point for the analysis may be chosen at random; for instance, one may choose a situation with a large number of emergents and with a minimum number of wind struck trees, which corresponds to a mature, but not yet collapsing stand. On Pio this formation type has a complex stratification with a very high density, which decreases progressively from layer three towards the ground layer: layer 1, $d = 0.43$; layer 2, 0.9; layer 3, 0.5; layer 4, 0.2. This formation type has the highest density in the tree canopy.

A second formation with fewer emergents and few wind struck trees had a simple structure (Types XI and XIII) with decreased density in the lower canopy and a tall undergrowth layer (layer 1, 0.2 or 0.3; layer 2, 0.7 to 0.9; layer 3, 0.2; layer 4, 0.1). This formation, apparently, corresponds to the beginning of a gradual break up of the community during which the growth of plants intensifies in all the layers and new emergents appear. Where the numbers of wind-struck trees were insignificant, the communities (V, VI) had a medium density in the three upper layers (layer 1, 0.5; layer 2, 0.2; layer 3, 0.2; layer 4, 0.3), they correspond to rejuvenated forests of low heights which appear after a hurricane has felled large numbers of trees. These areas may also have a very heavy and tangled undergrowth, resulting from increased light penetration to lower layers.

Table 24. Distribution of the types of stratification by layer density in plant communities on islands of the Southwest Pacific.

Island																	No.
Raoul			+ 4 0.12		2 0.06	+ 2 0.06	1 0.03		+ 3 0.09	+ 111 0.32	+ 6 0.18	+ 4 0.12	+ 1 0.03				34
Norfolk									+ 1 0.25		+ 3 0.75						4
Niuafo'ou		+ 1 0.03	2 0.05	+ 10 0.26	+ 7 0.18	+ 1 0.03	+ 4 0.10	3 0.08	1 0.03	2 0.05	+ 4 0.10	1 0.03			+ 2 0.05	+ 1 0.16	39
Bagaman			+ 3 0.16		2 0.11		1 0.05			1 0.05	1 0.05	1 0.05	+ 4 0.21	+ 2 0.11	+ 1 0.05	+ 3 0.16	19
Motu Atolls	+ 8 0.13	1 0.02		2 0.04	+ 9 0.16	1 0.03	+ 11 0.20	+ 16 0.30	+ 3 0.05	2 0.04	1 0.02						56
Suwarrow & Pukapuka					+ 3 0.14	+ 2 0.10				+ 1 0.05	+ 2 0.10	+ 3 0.14	+ 1 0.05	+ 4 0.19	+ 5 0.24		21
Philip			+ 1 1.00														1
	8	2	10	12	23	6	17	19	8	17	17	11	6	6	8	4	174
Proportion	0.05	0.01	0.06	0.07	0.13	0.03	0.10	0.11	0.05	0.10	0.10	0.06	0.03	0.03	0.05	0.02	

Table 25. Selected morphological characteristics of plant communities under different types of canopy stratification on Pio Island.

Stratification Type	Mean Height Of The First Layer (m)	Mean Diameter Of The First Layer (cm)	Number Of Emergents (40x40 m)	Amount Of Wind-fallen Plant Parts
V, VI	25	22	2	Average - High
XI, XII	31	58	2.6	Average
XIII, XIV	31	72	5.2	Nil - Very Low
XV	28	35	3.6	Low

On Pio, these types are found mainly near the windward coasts and are somewhat analogous to the results of forest clearing for food gardens, which provides the conditions necessary for the intensive growth of pioneer light-tolerant species following garden abandonment. As a result, similar, medium-height, single canopy forests appear in abandoned gardens and canopy differentiations is similar to the types described above for Niuafo'ou.

Thus, on Pio there are two types of successional processes affecting the stratification of the forest canopy: a relatively short cycle determined by the death and falling of some emergents; and a longer cycle following mass wind strike by hurricanes. The general scheme of seral stages in the forest structure may be presented as follows:

V, VI → IX, X → XI, XII → XV → XIII, XIV → XI, XII → XV, etc.,

Comparison of the above scheme with that of Bagaman Island indicates that stratification types are similar in both cases, with the heights and diameters of the trees serving as the primary criteria for identifying seral stages. On Pio variations in stratification result from endodynamic changes. One may assume that the initial stages of succession on Bagaman are followed by the formation of native forests like those of Pio. On Pio, however, the oldest forests with emergents correspond in stratification to the comparatively young forests without emergents on Bagaman. Further development of such forests on Bagaman may lead to the formation of communities like those of Pio. The available data do not indicate whether such a transition will be from existing communities directly, or whether further seral stages are needed prior to the climax formation. It is possible that on small islands such as Bagaman, tropical rain forest communities do not form because of low species diversity and an absence of emergent species.

DISCUSSION

Despite these limitations, the changes of vertical structure during the course of internally and externally influenced succession and cyclic transformations are relatively uniform and describe a single successional trend. Depending on the conditions present in any one location, such as the seral stage of development, climate, edaphic factors and anthropogenic activities, the changes to the canopy's vertical structure may cease altogether or pass into a closed cycle at different points, and result in the appearance of different stratification types. Depending on the intensity of factors external to the community and on the scale of environmental changes, succession may start with communities having different sets of lifeforms and associated vertical stratifications. These relationships may be united into one scheme during the later stages of the process. The scheme takes into account all of the factors involved. These relationships are shown in Figure 29.

Thus, changes in the vertical stratification of plant communities on small islands of the Southwest Pacific Ocean result from the interaction of different factors derived from within and outside the community, all of which operate on several different time scales.

The selection of islands of different geological ages allowed an analysis of the effects of time on community associations and interactions. An essential component in this process is the increase in the number of mainly shade-tolerant species with time. In turn, this results in a high density of the lower layers of the stand and natural reproduction under conditions of low incident solar radiation. The ecologically wide spectrum of species result in a pyramid of numbers based on vertical stratification with maximum diversity in the second and/or the third layers and minimum density in the layer of emergents and in the lowest layer. Under tropical conditions, climax communities are characterized by high species diversity. In the subtropics, the vertical structure of the climax community is simpler, having a maximum density in the lower canopy, while individual species abundance is approximately twice as low as in the early seral stages. The time necessary for island ecosystems to reach a climax may be tentatively defined as between tens and a few hundreds of thousands of years.

The most complicated and diverse processes are intra-community interactions, which are in general, coincident with successional trends. The formation of complex communities occurs with changes to individual species abundance and height. The complexity of the community and its rates of change are also a function of the magnitude and nature of disturbance. The most powerful impacts resulting in the most complicated and long-term transformations, are associated with volcanic eruptions. The rates of successional change on lavas without a covering layer of ash are a function of the slow rates of weathering and soil formation. Such a starting point for primary succession is apparently, very rare, as lavas are repeatedly covered by ash during subsequent eruptions. Few species are capable of colonizing bare lavas given the extremely arid conditions and shallow soils during the initial stages of succession. Under these conditions species diversity and density are far lower than those of tropical forest. Seed germination and successful growth of tropical rain forest species depends on high soil moisture and shade (Ashton *et al.*, 1978). These conditions are possible only under a continuous canopy of pioneer species. Under the extreme conditions given above, the restoration of a continuous canopy of pioneer species is a long-term process, and in some cases, is never achieved. Grassy plants with an extensive surface root system also seem to adversely affect tree propagation. The edge or boundary between forest and the herb-shrub formations is usually not very distinct; there are few species common to both forest and grassland communities, and these are often absent from islands. This is an indirect indication of the complexity of succession from the pioneer stage formed of grass and shrub lifeforms, to forest vegetation, a process which seems to require hundreds of years.

When the conditions of soil moisture are sufficient for the growth of pioneer tree species, the process of succession proceeds rapidly, and with considerable change to the environment, favors tropical rain forest species. Such conditions arise when the ash layer is thick and located in depressions of the lava surface. An analysis of vertical stratification allows us to discern under these conditions at least three or four different seral stages: the first is represented by a single canopy, low forest; the second, by a single canopy, low forest with a low density of plants in the other three layers; the third, by medium height forests with a high density of the lower canopy and a median density in the upper canopy, sometimes with emergents; and the fourth, by the true multi-layered tropical rain forests with emergents.

Ashton *et al.* (1978) suggest that the first pioneer stage is characterized by species capable of an early logarithmic phase of growth, and by a lack of shade tolerance (which leads to the distribution of leaves in one layer), and by a short life span of about 40 years. In the second stage the community is formed of more shade-tolerant species with horizontal branching and with the growth of leaves at the ends of the branches. Such species have high growth rates, are often able to fix nitrogen, and have a life span of around 100 years. In a mature state these species form hemispherical crowns, which create a favorable micro-climate for successive stages. Species, of the silk-tree genus are characteristic representatives of this stage.

In Ashton *et al.* (1978) classification, the third stage is defined as a mature stage of light tolerant species, and the fourth is a mature community with shade-tolerant species. The transition from the second to the third stage is associated with the appearance of emergents and increase in species characterized by lower light requirements, as well as shade-tolerant species. While the boundaries between the first two stages are clear, the transition between later ones is less distinct, being dependent on local environmental conditions and on the composition of interacting species. The time needed for all these transformations is estimated as a few hundred years.

The process of forming the vegetation's vertical stratification in the course of succession may stop at certain stages depending on the nature and scale of active external factors. Fires for instance, promote the preservation of the savannah vegetation and grasslands; the permanent rejuvenation of the motu atolls surface, due to the action of wind and surf, maintains the shrub stage in equilibrium with the environment. The widespread single canopy low forests on motus is accounted for by the influence of hurricanes; a permanent partial clearing of coconut palm plantations leads to the formation and maintenance of forests of the second successional stage. The age of young island ecosystems and the corresponding low species diversity combined with the thin and poorly developed soils limits the successional process and retards the formation of forest with a complex vertical stratification.

Alongside powerful external factors, such as a drastic change in the environmental conditions over large areas, there are factors of less effect: hurricanes of low intensity, anthropogenic tree clearings in small areas of tropical rain forest, and local landslides on slopes. All of these may bring about secondary successional changes. The process of succession and the restoration of a full climax in these cases proceeds at a rapid rate.

Finally, the materials discussed above permit us to distinguish the cyclic transformations of vertical structure, which are associated with the processes of break-up and renewal of a definite forest area within an established community. All the stratification types considered above represent an averaging of the structure, and characterization of its state in terms of the stage of succession. Cyclic, internally caused changes involved the inner spatial elements of communities-and characteristic patterns found in the third and fourth stages of a successional series. The third stage of the insular successional series may be considered a climax stage, and represents the influence of island age. For cyclic transformations to continue, it is necessary that light tolerant species with a long life-span are able to regenerate without intensive break-up of the upper canopy. The insular species in this category, evidently, do not possess this ability, or possess it to a limited degree. *Metrosideros kermadecensis,* for example, is unable to regenerate under its own canopy; however, it forms new trunks from fallen trees. On atolls, reproduction of *Pisonia* under forest canopy is also limited, but the recurrent impact of hurricanes provides for development.

The cyclic transformations are the most complicated in tropical rain forest. The wide ecological spectrum of species present leads to a mosaic pattern of successional stages at the community level. If there is a mass fall of emergents, then the cyclic stages involve a change in vertical stratification, starting at the early pioneer stage. When tree falls are less extensive, the process of cyclic transformation will be shorter, starting from a stage which includes elements belonging to the last two stages of the seral sequence.

The present results confirm and verify the suggestions of Richards (1952) and Cosems (1965), cited in Fontaine *et al.* (1978) that the "natural tropical rain forests always consist of a mosaic of seral stages of different ages, where the early, the middle, and the late components are represented in different proportions". In interpreting such patterns it is important to distinguish areas within which similar seral stages have been reached. This mosaic character of the community allows the determination of the potential capacity of the tropical rain forest to regenerate under the influence of different external factors. Under intermediate climatic conditions the felling or burning of tropical rain forest results in the formation of sub-climax communities such as grasslands and savannah; the transition from such seres to climax tropical rain forest is more complicated.

On the islands of the Southwest Pacific, one may distinguish processes that take place on different time scales: hundreds of thousands of years (co-adaptation under the influence of low-intensity factors, producing community types with prolonged internally generated cyclic transformations); tens to a few hundreds of thousands years where species interactions and selection within the community occur; and tens of hundreds of years where short cyclic transformations dominate successional patterns.

The islands control possible climax community structures, leading on the whole to simplification of communities in respect of individual species abundance and patterns of vertical stratification.

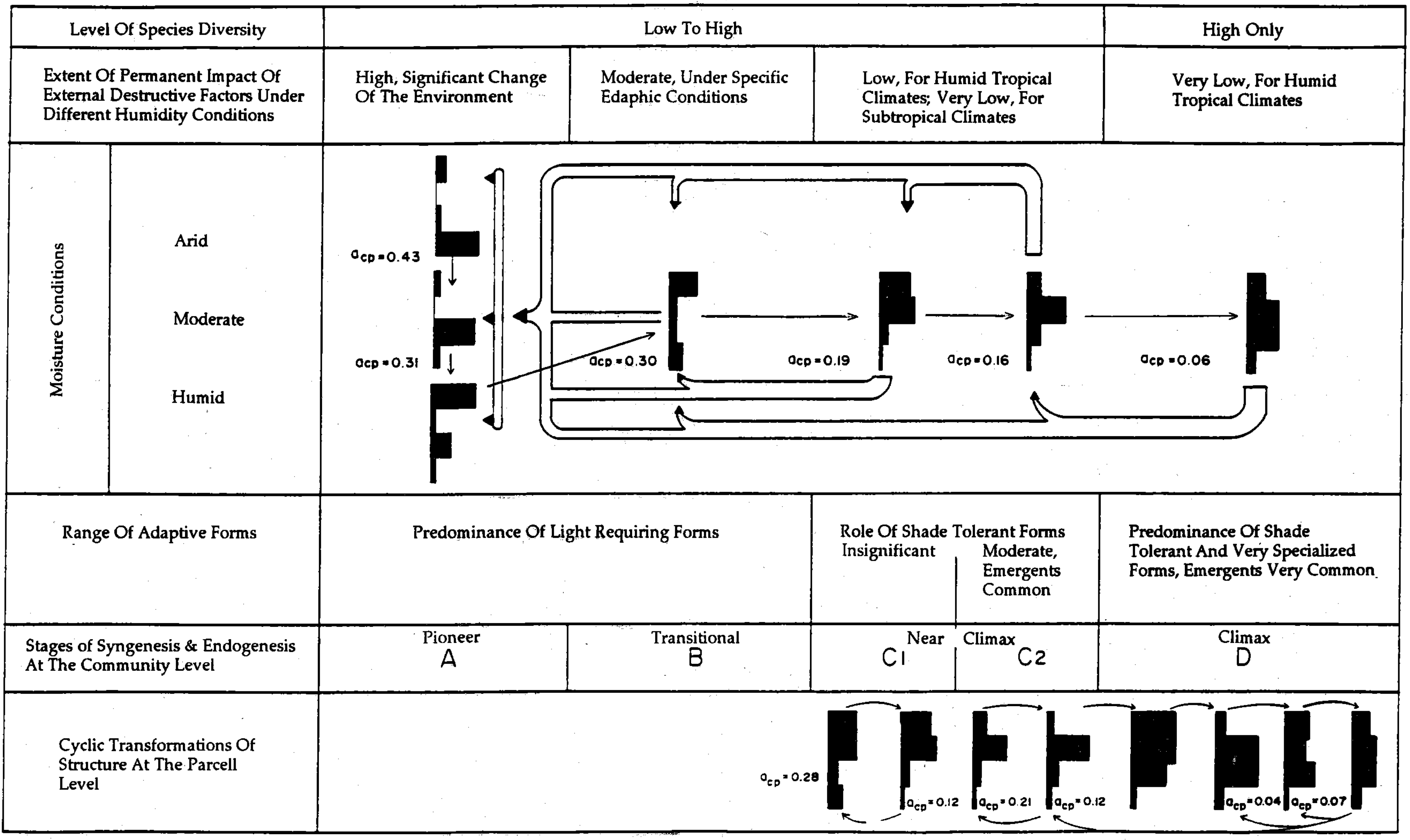


Figure 29. Conditions of intertransformation and stability of vertical stratification of plant communities; a_{cp} = Mean Transparency of Canopy. The double arrows show the possible ways of structural transformations under different disturbance regimes. The solid lines show the ways of self regeneration and the cyclic transformations at the parcel level.

CHAPTER VII. ASPECTS OF THE COMPOSITION AND ESTABLISHMENT OF INSULAR FAUNAL COMMUNITIES[1]

Y. I. CHERNOV

INTRODUCTION

The origin and development of animal communities on islands are related to fundamental ecological and biological questions: the role of migration in the life history of the species, the processes of micro-evolution, adaptive radiation and species formation; the structure and dynamics of closed populations; and the specificity of ecological niches in impoverished communities. A great number of publications are devoted to these questions (Gressitt and Yoshimoto, 1961; MacArthur and Wilson, 1967; Gunter, 1969; Nasimovich, 1973; Carlquist, 1974; Muhlenberg *et al.*, 1977; Voronov and Ignatiev, 1978). In this chapter we present some ideas which amplify or disagree with the generally accepted principles concerning animal communities on islands.

LIMITING FACTORS ON ISLANDS

The ecosystems of small islands develop under somewhat extreme conditions in terms of living space or the area of the habitat, which may be viewed as an environmental resource. From a landscape-geophysical viewpoint, two principal spatially related factors are distinguishable: energy limitation and shortage of moisture. The effects of these two factors on the animal community are different.

Energy availability determines ecosystem structure and function. In situations where energy is limited, this results in the qualitative impoverishment of communities and a weakening of energy-production processes. Under such conditions, a great decrease in the diversity of ecological niches is observed. No adjustments, either morphological, ecological or physiological, can compensate for energy shortage. In a cold climate, due to low diversity and the low intensity of production processes, the domination of individual species increases (Chernov, 1975, 1978), a situation which parallels that found in insular biotic communities.

In contrast, environmental extremes in aridity are relative; even in the most arid landscapes, some water is available in principle. In the process of adaptive evolution, different specializations arise, which help organisms to obtain, store and conserve water. In this regard, moisture shortage is a factor which intensifies morphological evolution and adaptive radiation. Thus, communities forming under arid conditions may exhibit low density and localized distributions, but are frequently characterized by high species diversity.

Shortage of living space which combines the impact of the two specific factors mentioned above has the following effect on the structure of communities. On the one hand, in a limited isolated area the community composition is impoverished, which in turn, leads to an increased density of insular animal populations and to domination of community structure by single species. On the other hand, under conditions of isolation and the availability of "free" ecological niches on islands, the intensity of local adaptive radiation increases. It is important to remember that shortage of space for organisms should not be considered only in terms of the area of a given island. The possibilities for permanent contacts may vary between species: for some, several adjacent islands may constitute the area inhabited by one population, for others - these may function as completely isolated populations.

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[1] Acknowledgments: The data for this chapter were collected during the Sixth voyage of the Research Vessel "Callisto" in 1976-1977. The following colleagues helped in the taxonomic analysis of the data: E.M. Antonova (Lepidoptera); S.I. Golovatch (Diplopoda); L.G. Grishina (Acarina); G.M. Dlussky (Formicidae): A.F. Yemelianov (Homoptera); V. Zherikhin (Myriapoda); I. M. Kerzhner (Heteroptera); O. L. Kryzhanovsky (Coleoptera); T. S. Perel (Lumbricidae); L. Pritykina (Odonata); M. Il Falkovich (Lepidoptera). To all of them the author extends his sincere thanks.

SPECIES IMPOVERISHMENT

No matter where a community develops, its qualitative impoverishment leads to similar ecological consequences. One such consequence is the compensation through increases in single species density for the decrease in species diversity. This is true of both tundra and island communities, which allows one to consider the island ecosystem not as an ecological paradox, but in comparison with other types of ecosystems.

Usually the paucity of island faunas is explained by the fact that colonization is difficult for certain species. The examples of animals and plants that have been introduced to islands by man and successfully established feral populations are often cited as proof of this thesis. However, the question is not answered by such examples since in comparison with the length of time for which most morphospecies persist, the time that these populations of introduced species have existed is extremely short. There are no grounds for believing that such species can continue to exist as long as native species. Secondly, the establishment of feral populations is most often successful on those islands that have been greatly changed by man. Numerous Palaearctic species which have successfully established populations in New Zealand, on Norfolk island, in the Kermadec Archipelago, and elsewhere in the Pacific, inhabit those biotic communities that are strongly or completely modified by man (pastures, meadows, agricultural lands) but are absent or at low frequency in typically local plant communities, where native animal species predominate (Pernetta and Watling, 1979).

Many [different] papers have dwelt upon aspects of disequilibrium, aggregation, dispersion, and the random nature of the fauna of islands, and have accounted for these features in terms of the colonization process and the difficulty of access to such islands. Time of arrival is believed to be important, with the first colonizers supposedly having advantages compared with later migrants, since they have a longer period of time in which to adapt to local environments (Voronov, 1978). If one accepts that in the case of island faunas the settlement process is of fundamental importance, then these aggregated and random distributions will be characteristic features of such faunas. When analyzing the faunal composition of a number of taxonomic groups on some small islands in Oceania, a contrary picture is apparent. The specific characteristics of an island environment are so great that they dominate the biotic composition of the community more strongly than do zonal and regional climatic features, and frequently limit and determine the faunal composition. For example, large vertebrates cannot live on small islands regardless of the island's climate or remoteness.

INSULAR TAXA AND THEIR CHARACTERISTICS

In different taxa of animals there are some groups and species, which when compared with the majority of species, are particularly likely to colonize islands, although it is often impossible to discern any significant advantages to the species concerned. Certain population mechanisms may affect the ability to survive and develop as island forms, and many islands may have endemic representatives of traditional "island" groups of animals, which display a degree of adaptive radiation.

It might be suggested that the possibilities of different animal species colonizing an island are much greater than the possibility of their subsequent establishment of permanent populations. The dispersal abilities of many species, especially invertebrates, are practically limitless within the time span of a species existence. They are capable of crossing any distance and obstacle, as evidenced by the long-distance transfer by the jet stream of many aeroplanktonic insects. There exists no problem for many flying insects and other passively dispersing invertebrates to reach even the remotest parts of the earth, although few of these succeed in establishing island populations. It is unlikely that the island faunas result from chance settlement or according to the principle "the first to come the first to settle". In this respect, our views correlate with those authors who believe that the principal factor in the formation of island faunas is not geographical remoteness, but ecological, i.e. diversity of biotopes and ecological niches (Oulett, 1967; Lack, 1969, 1970; Harris, 1973). Of particular importance are the biological and ecological peculiarities of species which predispose them to establish populations under the specific conditions of small islands; such characteristics have been little studied to date.

When studying the process of the formation of island communities, it is necessary to pay attention to "inherent" factors, such as the peculiarities of island life and the operation of biological processes within a limited, closed area. In qualitatively-impoverished, island ecosystems the ecological adaptability of a species, their ability to occupy different ecological niches and to establish populations in widely different habitats becomes very important. In analyzing the structure of island ecosystems, we frequently encounter a phenomenon which may be called "broadening of ecological niches". Here a single species plays a dominant role in diverse habitats or species associations, displays high ecological plasticity, and on one island may even be represented by several ecological forms (a phenomenon called "superdominance"). Such a feature is also characteristic of other types of communities with impoverished species composition, such as tundra communities. All these factors result in many peculiarities in population and community relationships, and in the species composition of insular floras and faunas.

THE COASTAL COMMUNITY

In considering the specific features of community composition on the small islands of Oceania, the coastal complex seems to be a most important aspect. On small islands the supra-littoral fauna is quite rich due to the fact that the coastal belt occupies a considerable proportion of the islands. These rich, supra-littoral communities of small islands in the tropical zone include diverse forms of many animal groups - shore crabs, molluscs, pseudoscorpions, ants, isopods, amphipods, crickets, diplopods, geophilous insects, spiders, collembolans, Acarinae, lepidopterous and dipterous larvae. In sandy, littoral habitats this complex is richest on the top of the storm-deposited bank, however, the influence of this community is seen far inland, sometimes 100 - 200 m from the shore. Consequently many typically supra-littoral molluscs, crabs and the young of robber crabs are found everywhere on small islands.

The coastal environment is relatively uniform, even under different macro-environmental conditions. It is, for instance, not affected by climate so much as by the proximity of the ocean and wave action, which tend to ameliorate air temperatures and humidity differences. Substratum types and food sources such as algae in the drift debris in these habitats also tend to be quite similar over wide geographic distances. Thus, the geographical distribution of many supra-littoral forms tends to be dominated by these factors rather than by macro-climate. Occupying considerable ranges, such species tend to demonstrate independence of climatic gradients, which should be looked upon as an example of the law of environmental levelling (Chernov, 1974; 1975). The larvae of species of the families Coelopidae, Muscidae, Scatophagidae which feed on rotting algae display such distributions. *Fucomyia frigida F.* and *Fucellia fucorum F.* for example, are found on sea coasts from the Arctic to the south of America and to tropical latitudes of Asia and Australia. These species are also found in the coastal zones of some islands of Oceania. We found *F. fucorum* on Norfolk Island and in the Solomon Islands.

Many species of the supra-littoral complex are purely tropical, but are often extremely widespread with pan-tropical distributions. Others are also found in the subtropical island zone as is the case with many shore crabs, molluscs, littoral amphipods, isopods, and pseudoscorpions - the dominant inhabitants of the supra-littoral of Pacific islands. On almost all the islands studied the same molluscs and pseudoscorpions (*Xenolpium salomonis*) were found in abundance in mangrove thickets, in algal heaps, and in the litter of storm banks.

Sea birds are widespread, inhabiting the coasts of small islands. On the remotest and smallest islands, such as Suwarrow Atoll, sea birds are the only representatives of the avifauna, and all species have extremely wide distributions: for instance, *Phaethon rubricauda*, which is common on all the islands of the Pacific and Indian oceans; *Fregata minor*, which inhabits islands of the tropical belt of all three oceans; *Sula sula*, which lives on islands in both the tropics and subtropics; several species, such as *Gygis alba, Anous stolidus,* and *Sterna fuscata* inhabiting numerous oceanic islands within the warmer zones. The distributions of these species do not reflect any phylogenetic relationship but [reflect] biotope specificity, which retains similar features in different regions and under different climatic conditions.

It should be stressed that the distributional range of species in the coastal complex is not simply due to the ease of dispersal and settlement. Some species are good fliers or are easily dispersed by water (for example planktonic larvae). In contrast, *Sula sula* is not a strong flier over long distances. In some widely distributed flies, the ability to fly is poor (e.g. *Fucomyia frigida*) and some species have shortened wings.

Thus, the coastal fauna of the small islands of Oceania is quite uniform over long distances, a feature which reflects the nature and similarity of this biotope on different islands.

TERRESTRIAL FAUNA

Features of the composition terrestrial fauna of small islands are illustrated by some groups of animals studied during the voyage of the Callisto.

CURCULIONIDAE

The presence in different taxa of traditional "island" groups is well illustrated amongst the Curculionidae. On the small islands of Oceania this huge family is largely represented by species of one tribe Celeuthetini of the subfamily Otiorrhynchinae, which as a result of broad adaptive radiation, have formed numerous endemic genera and species with different morphologies. They inhabit both large archipelagoes within the zone of direct influence of the New Guinea fauna, and remote, small islands and atolls. Species of the genus *Platysimus* are found on islands of Tonga, Samoa, Fiji, and Vanuatu. Our collections show that several species in this genus are the only representatives of the family Curculionidae on Niuafo'ou. On the island of Pio in the Solomon Islands archipelago, we found a species of *Trigonops* as the sole representative of the family Curculionidae. On Bagaman Island we only collected a representative of the typical New Guinea genus of the same tribe, *Apirocalus cornutus* Pasc. In the Fiji Islands the fauna of this group of weevils is quite diverse. Species of the genus *Levoecus* are quite common, as well as species of the tribe, Elytrurini, which is close to Celeuthetini.

HETEROPTERA

Some of the characteristics of the oceanic, weevil fauna are also illustrated in the composition of some groups of Heteroptera. On the isolated islands of Oceania this group of insects is mainly represented by the families Nabidae, Lygaeidae, and Miridae, which are generally small forms. On remote islands there are none of the large predaceous bugs normally found in tropical faunas.

Kerzhner (1979) analyzed the species composition of the Nabidae from the islands of the Pacific, and recognized three species groupings on the basis of their distributional patterns. The first of these groups are representatives of the continental faunas of the Palaearctic, Australian and Palaeotropical regions. These species are mainly found on large islands such as New Zealand and New Caledonia, or in archipelagoes with a large number of small, closely located islands. The second group in this family are complexes of endemic species typical of individual large island systems, such as the Hawaiian, the Marquesas, and the Galapagos archipelagoes. These complexes are largely the result of species radiation in one genus, *Nabis sensu lato.* The third group is denoted by Kerzhner (1979) as an "almost cosmopolitan" element - species of the genus *Tropiconabis,* which colonize even the smallest and most isolated islands.

The genus *Tropiconabis* displays extensive adaptive radiation on different island systems and in the isolated islands and atolls of Oceania. Widespread species are: *T. nigrolineatus* Dist., which inhabits Australia and the whole of Oceania, and *T. capsiformis* Germ., which is common in all tropical and subtropical regions, except the central part of Oceania. On Raoul Island in the Kermadec Archipelago we found great numbers of *T. nigrolineatus.*

Small black bugs of the family Lygaeidae are the most common representatives of Heteroptera on the smallest and most remote islands. Among them, species of the genera *Remaudieriana* and *Pachybrachius* are particularly characteristic of Oceania. On all the small islands visited (Suwarrow, Danger, Niuafo'ou, and Raoul) we found two small transoceanic species, *R. nigripes* Dall and *P. pacificus* Stol. In addition to these two widespread species, Oceania is inhabited by several other representatives of these genera. Except in the case of Suwarrow one or two species were found on all the islands visited.

Bug species in the family Miridae are also quite common on small islands. On Raoul we found three species: the trans-oceanic *Cyrtopellus nicotinianae* Kon., *Tigonotylus dohertyi* Dist., and one species of *Kygoris*; on Danger atoll, *Creontiades pallidifer* Wall. was the only representative of this family. This latter species is widespread throughout the whole of the Oriental Region and are found even on the smallest and remotest islands visited during the expedition. Widespread species with large distributional ranges dominated the fauna.

On the islands close to New Guinea (Louisiades, Bismarcks, Solomons) as well as Fiji, the bug fauna is more diverse and contains both New Guinea faunal elements and numerous local endemics.

Weevils and bugs are comparatively small in size and most are weak fliers. Some of them do not fly at all or use their wings infrequently; passive migration and dispersal predominate amongst such groups. Of the bugs, for example the Lygaeidae, fly infrequently while some species of Nabidae and Miridae fly comparatively well. According to Kerzhner (pers. comm.) *Tropiconabis* species are often caught in elevated traps and are part of the achroplankton.

LEPIDOPTERA

Many day flying Lepidoptera readily form island populations and several genera and species have radiated widely on the islands of the Southwest Pacific. *Precis villida* F. for example, a representative of a genus which replaces the genus *Vanessa* of the Oriental Region in Oceania has many subspecies and forms on different islands. We found this species on Danger Atoll, and on Bagaman and Pio islands. On Danger Atoll the genus was represented by high density populations of *P. villida taitica* Seitz.

Hypolimnas bolina is another example of a widespread species with typical insular forms. It should probably be considered a superspecies complex. On the islands of Oceania this taxon is represented by a multitude of forms, subspecies, and varieties. For instance, on Danger Atoll we met with two sympatric forms of these butterflies - the dark and the light (or to be more precise, reddish) *H. bolina alcmene* Cv. The butterflies *P. villida* and *H. bolina* are extremely widespread on small islands of Oceania, and on some of the islands they are the only representatives of the Lepidoptera.

The Lycaneidae are another widespread and interesting group of butterflies, found on almost all the islands visited including the remotest atolls, where we collected *Jamides bochus* Cr., a blue butterfly that is common from the Himalayas to Australia. On Raoul Island and on Suwarrow Atoll this species is probably, the only species of diurnal butterflies, while on Danger Atoll it is one of only three species. On Niuafo'ou Island, a blue butterfly, *Lycaena* sp., which is an example of a widespread species, demonstrates a tendency to form local populations under different conditions and on islands. The tendency to colonize small and remote islands seems to be a distinctive feature of blue butterflies.

Some groups of Lepidoptera have rich island faunas, but their distribution is mainly limited to large island systems lying in the zone of influence of certain faunal centers of diversity. For instance, there are numerous island forms of the diverse Oriental genus *Euploea.* These black-and-white mottled butterflies are common inhabitants of islands near New Guinea (Louisiade, Solomon and Bismarck Archipelagos). On some islands (Pio and Bagaman) population numbers of these butterflies were the highest we observed. In this genus, *E. eurypon* Hew. was the most abundant and commonly encountered species. On the more remote, smaller islands of Tonga, Samoa and the Cook Islands Archipelagoes, this genus was absent.

The large genera, *Papilio* and *Danais*, are distributed in Oceania in a similar manner; they are diverse and numerous on the archipelagoes close to New Guinea, but to the east their numbers decrease sharply, and they are absent from the greater part of Polynesia. The monarch butterfly, *Danais archippus* F. which makes regular flights over the ocean, reaches only some of the remote islands in the subtropical zone. On Bagaman and Pio islands the large black *Danais alfinoides* F. and the very beautiful swallow-tail butterfly with green spots - *Papilio agamemnon* L. were especially numerous. We also met with these species in Fiji, which is the eastern limit of their distribution.

DRAGONFLIES

Of special interest is the strong and rapid flying dragonfly fauna. On the most isolated islands visited by "Callisto" (Niuafo'ou, Raoul, Suwarrow, and Danger) we identified 10 species of dragonflies. Most of the species inhabiting such islands are widespread species which may also be found in Asia and Africa. For instance, *Ischnura aurora* Br. inhabits all the islands of the Indo-Pacific and those within the Oriental region. It is also found on all the archipelagoes of tropical and subtropical regions and we encountered this species even on remote Suwarrow Atoll. A typical transoceanic species is *Ischnura torresian* Till. which we managed to catch on Raoul and Niuafo'ou. *Orthetrum sabina* Drury, *Macrodiplax cora* Br., *Anax guttatus* Burm., and *Tholimus tillarga* Fabr., which are abundant on many islands of Oceania, are also common throughout the Oriental and Indo-Pacific regions. There are great numbers of them on Niuafo'ou which has favorable conditions for dragonflies; a large expanse of water and a landscape of thin forests with edges and glades suitable for hunting.

Part of the dragonfly fauna of Oceania belongs to regional faunal complexes; among our specimens the Samoan endemic species, *Rhyothemis regia chalcoptilon* Br., turned out to be abundant on Niuafo'ou. A number of species, for example *Aeschna brevistyla* Ramb. and *Hemicordula australiae* Ramb., which we also found on Raoul Island, are characteristic of the fauna of the western part of Oceania near Australia and New Guinea.

We may conclude that on the small, remote islands of Polynesia, the Australian New Guinea element of the dragonfly fauna is rather impoverished with widespread species having a tendency to form island populations dominating the fauna in this region.

ANTS

Ants occupy a special place in the animal world of tropical regions, and as active predators and consumers of "offal" they are extremely numerous on the islands of the western Melanesia. Among them tree ants of the genus *Oecophylla* are notable for their numbers, aggressiveness, and the fact that they "sew" leaves together to form their huge nests. This genus, consisting of only two species, is represented on the by the very widespread *O. smaragdina.* To the east the frequency of *Oecophylla* declines, and on the majority of the small islands of Polynesia, the species is absent. We did not encounter them on Niuafo'ou, Suwarrow and Danger atolls. Other comparatively large ants, such as the tree ant, *Polyrachis* sp., are also found mainly in the western part of Oceania. In Melanesia, *Polyrachis* is numerous on the Louisiade and Solomon islands. On the small islands of eastern Oceania there is a clear tendency towards the "miniaturization" of ant forms, with mainly small and very small species being found in this region. The peculiar *Odonatomachus insularis,* which is black, with long mandibles and emits loud sounds (clicks), is the only medium sized species which is widespread in eastern Melanesia and spreading into Polynesia. We encountered this species on all the tropical islands, except Suwarrow Atoll.

Another feature of the ant fauna of Oceania is a sharp decrease in the numbers of endemic species to the east of Melanesia. On small islands of the Louisiade Archipelago, in the Solomon Islands and in Fiji, the ant fauna is extremely rich, ecologically diverse, and includes many endemic forms. For instance, in our collection from Pio Island, Dlussky (pers. comm.) noted many unique, probably strictly endemic species of *Camponotus, Tetraponer, Iridomyrex* and *Opisthopsis.* For the Polynesian islands, such as the Niuafo'ou and Suwarrow, the picture is different; on the former we discovered widespread pantropical or transoceanic species such as *Odontomachus insularis, Anoplolepis longipes,* and *Pheidole megacephala.* On Suwarrow the ant fauna was composed of small species having widespread tropical distributions: *Olygomyrmex atomus* Em., *Paratrechina bourbonica, Topinoma minutum, Solenopsis geminata,* and *Paratrechina longiconis.* Of these, only *O. atomus* may be considered characteristic of Oceania; the rest are pantropical.

SOIL ARTHOPODS

Data on the distribution of small soil arthropods such as the Arachnida and Apterigota are particularly important in defining the peculiarities of insular faunas. There are sufficient grounds for assuming that differences in the distribution of the species of this complex are at least partially influenced by differences in dispersal abilities. Most small arthropods do not possess adaptations for long distance dispersal and are mainly transported in a passive manner. Unfortunately, the bulk of the material collected by us during the voyage has not been analyzed to date, but preliminary results conform to the patterns discernible in the materials of the larger invertebrate groups discussed above. The following data for two different ecological groups of arachnids, the Pseudoscorpions and Oribatid ticks of the family Galumnidae, are representative of the patterns displayed by soil invertebrates.

The Galumnidae are one of the dominant groups in microarthropod communities: their densities reach 200 specimens per 1 sq. dm., and they may form about one third of all the Acarimorpha in some communities. Their species composition on small islands is interesting; we found six species on Raoul Island, all at low density. Of these, four species are probably undescribed, and endemic to the New Zealand region. One species, *Acrogalumna longiplum* Berl., is a typical cosmopolitan species known from the Holarctic, Australia, and New Zealand, and was the dominant species in most biotopes on this island. It was one of five species found on Niuafo'ou Island and on Suwarrow Atoll. On both of these islands, *Galumna flabelligera* Hamm. was the dominant species in all the biotopes examined. Large numbers of specimens were collected in habitats such as coconut plantations, the various forest types, on lava substrates and in coastal areas. This pantropical species is known from numerous islands of Oceania, as well as South America.

The composition of the pseudoscorpion fauna of the islands shows similar patterns. According to Beier (pers. comm.) our material contains twenty species, many of which are endemic to different island groups in Melanesia. Among them there are also several species such as the transoceanic *Xenolpium salomonis* Beier, *Paraliochthonius vlassicsi* Dad., and *Smeringochernes salomonensis* Beier, which have colonized even the remotest, small islands.

Thus, among small arthropods a similar pattern emerges: namely, the fauna of small islands is composed of certain species and groups which have an increased tendency to form insular populations, and, hence, tend to dominate the invertebrate communities in such locations.

VERTEBRATES

Data on vertebrate distributions collected by the expedition generally conform to the patterns of distribution revealed by various groups of invertebrates. Among the reptiles, geckos and skinks demonstrate a tendency towards the formation of insular races. These lizards are a trophically and dynamically important component in the ecosystems of all the islands of the tropical Pacific. On Suwarrow and Danger atolls these two groups of lizards are the only reptiles present. The skinks (of undetermined taxonomic rank) are of many diverse forms. On the volcanic island of Niuafo'ou we encountered many forms which differed in color, preferred biotope, feeding habits, and other aspects of their ecology. These included large, black, terrestrial species which were camouflaged against the lava substrate covering the island; a green species, the color of leaves, and others with a mottled pattern.[2]

Skinks are excellent climbers and often live in tree hollows. On the smallest islands where there are no other groups of lizards, skinks and to a lesser extent, geckos, display extremely high population densities: on Suwarrow Atoll up to 1,000 specimens per ha. In contrast on New Guinea, where the reptillian fauna is more diverse, the density of individual species are hundreds of times as low.

The avifauna of small islands is impoverished. However, some groups, such as the Megapodiidae, Rallidae and some individual species of parrots and doves, display a remarkably wide distribution and the formation of insular species and races. None of these groups of birds possesses any special migratory abilities, and for some the ability to fly is clearly low. It is most probable that their limited flying abilities and inclination to remain in one location favors the formation of distinctive island populations.

The distribution patterns of birds on the islands of Oceania are similar to that of insects, in particular the Lepidoptera. On islands close to New Guinea, such as the Louisiade and Solomon Islands archipelagoes, the bird fauna is comparatively diverse, variable in species composition and relatively rich, having about two dozen land bird species even on the smallest islands. These faunas are derived from the rich New Guinea avifauna. The avifauna of the Fiji archipelago is also quite rich but many species and whole groups of the New Guinea avifauna are absent. On the largest island of this archipelago, Viti Levu, 55 species of land birds including several local endemics have been recorded. On the 18 km^2 island of Niuafo'ou, situated between the archipelagoes of Fiji and Tonga, there are only eight land birds. In contrast, on Pio in the Solomon Islands, with an area of 2.5 km^2, our expedition recorded 14 nesting species of land birds; on Bagaman Island (8 km^2) in the Louisiade Archipelago, no less than two dozen species were recorded.

The zoogeographical composition of the bird fauna of Niuafo'ou is quite interesting. The avifauna of this island consists of:

1. *Megapodius pritchardii,* which is endemic to this island.
2. *Rallus philippensis,* a species of rail which is widespread in the Pacific from the Philippines to Tasmania. (This poorly flying bird forms numerous island races in Oceania and has a tendency to settle on small, isolated and remote islands. In this respect it is similar to the butterfly, *Hypolimnas bolina,* which is widespread with many insular forms).
3. *Ptilinopus porphyraceus,* a small species of dove which is also a common inhabitant of many islands in Oceania.
4. *Vini australis,* a small parrot endemic to Central Polynesia.
5. *Collocalia spodiopygia* which is widespread on the islands of Oceania.
6. *Pycnonotus cafer,* the introduced Indian red-vented bulbul.
7. *Aplonis tabuensis,* a local subspecies of the Polynesian starling.

It is interesting to note that *M. pritchardii, R. philipensis, V. australis,* and *A. tabuensis* are all distinctly poor fliers while at the same time, display an increased tendency to form distinct island populations. Among this fauna there is not a single representative of the New Guinea avifauna or even of the fauna of Fiji. The species are either local endemics characteristic of Central Polynesia or single islands, or are widespread in Oceania. Of particular interest is the absence on Niuafo'ou of

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[2] The black species is probably *Emoia nigra,* the green species *Emoia concolor* and the mottled species *Emoia trossula* (= *samoensis*). Editors note.

nectar-feeders (Drepanididae), which are common inhabitants of the island archipelagoes in close proximity to New Guinea.

Still further to the east, on the small islands of the Cook Islands Archipelago, land birds are either completely absent or are represented by a single species. On Danger Atoll only one species of land bird (an unidentified dove) was nesting.

Thus, the species composition of many animal groups on small, isolated islands is rather typical and constant, which is probably a reflection the specific habitats and of the relationships between populations in small areas. One gets the impression that the differences in the taxonomic composition of the animal communities of small islands in Oceania are much smaller than the regional peculiarities of continental faunas.

At the same time, different groups of animals display different patterns of distribution on oceanic islands. The data for islands of the tropical zone in Table 26, show a number of patterns reflecting differences in their remoteness from the main centers of faunal diversity. Land birds decline sharply in the number of species while oceanic species constitute an increasing proportion of the avifauna with increasing distance from the source.

The distribution of reptiles is different. Pio, a small island in the Solomon Islands, is covered by a tropical forest, and is subject to the direct influence of the rich New Guinea fauna. Here, in addition to the widespread geckos and skinks, we found snakes, agamid and varanid lizards. On all of the other islands visited the number of species is approximately the same. Even on isolated Suwarrow Atoll which consists of several small islets (motus) only hundreds of meters in diameter, and periodically destroyed by hurricanes, we found three species of skinks and one gecko. Four or five species are most probably the limit of diversity of this group of animals on small isolated islands.

Table 26. Number of species of major animal taxa recorded for islands visited by the research vessel "Callisto".

Taxon	Bagaman & Louisiades Archipelago	Pio, Solomon Islands	Niuafo'ou	Danger Atoll	Suwarrow Atoll	Raoul Island
Sea birds	0	0	1	5	10	9
Land birds	20	17	9	1	?	7
Reptiles	n.d.	7	5	4	3	1
Butterflies	18	4	3	3	1	1
Bugs	n.d.	n.d.	5	4	1	7
Cicadidae	n.d.	10	3	1	1	8
Dragonflies	n.d.	2	9	1	1	5
Diplopods	8	3	3	2	2	2

n.d. = numerous but not determined.

A similar pattern is illustrated by the diplopods. On Bagaman Island near New Guinea, the number of species of this group is high (there are probably many more species than we managed to collect), while on all of the remote and small islands, the number of species of this group is approximately two or three.

The numbers of species of Lepidoptera and Cicadidae show similar patterns. In the Louisiade Archipelago are the representatives of the richer New Guinea fauna; the actual number of species on Bagaman island is probably several times as great as the number we discovered during several days of work. At relatively short distances to the east, the number of species in these groups decreases sharply and continues to decrease with distance from New Guinea. On the remotest islands only the most widespread forms are found. *Exitianus plebeius* Kirk (*Cicadidae*), a transoceanic relative of rice cicada, was the only species discovered on Suwarrow and Danger atolls.

DISCUSSION

In a number of cases a group's species diversity on an island does not depend on its remoteness, but is determined by the biology of the species and the availability of suitable habitats. Dragonflies serve as an example to illustrate this point. On most small islands, dragonfly species are few, due to the lack of water basins suitable for larval development. On islands where water lenses are available (e.g., Niuafo'ou and Raoul), their density and species diversity are both higher.

An analysis of the species composition of different animal groups on the islands of Oceania reveals that maximum species diversity is found in western Melanesia, the faunas on the islands being derived from those of New Guinea and Australia. Although the fauna of eastern Melanesia and of New Zealand is impoverished, local secondary centers of species formation have developed with characteristic endemics related to the New Guinea and Australian faunas. The faunistically impoverished eastern Polynesian section of Oceania is mainly settled by widespread pantropical or polyzonal species with high dispersal abilities.

ANTHROPOGENIC IMPACTS

On remote and small islands the fauna consists of two groups; the widespread transoceanic or pantropical species and representatives of local centers of endemicity. It is commonly believed that some representatives of the first group are accidental anthropogenic introductions, or those which have followed with the change of landscape. In a number of instances some species have been introduced. Species such as the pigeon, *Columba livia*, the mynah birds, *Acridotheres tristis* and *Acridotheres fuscus*, and the muckworm *Eisenia foetida* have spread together with people and at present have occupied many remote islands and archipelagoes. However, despite their ability to occupy anthropogenic biotopes neither the mynahs nor the pigeon have established populations on remote islands where there are no urban settlements.

Several species not so closely associated with people, but with high dispersal abilities have colonized many small and remote islands. Such species are comparatively few, but they emphasize the importance of population-specific characteristics and the importance of the island habitats in the process of colonization and establishment. Examples of such species are, the rail(*Rallus philippensis*); the butterflies (*Jamides bochus, Precis villida,* and *Hypolimnas bolina*); the dragonfly, (*Ischnura aurora*); and the bug (*Tropiconabis nigrolineatus*).

In general, the role of humans in the process of species range extension is often exaggerated. In a number of cases the specificity of the species habitats and its ecological relationships are more important determinant factors in successful establishment of insular populations. The widest ranges are generally displayed by species which are independent of human influence (Chernov, 1975).

In the formation of insular communities the island's landscape and environment, particularly the degree of preservation of primary vegetation plays an important role. True tropical forests characteristic of large equatorial islands are found in western Oceania on the archipelagoes close to New Guinea. To the east, with increasing aridity, typical rainforests are less, and less well developed. On small islands and atolls of the central and eastern parts of Polynesia the plant communities tend to be dominated by screw pine (*Pandanus*) and coconut palms, mangoes and other cultivars. The environment of such islands is by and large an anthropogenic landscape. This feature of the island environment may account for the weak penetration of representatives of the tropical New Guinea fauna to the islands of eastern Oceania.

All of these factors make it difficult to generalize about the formation of island faunas. If we compare Pio and Niuafo'ou, for example, one may note that on Pio there is a typical rainforest fauna, but on Niuafo'ou there is an impoverished, typically insular, Polynesian fauna with a predominance of widespread transoceanic and pantropical species, and some endemics. It is therefore very difficult to decide whether this difference is due to differences in distance from New Guinea or to the specificity of the different environments. On Pio, the equatorial rain forests are largely untouched; on Niuafo'ou the vegetation is partially anthropogenic and partially natural, based on recent lava flows which cover much of the island. In addition, the climate of Niuafo'ou Island is much drier.

These questions touch upon an important general biological problem concerning the role of specialization and generalization, and the ecological plasticity of species under different conditions. Available data suggest that under extreme conditions r-adapted species very often dominate in insular communities with impoverished diversity. Such species are often geographically widespread and/or coastal species, or species with wide ecological tolerances.

The above view is probably of more general significance since one encounters an analog of such relationships when analyzing the fauna of transpolar landscapes (Chernov, 1975). In this region an apparent paradox is observed: the northernmost variants of tundras with very harsh conditions are settled more frequently by widespread forms usually of southern origin rather than by species characteristic of the closest environments, the tundras. Such comparisons support the idea expressed above that questions concerning the formation of animal communities on small islands should be resolved within the general ecological framework of extreme environment problems.

FACTORS AFFECTING FAUNAL COMPOSITION

Different factors involved in the formation of animal communities on small islands are discussed below. Using materials collected during the voyage of the Callisto, the factors are ranked according to their general significance.

DISTANCE FROM FAUNAL CENTER OF DIVERSITY

The role of this factor is best illustrated in a comparison of Norfolk and Raoul islands which lie in the subtropics. There are basic differences between the faunas of these two islands. On Raoul and on the nearby small island of Meyer, *Prosthemadera novaezeelandiae* and *Cyanoramphus novaezeelandiae*, both typical representatives of the New Zealand fauna are the most characteristic and abundant bird species. On Norfolk Island they are absent. The ant fauna of Norfolk is very diverse. It includes *Ponera leae ovulata* Don., *Amblyopone australis caphalotes* Smith, *Pheidole ampla norfolkensis* Wheeler, which are typical derivatives of the Australia fauna. On Raoul there are practically no ants. We only collected one species of the widespread genus *Pachycondyla* close to human settlements. This was probably a recently introduced species and not yet fully naturalized. This observation is in conformity with the extremely low diversity of the New Zealand ant fauna, which is a characteristic feature of this zoogeographical sub-region.

The only species of leaf beetles on Raoul, *Psylliodes solanae* Brown is also a representative of the New Zealand fauna. On Norfolk Island, in contrast, Australian and Melanesian elements are represented (see Medvedev, this volume). Thus, the proximity of these islands to different zoogeographical centers of origin (Australia and New Zealand) results in the basic differences in their faunas, despite their location within the same climatic zone.

The influence of the New Guinea fauna is strongly felt on the islands of the Louisiade Archipelago where speciation is quite intensive. This is well illustrated by the leaf beetle fauna, where all three species collected on Bagaman island are probably endemic to the Louisiades. Of special significance is the discovery of a new species of *Luisiadia*, with unique characteristics. In the Solomon Islands the role of the New Guinea elements is less significant, but the fauna of these islands is undoubtedly derived from New Guinea. The Fiji Islands, where endemism is common, are also greatly influenced by the New Guinea faunal center. On the islands of Samoa and Tonga the influence of the continental fauna is diminished. The widespread transoceanic or pantropical forms predominate and are the only representatives of many groups on more remote small islands.

Thus, from a zoogeographical, viewpoint the possibility of contacts with different faunal centers of origin is of greater importance than the isolation of islands as such. The fauna of oceanic islands reflects the center of origin within whose sphere of influence the island is located. Another aspect of this question is how the specific composition of the fauna changes in the process of formation of animal communities and ecological linkages which are affected by environmental and climatic factors.

ISLAND SIZE

This factor is of a great importance, since it determines the living space and carrying capacity of the environment. The smaller the island, the less diverse the faunal community. At the same time, however, the effect of having a closed area may lead to opposite results: that of concentrating within a single area a greater numbers of species with relatively high population density.

Within a comparable area on a continent or large island the number of individuals of a species would be less. On a small island a naturalist may easily collect all possible species of a certain group not only because they are comparatively few, but also because of the comparatively high population numbers of each species. Insular populations on small islands apparently compensate for the lack of space by maintaining high densities. Consequently the proportion of common species on small islands is greater than on large ones.

CLIMATIC CONDITIONS

When analyzing the mode of formation of insular faunas, there arises the problem of distinguishing between the zonal climatic factors and the influence of subregional climates, which in Oceania are expressed by increasing aridity from west to east. The complexity of this problem is increased by the fact that in the tropics and subtropics the boundaries are often less distinct than in temperate and colder regions.

The materials obtained during the voyage show that there are clear differences between the island faunas of the equatorial and subequatorial zones. The Louisiade and Solomon islands belong to the former and the Fiji and Tonga archipelagoes to the latter. Similar elements in the island communities of the tropics and subtropics are mainly found among the coastal faunas, as for example in the case of the colonial sea birds. This is well illustrated by a comparison of the sea birds nesting on Suwarrow Atoll, the islands of Fiji, Philip Island (Norfolk I.), and on Meyer Island near Raoul. The only difference between the tropics and the subtropics is the absence of frigate birds in the latter. Other differences in faunal composition may be conditioned by environmental and ecological factors such as the island's elevation and the nature of the vegetation. A number of typical sea birds, for example, *Phaeton rubricauda, Sterna fuscata, Anous minutus*, and *Gygis alba* (Table 27) with high population densities nest on both tropical and on subtropical islands despite considerable ecological differences between them. Such breeding is determined by the nature of coastal habitats and reflects the tendency of coastal species to spread into different climatic zones.

In terms of their population dynamics, animal populations on tropical and subtropical islands differ markedly. These differences are especially obvious among the soil fauna. From preliminary counts, the total biomass and population density of microorganisms in the litter and the soil are lowest on humid equatorial islands.

Very low values for population numbers (between 10,000 and 40,000 m^{-2}) and biomass of micro-arthropods are characteristic of the forests of New Guinea and of the Louisiade and Solomon Islands. These indices increase to the south on the tropical islands of Fiji and Tonga, and is even greater on the subtropical islands of Norfolk and Kermadec, where the total biomass of soil invertebrates is almost 200 g m^{-2}.

In contrast, taxonomic diversity decreases from the equator southwards to the subtropics. Within the equatorial-tropical region there is also some increase in quantitative values and a decrease in taxonomic diversity eastwards from New Guinea. It is obvious that this tendency is due not only to climatic changes, but also to the decrease in size and increasing isolation of the islands in the eastern part of the Pacific, where the soil fauna has an obvious fragmented character.

Table 27: Distribution of sea birds on some small islands of the southwest Pacific.

Species	Raoul (Meyer)	Norfolk (Philip)	Suwarrow Atoll	Danger Atoll
Fregata minor	-	-	x	x
Pterodroma solandri	-	x	-	-
Pterodroma neglecta	x	-	-	-
Pterodroma hypoleuca	x	-	-	-
Puffinus pacificus	x	x	-	-
Phaeton rubricauda	x	x	x	-
Sula sula	-	-	x	x
Sula dactylata	x	x	-	-
Sula leucogaster	-	-	x	-
Sterna fuscata	x	x	x	-
Anous minutus	x	x	x	-
Anous stolidus	-	x	x	x
Procelsterna cerulea	x	x	-	-
Gygis alba	x	x	x	x

Note: x = nesting; - = not encountered.

AGE OF ISLAND

Island age exerts a diverse and often indirect influence on faunal composition. In the first place, it determines the possibility of endemic and subspecies formation. Endemic subspecies are found on many islands of the Pacific; for example, the subspecies *Cyanoramphus novaezelandiae cyanurus* is found in the Kermadec islands while *Aplonis tabuensis nestiotes*, a subspecies of the Polynesian starling is found on Niuafo'ou. Island endemic species are also well represented by such species as the megapode, *Megapodius pritchardii* which is endemic to Niuafo'ou, and the parrot, *Vini australis*, which is characteristic of the islands of Central Polynesia, as is the leaf beetle, *Luisiadia tschernovi*.

Naturally, the age of the island also determines the formation of endemic forms indirectly through soil cover, relief and vegetation. There are quite distinct differences for instance between the soil faunas of Raoul and Kermadec. On the former, earth worms of five species are abundant (up to 600 m^{-2}, but averaging 200 m^{-2}). Of these the introduced species, *Lumbricus rubellus* Hoffm., *Allolobophora caliginosa* Sav., *Octolasium cyaneum* Sav., and *Eisenia foetida* Sav., are the most abundant and out-compete the native *Pheretima peregrina* Fl. On Kermadec, earth worms in forests are uncommon, being represented only by subtropical forms of the Australian fauna. The mudworm *Eisenia foetida* is found only in vegetable gardens and in manure near human dwellings.

On Raoul there are only two species of molluscs (one slug and one species of gastropod), while on Norfolk the gastropod and slug fauna is rich, with not less than ten species of several families (Iredale, 1945). As noted above, the ant faunas of these islands are distinctly different. These profound differences cannot be fully explained merely by reference to the centers of origin of the New Guinea and Australian faunas. Rather, the peculiarities of the soil cover which reflect differences in island age, on these islands seem to play a significant role. Norfolk Island is about two million years old, with ancient red-colored laterite-like soils developed on it. In contrast Raoul is only about 2,000 years old (Voronov, *et al.*, 1977), and its soils are young, strongly humified and undoubtedly more favorable for earth worms. At the same time, these conditions are not favorable for supporting a diverse fauna and high density of shelled molluscs.

Niuafo'ou is also interesting in this respect, as a considerable part of its volcanic surface is only about 100 years old. Large areas are covered by recent lava flows. Such a highly dynamic island surface must accelerate micro-evolution and the development of insular forms in some groups of animals. The Scincidae are very diverse here, and some may well be locally adapted, ecological forms. The specific environmental conditions on this island may also account for the establishment of *Megapodius pritchardii*, an endemic species which uses geothermal heat to incubate its eggs.

On the whole, the smaller the island, the less important the role of its age in the formation of the animal community. On small islands, the time factor is distorted by diverse influences of an ecological, climatological and landscape character.

ECOLOGICAL CHARACTERISTICS OF SPECIES

The ecology of a species and its relationships with other species play an important role in the establishment of island faunas. One of the principal aspects of the ecology of animals and plants on islands, is what may be termed "broadening of ecological niches". Due to the low species diversity of the fauna and flora and the absence of certain groups on islands, many individual ecological niches may be filled by single species. In the forests on Pio the major consumer of the litter was a single species of diplopod, while the role of insect predator in the lower canopy was filled by a single species of tiger beetles (Cicindelidae). On Raoul, birds feeding in the tree canopy are represented by one species, *Prosthemadera novaeseelandiae* (family Meliphagidae) which feeds both on the nectar of the only species of tall trees (*Metrosideros kermadecensis*) and on insects; it may also eat the fruits of some cultivated plants. On many small islands omnivorous birds feeding on the soil surface are represented by only one species of either the megapode or rail.

One of the consequences of having single representatives of certain ecological "professions" is extremely high population numbers and a wide habitat distribution of such species when compared to continental or large island communities which have a more complete set of fauna. On Bagaman and Pio the density of the most ecologically important forms - gigantic diplopods, tree ants, tiger beetles, spiders, doves, and parrots - are several orders higher than in the forests of New Guinea, where these groups are represented by a high diversity, but of lower individual density.

The term super-dominance, referring to the characteristic of low species diversity and high individual species density, is applicable here. As noted for the tundra zone by Chernov (1975), population numbers of the only species of earth worm present are greater than in forests where several species are present. On Norfolk the density of terrestrial amphipods in the hay-scented fern litter reaches several thousand m^{-2}, on Suwarrow Atoll, up to 200 skinks are present ha^{-1}, while on Pio there may be up to 10,000 millipedes ha^{-1}. According to our observations in New Guinea such high individual numbers of species of millipedes, lizards, birds, and ants are found only in anthropogenic biotopes, i.e., in communities with an impoverished species composition.

The representation of many ecological "professions" in island ecosystems by single species and the corresponding occupation by one species of a wide spectrum of habitats seems to play a very important role in the establishment of island communities. There is no doubt that the occupation of niches by a single competitive species hinders successful colonization of islands by newcomers, thus maintaining low faunal diversity. This may be considered one of the factors contributing to the structural stability of island communities.

In island ecosystems, selection favors generalist species to the detriment of species diversity. Some species display an increased evolutionary rate and are represented by many forms. Thus despite the poverty of the fauna, such species fill the main ecological niches and cover "the ecological space."

Such factors should be taken into account when considering those instances where species introduced from other zoogeographical regions and natural zones, in particular from the Palearctic and Oriental regions, turn out to be more competitive when compared to the native species and successfully established populations on many islands. The biology of these species seems to reflect inherently "strong" competitive characteristics. In particular, the competitive ability of Palearctic migrants, when compared to subtropical forms from the New Zealand and Australian regions, is probably due to the fact that they evolved under conditions of high competitive intensity within the rich and young Palearctic fauna.

POPULATION DYNAMICS

There are grounds for believing that population fluctuations are quite common in the islands. In isolated populations such processes may lead to the complete extinction of certain forms and such events may be more frequent and correlated with small population size. Such phenomena (known as genetic drift) have been studied in detail in population genetics. There is no doubt that such processes are also important in island populations, where individual forms or species may become extinct due to extreme numerical fluctuations.

Data from the atolls of the Cook Islands Archipelago show that such phenomena are possible. In particular, on Suwarrow Atoll one species of millipede, *Rhinocricus* sp., is very numerous, while on Danger Atoll although we did not catch any living millipedes, we repeatedly found remains of diplopods of a similar size and form in the litter. On Danger Atoll the butterflies, *Hypolimnas bolina* and *Precis villida*, were abundant; they were completely absent on Suwarrow where there were great numbers of two species of Noctuid moth, which were absent on Danger. These differences are not explained in terms of migration since these are widespread forms, inhabiting numerous small and remote islands of the Pacific, and have little difficulty in getting to the most remote fragments of dry land. It is doubtful that these species, having reached the atoll of Suwarrow which is rarely visited by people and periodically destroyed by hurricanes, could not also get to Danger Atoll, which is inhabited. Their periodic extinction on small islands seems a more likely explanation.

BIOTOPE DISTRIBUTION AND MICRO-CLIMATE

There is a general ecological principle that the greater the difference between a species preferred micro-climate and the macro-climate, the more widespread its distribution (Chernov, 1974, 1975). In particular, species of soil invertebrates are usually more widespread than those living on the surface. In addition, smaller species are generally more widely distributed than larger species, since it is easier for small animals to find suitable micro-climatic conditions in larger environments. Such phenomena are undoubtedly important in the formation of island faunas. As an example we have already noted the similarity and widespread nature of the coastal complex of species. This is a consequence of the specific nature and stability of the environmental conditions in coastal biotopes, and the similarity of such conditions under different macro-climatic conditions. One should also bear in mind that the coastal biotopes play a particularly important role in island community structure and that the smaller the island, the greater the importance of coastal biotopes.

In the whole of Oceania, including the smallest and the remotest islands, small skinks and geckos are quite common, while larger reptiles, such as agamids, monitor lizards, and snakes live only on those islands that are situated close to centers of faunal diversity such as New Guinea. Numerous examples of this relationship are found amongst the insects; on Suwarrow and Danger atolls there are none of the omnipresent tree ants of tropical forests. However, the small peculiar *Odontomachus insularis* and small soil dwelling *Solenopsis geminata, Olygomyrmex atomus,* and *Paratrechina bourbonica* are abundant.

It is possible that the settlement of small remote islands by predominantly small species is a reflection of their high dispersal potential. The main factor, however, seems to be the nature of the environment, and its lack of suitable micro-habitats necessary for the survival of larger animals. The larger the organism, the lower the probability of finding a suitable biotic and abiotic environment for its survival. The frequently noted tendency of "dwarfing" of animal species on small islands may reflect this aspect of island biology.

ANTHROPOGENIC IMPACTS

The influence of humans on the fauna of islands is seen in different ways. One important aspect is in the introduction of species. However, the successful establishment of such species depends on the diversity of aboriginal fauna, the biological requirements of the species, and the degree of anthropogenic transformation of the island's environment. The latter is of particular importance on islands, since the creation of biotopes suitable for immigrant species may determine the establishment of feral populations of such species. For example, breeding of cattle on Raoul over a long period and the creation of permanent pastures has resulted in the establishment of a rich fauna of coprophagous Diptera. Some of these are representatives of the New Zealand and Australian faunas, but the majority are widespread. Immigrant birds, such as the starling, *Sturnus vulgaris* and yellow bunting are also associated with pastures on this island.

The anthropogenic meadow community formed on Raoul Island also includes several species of leaf hoppers, leaf bugs and grasshoppers; all of these insects have wide climatic tolerances. On many islands with disturbed habitats which differ from the true climax communities, species from other zoogeographical regions, as well as generally widespread ones, often appear to be more competitive when compared to endemic and native species. There may be several reasons for this; a relatively low diversity of native island fauna, combined with the fact that introduced species are generally adapted to anthropogenic conditions and disturbed landscapes. Where typical or near climax communities are preserved, introduced species do not normally occupy such habitats or are found in them only at low density.

Many economic activities of island people stimulate the formation of particular groups of animal species. For example, a relatively rich complex of animals is often associated with the waste products of copra production. In the heaps of decaying nut shells are different species of lizards, especially geckos, the Polynesian rat, land crabs, earth worms, wood lice, myriapods and others. Furthermore, many species of ants make their nests in empty shells of rotten nuts.

On all of the islands settled by people, including the remotest atolls, the fauna of symbiotic dipterans is quite abundant. The larvae of these species inhabit excrement, food wastes, and corpses. Many of these species are representatives of the local tropical or subtropical fauna, but there are also cosmopolitan ones such as the typhoid fly, and the gray redback fly. In warmer climates the relationship between symbiotic flies and human habitation decreases; such species are widely distributed and occur in natural habitats far beyond the limits of settlements in the islands visited. Some species of Diptera are also abundant on uninhabited islands.

Of great interest is the animal population of uncultivated areas, in particular the communities of small soil animals, which can be accurately counted and whose community structure reflects the merest nuances of changes in habitat chemistry, the biotic environment, and physical factors. The study of this community should be considered particularly important for future work.

CHAPTER VIII. THE ANIMAL COMMUNITIES OF ISLAND ECOSYSTEMS

R. I. ZLOTIN

INTRODUCTION

Studies of the organization of island ecosystems and their animal populations undertaken during the sixth voyage of the Research Vessel "Callisto" included the examination of two sets of questions. The first involved examination of the structure and functioning of ecosystems in tropical latitudes, which are the oldest, most complex and highly evolved of all communities. According to UNESCO, ecosystems of the tropics occupy 37% of the total continental area, and over half of them are humid tropical communities. The island ecosystems of Southwest Oceania belong to this type.

At present there have been few studies of the organization of tropical ecosystems and their animal populations. Information on the population structure of most animal groups is available only for a small number of tropocal communities, and in the Soviet literature there is practically no information on this subject

Knowledge of tropical communities allows the evaluation of the younger ecosystems of temperate latitudes, from the broader perspective and the methodology of comparative geography, in order to determine those mechanisms that regulate community stability.

The second set of problems includes examination of the role of such factors as origin, age, lithological-geomorphological properties, island size, distance from continents and large islands, latitudinal and regional location, frequency of destructive abiotic events, and the influence of people and domestic animals on the structure and composition of the animal communities. Such questions, comprised part of the research program of the sixth "Callisto" voyage. The answers to these questions are valuable in determining the optimal utilization and conservation of small island ecosystems.

RESULTS

HABITATS AND ISLANDS

Background information on the islands visited, including their age, origin, geological and geomorphological peculiarities, soils, and vegetation cover is given elsewhere in this volume. Table 28 summarizes such information for those ecosystems where animal ecological studies were made. The origin and age of an island are important features in differentiating between ecosystems, and it will be shown below that these factors determine the principal features of the structure and functioning of animal communities, as well as the biota as a whole.

ANIMAL COMMUNITIES ON THE GEOLOGICALLY OLDER ISLANDS

The animal communities of the ancient, volcanic and sedimentary islands will be described first as specific "reference points" in the analysis of insular biotic communities. This group includes volcanic and sedimentary islands which are hundreds of thousands through millions of years old, in contrast to the raised coral islands (high atolls) which are tens of thousands of years old. Ecosystems on the older islands have a mature "tropical" profile of strongly weathered and leached soils with a poor absorption complex (Targulian and Yelpatievsky, 1979). Red and brown ferrallitic and ferrasiallitic soils derived from ancient volcanic ashes on these islands contrast sharply with ferrallitic-carbonate soils of high atolls which are oligotrophic and generally unsuitable for many organisms.

Table 28. Typological characteristics of the island ecosystems studied.

Age	Origin	Soils	Vegetation	Island
Ancient	Sedimentary and Volcanic	Red ferralitic	Tropical Primary Rainforest	New Guinea Viti Levu Bagaman
			Secondary Forest	Norfolk
		Brown Ferrasiallitic	Secondary Forest	Bagaman
		Humic-brown & Brown	Tropical Rainforest	Bagaman
		Humic-brown Gley	Tropical Savannah	Bagaman
	Raised Coral	Red Ferralitic-carbonate	Tropical Rainforest	Pio
Young	Volcanic	Soft Humic	Tropical Rainforest	Niuafo’ou
		Al-Fe-humic	Subtropical Evergreen Forest	Raoul
		Dark Gray-humic	Subtropical Evergreen Forest	Raoul
	Coral (Low)	Humic-carbonate Rock Debris, Sands	Open Canopy Forest	Suwarrow & Pukapuka Atolls
		Bog Soils Al-Fe-humic-carbonate	Tropical Forest	Suwarrow & Pukapuka Atolls

THE SOIL MESOFAUNA

All older islands have a soil mesofauna of invertebrates of similar structure and level of total abundance (Table 29). The numbers of invertebrates vary from 100 to 500 m^{-2} (average about 300 m^{-2}), and biomass of between 24 and 39 g m^{-2} live weight. Isopoda (wood lice) predominate numerically, followed by oligochaetes, (megascolecites). In our collections the length of the latter reached 50 cm, the thickness - 1.5 or 2 cm. Numerous larvae of may beetles, darkling beetles, ground beetles, together with the larvae of Diptera, of true cicadas and crickets, small molluscs and millepedes were also encountered.

Earthworms formed the largest part of the mesofaunal biomass (over 90% of the total) at all sites. The minimum biomass (24 g m^{-2}) was found on Bagaman in a *Themeda* sp. savannah ecosystem. The maximum biomass of 38.6 g m^{-2} was found also on Bagaman on a slope covered by secondary forest.

All live animals were found in the upper layer of soil (between 0 and 5 cm). None were encountered deeper than 15 cm, with the exception of the larvae of cicadas and may beetles, whose tunnels stretched up to 50 or 60 cm in depth.

THE SOIL MICROFAUNA

Included in the soil microfauna are representatives of three groups of organisms of different sizes and systematic affiliations which required special methods for their quantification. These were:

1. Nematode worms together with Tardigrada, Rotatoria, Ostracoda, small larvae of Diptera (Nematocera).

2. Enchytraeidae.

3. Microarthropods - ticks, myriapods, lower insects, etc.

The abundance of free living nematodes varied greatly and is presented in Table 30. The maximum numbers and biomass were found in tropical rainforests on Pio Island while the minimum was found in a similar ecosystem on Viti Levu, Fiji.

Tardigrada and Rotatoria were encountered mainly in ecosystems where the numbers of nematodes and Enchytraeidae were comparatively low. There were no Enchytraeidae on Bagaman, although the other two taxa were collected. On other islands the biomass of enchytraeids exceeded that of nematodes. A maximum biomass of Enchytraeidae amounting to 23 g m^{-2} was found on Pio.

Worms were not evenly distributed in the soil profile. Enchytraeidae were found only in the upper 10-cm, while nematodes were found down to a depth between 50 and 70 cm, with 50% of their total numbers being found between 0 to 5 cm in depth.

The composition and numerical abundance of the soil microarthropod community is surprisingly high as illustrated by the data in Table 31. It can be seen from this table that the biomass of microarthropods is dominated by six or seven taxa: beetles, ticks, ants, lepidopterous larvae, spiders, and Miriapoda. The species composition of these co-dominant groups of microarthropods is also very diverse, but between three to six species generally form the bulk of each taxon.

In terms of the vertical distribution of microarthropods about 90% are characteristically found between 0 and 10 cm depth, with between 70 and 80% of all arthropoda occurring between 0 and 5 cm.

A major feature of the distribution of the soil fauna in these ecosystems is the existence of two zones of animal abundance and an intermediate zone between them. These zones are associated with the distribution of the tallest emergent trees, essentially near the trunks and among the buttresses, or above

Table 29. Abundance of soil mesofauna in the ecosystems of ancient islands (m^{-1}).

Mesofauna Groups	Number of Specimens							Biomass (in mg)						
Plot Number:	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Megascolecidae	200	35	120	6	99	64	80	30000	37060	30000	23500	24310	21150	--
Isopoda		+	50	60	--	112	220	+	+	250	300	--	800	1320
Coleoptera	15	50	15	+	5	70	+	200	900	150	+	200	3280	--
Cidadidae	--	3	2	--	5	+	+	--	70	50	--	180	+	--
Chilopoda	20	15	6	+	5	25	32	150	20	10	+	10	150	30
Others	35	30	6	100	30	55	--	300	400	20	500	330	720	--

Table 30. The abundance of nematodes, Tardigrada, Rotatoria and Enchytraeidae in ecosystems of ancient islands (No m^{-2})_

Island And Habitat		Nematodes	Tardigrada	Rotatoria	Enchytraeidae
Bagaman, Rainforest	Nos 000's	790	800	+	--
	Weight mg	658	480	+	--
Bagaman, Savannah	Nos 000's	1070	--	--	--
	Weight mg	283	--	--	--
Viti Levu, Rainforest	Nos 000's	582	--	--	22
	Weight mg	95	--	--	4,200
Norfolk, Secondary Evergreen Forest	Nos 000's	720	--	340	44
	Weight mg	300	--	340	3,000
Pio, Rainforest	Nos 000's	4,184	--	+	233
	Weight mg	1,722	--	+	23,000

Note: + = Present in insignificant numbers.

Table 31. The density and biomass of soil microarthropods in the forest ecosystems of two ancient islands of the Southwest Pacific.

	Viti Levu, Fiji Lower Montane Rainforest		Pio, Solomon Islands Rainforest On The Highest Highest Terrace	
Taxa	Density (N/m^2)	Biomass (mg/m^2)	Density (N/m^2)	Biomass (mg/m^2)
Collembola	8,500	310	9,200	170
Acarina	22,850	145	34,600	552
Formicidae	2,300	920	2,000	820
Coleoptera	570	360	810	500
Lepidoptera, Larvae	400	800	40	100
Araneida	350	350	25	25
Homoptera	350	60	200	34
Hemiptera	100	30	50	15
Chilopoda	100	30	230	70
Diplura	300	60	160	30
Symphyla	600	60	550	55
Pauropoda	300	30	320	32
Diptera, Larvae	250	35	230	40
Hymenoptera	550	45	20	6
Isopoda	50	50	30	30
Others	815	82	345	45
Total:	48,385	3,357	48,800	2,524

the ground roots where plant debris accumulates forming a comparatively thick litter layer.

The numbers of invertebrates are highest in this zone, whose radius reaches up to 3 m. Towards the periphery of the crown, the litter layer thins out and the abundance of soil animals decreases. The second zone includes areas between the crowns of the emergent trees. In this zone the abundance of animals is 1.5 to 4 times lower than the trunk area.

SURFACE INVERTEBRATES

These are inhabitants of the soil surface including litter, grass and tree trunks. In addition to the soil meso- and microfauna, a group of arthropods are found in association with the surface litter. Counts of these animals were made in the tropical rain forests of New Guinea, Bagaman, and Pio; and the number of specimens crossing a 1-meter line during one day were also determined. This index reflects the mobility of the surface arthropods (Table 32).

Ants of 2 or 3 species and beetles were the dominant forms in this survey. Beetles were represented by one or two species of Curculionidae, Carabidae, Lampiridae, Staphilinidae, and Scarabaeidae, while other arthropods were represented by single specimens. The comparatively high number of juvenile crickets on Pio and diplopods on Bagaman may reflect a seasonal pattern of reproduction for these species.

The grassy *Themeda* habitat on Bagaman was mainly inhabited by savannah species which were absent under the forest canopy. The following numbers of arthropods were found m^{-2} in this habitat:

Herbivores -	Halticinae, 5; Cicadodea, 3; Lygaeidae, 3; Acrididae, 0.5.
Carnivores -	spiders, 3; ants, 2; Tromidiidae, 2; Chacidodae, 2; crickets (Tettigoniidae) 1.

In addition 25 specimens m^{-2} having a live weight of 75 mg but with indeterminate trophic status were also found.

It is notable that all surface arthropods were of small size: the mean weight of the litter forms was between 3 and 5 mg, and for the grassland species, 3 mg. Some data concerning arboreal communities were obtained through visual observation and collection of invertebrates on the lower branches of trees, and an assessment of herbivore damage and defoliation (on Pio island only). On most islands we collected the meso and microfauna of epiphytes.

Table 32. Number of individuals of different taxa crossing a 1 meter line day[1].

Taxon	New Guinea	Bagaman	Pio
Formicidae	16	24	14
Coleoptera	12	4	2
Isopoda	6	8	-
Crylloidea	2	6	40
Blattodea	2	-	-
Araneida	2	-	2
Dermaptera	2	-	-
Diplopoda	-	12	-
Thysanura	-	-	2
Total	42	54	60

The invertebrate inhabitants of the tree canopy were not numerous. On leaf surfaces there were larvae of Lepidoptera (mainly Geometridae, Noctuidae, and Microlepidoptera), Homoptera, and Heteroptera; among predators there was a predominance of ants, in particular *Oecophylla* which build hanging nests of green leaves.

Visual estimation of leaf damage on Pio showed maximum damage/defoliation in the upper story and less damage in the lower and middle stories. The greatest damage was done to leaves at the end of branches. In the upper story, up to 80% of all leaves had traces of damage. The mean loss of leaf biomass was up to 30%, with individual leaves having lost up to 60 or 70% of their total area.

The mean indices of damage for the canopy layers as a whole are as follows:

1. The upper story - 60% of all the leaves damaged with 15% of their total mass and surface destroyed.
2. The middle story - 40 or 50% of all the leaves damaged with between 5 and 10% of their total mass and surface destroyed.
3. The lower story - 20 or 30% of all the leaves damaged with up to 5% of their total mass and surface destroyed.

Termite nests were found in the lower tree trunks and the covered galleries of these insects ran between the tree-tops and the dead trunks of fallen trees. In the lower montane, primary rainforest of Viti Levu the mean biomass (live weight) termites was about 2 kg ha^{-1}.

The epiphytic micro-habitats were dominated by similar groups of invertebrates as found in the leaf litter. The proportion of Thysanura was greater, with higher numbers of large pigmented forms. The species diversity and the general abundance of the epiphytic microfauna were lower than in the soil and litter. Amongst the mesofauna, large cockroaches, crickets and diplopods were prevalent. In the epiphytic fern *Asplenium nidus*, growing at tree heights between 2 and 7 m, were found several specimens of Julid diplopods 12 to 20 cm in length; their feces filled up to 40% of the volume of the epiphyte's peaty mass. These animals consume strongly lignified materials.

VERTEBRATE ANIMALS

Of the vertebrates only reptiles were quantitatively estimated. The abundance of birds was estimated visually and the estimates converted to numbers and biomass. In the estimation of mammal abundance, evidence of their activity was also taken into account.

The tropical rain forests of the geologically older islands have particular groups of bird species. The density and biomass (tens of g ha^{-1}) are extremely low with frugivorous and insectivorous forms predominating.

The mammalian fauna is impoverished. It includes rodents, and frugivorous and insectivorous bats. On the tropical islands of Oceania which are not rich in species (Darlington, 1958), the biomass of mammals is low.

The distribution of amphibians on the islands is largely determined by the availability of fresh water. On large, old islands such as New Guinea and Viti Levu, with abundant natural and man-made surface water bodies, the introduced cane toad, *Bufo marinus* is widespread. It was introduced from Central America as a biological control agent of sugar cane pests. On small islands without surface water, *Bufo marinus* and other amphibians are generally absent.

A species of frog, probably of the family Hylidae[1] was discovered on Pio. Its population numbers were low. During the two days of study on the island, only three specimens were seen, but unfortunately, not collected.

From our data most of the reptiles on the older islands were lizards of the family Scincidae. On small islands the abundance of skinks, represented by two or three species, varied from 0.3 to 10 100 m^{-2}, with mean values of density in all habitats being between 2 and 4 per 100 m^{2}. We noticed a decrease in the

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[1] This is almost certainly a species of *Platymantis*, a genus in the family Ranidae which is morphologically convergent with the Hylidae. Editors' note.

abundance of this group of lizards with an increase in the islands' age and size (judging from data based on Pio, Bagaman, Viti Levu, and New Guinea).

Gekkonidae are also quite common on large islands. These are usually nocturnal, secretive, and being arboreal, are often associated with epiphytes, especially the "bird's nest" fern. Several species of gekkos were discovered, with densities somewhat similar to those of skinks.

On the islands of Bagaman and Pio we found large monitor lizards (*Varanus* sp.). The iguanid lizard, *Brachylophus fasciatus* and the small (70 cm long) python, *Candoia bibronii*, were also quite common on Pio. Both the iguanid and the python are arboreal and were previously thought to be endemic to Fiji and Tonga.

ANIMAL COMMUNITIES OF GEOLOGICALLY YOUNG ISLANDS

Both volcanic and coral islands with ages in hundreds or a few thousands of years are classed as young islands. Volcanic soils (andosols) form on islands of volcanic origin, while atolls are characterized by carbonate rock-debris-sandy and bog soils (Table 28). The volcanic soils developed on andesite-basalt pyroclasts are generally fertile, while the coral sands are extremely low in nutrients and have poor water retention properties.

SOIL MESOFAUNA

The communities of soil mesofauna may be divided into two groups (Table 33). The volcanic islands have high mesofaunal population densities and biomass, while the corresponding indices for the atolls are approximately one order of magnitude lower. The maximum biomass, recorded in forest ecosystems dominated by *Metrosideros kermadecensis* on Raoul, was between 100 and 170 g m^{-2}. The mean biomass of the soil mesofauna in the tropical forests of Niuafo'ou was between 55 and 75 g m^{-2} and the minimum of about 6 g m^{-2}, was encountered on Suwarrow and Pukapuka atolls.

In addition to coconut palms, the low atolls are characterized by natural growths of *Pisonia* (*Pisonia grandis*), which are generally small in area and occupy the depressions in the central part of the island. Under the *Pisonia*, bog soils are formed with a thick peaty litter weighing up to 2,500 g m^{-2}. In close proximity to the *Pisonia* trunks, the mass of mesofauna was three times as much, and under the crown 5 m from the trunk, twice as high as in the nearby coconut stands.

On the volcanic islands, oligochaete worms dominated in both numbers and biomass; on Niuafo'ou, the Megascolecidae and on Raoul, the Megascolecidae and four species of Lumbricidae introduced from New Zealand (Watt, 1975). On the atolls, Isopoda were co-dominant with Megascolecidae worms.

Other groups of invertebrate mesofauna included Cicadidae, molluscs, diplopods and chilopods, although these groups were not numerous. Larvae of Pyralidae were quite common in the *Pisonia* forests. In general these invertebrates were concentrated in the upper horizons of the soil to depths between 5 and 10 cm.

SOIL MICROFAUNA

The distribution and abundance of free living soil nematodes and Enchytreidae in the ecosystems of young islands displays the same general pattern as the mesofauna (Table 34). The highest numbers and biomass of nematodes (1,400,000 to 2,100,000 m^{-2} and 0.6 to 1.2 g m^{-2}) are found on the volcanic islands and on the atolls under *Pisonia* (4,000,000 through 6,000,00 m^{-2} and 1.3 through 1.8 g m^{-2}). The smallest numbers and biomass were encountered on the atolls in sandy soils under palm trees (1,100,000 m^{-2} and 0.2 g m^{-2}).

Enchytreidae are extremely abundant in the volcanic forest soils of Raoul. At higher altitudes the

Table 33. The abundance of soil mesofauna in the ecosystems of young islands (Nos m^{-1})

Taxa	Numbers Of Individuals per m^2								Fresh Weight (mg/m^2)							
Location	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
Oligochaeta	452	536	576	368	138	8	40	36	100,320	130,400	164,480	14,400	54,450	2,500	15,000	10,400
Isopoda	40	40	20	10	6	25	450	100	320	320	160	80	500	200	3,200	800
Diplopoda	15	64	354	–	–	+	+	+	225	100	520	–	–	+	+	+
Cicadodea	–	3	30	3	5	–	–	–	–	40	60	200	300	–	–	–
Mollusca	10	22	10	+	+	+	+	+	50	110	50	+	+	+	+	+
Chilopoda	+	+	+	3	15	2	10	8	+	+	+	30	140	20	80	60
Others	45	10	40	4	7	5	50	35	150	140	250	35	370	80	150	190
Totals	562	675	1030	388	191	40	550	179	101,065	131,110	165,520	74,745	55,310	2,800	18,430	11,450

Legend

+ = Presence in the counts of single specimens.

1 Raoul; primary everygreen subtropical forest at 480 m altitude on a flat slope of eastern exposure.

2 Raoul; around 350 m altitude on the same slope.

3 Raoul; around 200 m altitude on the same slope.

4 Niuafo'ou; secondary tropical forest dominated by coconut palms, on a slope of northwest exposure;

5 Niuafo'ou; primary tropical forest on the same slope.

6 Suwarrow Atoll; natural stand of coconut and *Pandanus*, in the central part of a motu.

7 Suwarrow and Pukapuka atolls; natural growth of *Pisonia grandis*, near a *Pisonia* trunk.

8 Suwarrow and Pukapuka atolls; natural growth of *Pisonia grandis*, 5 m from the trunk.

Table 34. The density (Number x 1000 m^{-2}) and biomass (mg m^{-2}) of nematodes, Enchytraeida, Rotifera, and dipterous (Nematocera) larvae in the ecosystems of young islands.

Island & Ecosystem		Nematodes	Enchytraeidae	Rotifera	Diptera
Raoul					
High Altitude Forest	Nos	2,080	123,500	--	--
	Weight	1,275	145	--	--
Mid-altitude Forest	Nos	1,830	38,800	--	--
	Weight	990	80	--	--
Low Altitude Forest	Nos	1,920	8,600	--	--
	Weight	631	30	--	--
Niuafo'ou					
Rainforest	Nos	1,355	--	--	--
	Weight	900	--	--	--
Suwarrow					
Tropical Forest	Nos	1,106	3,600	--	--
	Weight	220	60	--	--
Pukapuka					
Rainforest	Nos	4,340	76,200	140	840
	Weight	1,830	305	14	168,000
Rainforest	Nos	5,800	25,600	350	9
	Weight	1,320	100	35	1,800

biomass of these worms was greater than that of the earthworms (up to 76 g m^{-2}).

The larvae of nematoceran Diptera were abundant (biomass up to 162 g m^{-2}), a feature also characteristic of temperate zone bog soils. The sandy soils under palm trees were distinguished by the lowest biomass of enchytraeids (4 g m^{-2}).

The worms and the Dipterous larvae in the ecosystems of young islands are clearly associated with the surface horizon of the soil (0 through 5 cm).

To date, only the soil microarthropods from the atolls have been examined in some detail (Table 35). The total abundance of microarthropods in volcanic soils, although not yet fully analyzed is greater, probably weighing between 10 and 20 g m^{-2}, and on Raoul may reach several tens of grammes.

The features common to all communities of soil invertebrates in the ecosystems of young islands are as follows: relatively low species diversity, with some species dominating the whole community; high total biomass on volcanic islands and low total biomass on atolls; and a distinct spatial heterogeneity of soil animals on atolls.

SURFACE INVERTEBRATES

The surface active arthropod community on young islands includes cockroaches, crickets, ants, and diplopods. The density of these invertebrates is low, as measured by the number of individuals crossing a one meter line each day. On the volcanic islands several dozens of specimens crossed such a line but fewer than ten specimens did so on low atolls. On the atolls hermit crabs and coconut crabs (*Birgus latro*) are the dominant surface active species; their total biomass is approximately 3,100 mg m^{-2}.

The herb layer of a closed canopy forest is insignificant, averaging 5% of the projective cover. Consequently the community of invertebrate herbivores is represented by few bugs, Cicadidae, Microlepidoptera, and spiders. The herbivores living on hard-leaved species such as palm trees and *Pandanus* were few, in contrast to the evergreen forests of *Metrosideros kermadecensis* on Raoul which were considerably damaged. On average about 40% of the leaves in the crown was damaged. The damage was mainly caused by pyralid leafminers which accounted for 60 to 90% of all damage. In addition there were necrotic spots left by hemipteroid insects (bugs, cicadas, and aphids) which accounted for 10 to 40% of all damage. The number of herbivores on *Metrosideros kermadecensis* was low. Thus leaf surface losses were around 15%. The damage to soft-leaved tree species (Leguminosae) on tropical, volcanic islands and to *Pisonia* on the atolls was also relatively insignificant.

On Suwarrow Atoll and to a lesser degree, on Pukapuka Atoll there was a high density of Lepidopterous larvae (Noctuidae), which had caused extensive damage to the leaves of *Pemphis* sp. Thus it was difficult to choose an undamaged herbarium sample.

On young islands there were few colonies of tree ants or termites. The invertebrates of epiphytes, including cockroaches, wood lice, and crickets were similar to those of old islands.

Table 35. The abundance and biomass of soil microarthropods in the ecosystems of low atolls. Abundance expressed as Numbers per m^2, and biomass in mg per m^2.

Island	Suwarrow Atoll		Suwarrow And Pukapuka Atolls			
Ecosystem	Coconut & *Pandanus* Forests, Centre Of Motu		Near *Pisonia* Trunks		Under *Pisonia* Canopy 5 m From Trunk	
Taxon	Nos	Mass	Nos	Mass	Nos	Mass
Acarina	10,000	128	498,500	17,000	724,150	102,500
Collembola	3,200	68	118,000	3,450	84,600	2,855
Formicidae	550	220	30,900	12,400	2,000	800
Diptera, Larvae	250	40	9,500	1,450	1,950	280
Lepidoptera, Larvae	150	550	4,500	8,100	800	1,600
Coleoptera	650	400	19,500	11,300	800	480
Pauropoda	2,220	200	2,700	270	200	20
Chilopoda	110	33	100	30	600	180
Symphyla	30	3	2,000	200	3,600	360
Campodea	--	--	250	50	1,000	200
Diplopoda	330	230	7,500	3,100	14,200	5,680
Others	660	137	3,500	300	1,750	345
Total	17,950	2,009	696,450	57,650	835,650	23,050

VERTEBRATE ANIMALS

Reptiles were the most common vertebrates on small, young islands, with mammals being represented only by the Polynesian rat, *Rattus exulans*, and introduced species such as feral goats and cats (Raoul), the Norway rat (on many islands) and rabbits. The total biomass of mammals may reach 0.5 kg ha^{-1} while the mean values was about 150 g ha^{-1}.

The bird communities of young islands include passerines, parrots, and pigeons, living permanently on the islands, and members of the Laridae, Pelecaniformes, and Procellariiformes, which only nest on the islands but feed at sea. The species diversity of terrestrial birds was not great: in the tropical forest on Niuafo'ou, we recorded only 7 species; in the evergreen forests of Raoul only two species (*Prosthemadera novaeseelandiae* and *Cyanoramphus novaezelandiae*); in anthropogenic habitats however, introduced species are abundant (Watt, 1975) and included the starling, *Turdus philomelos* and *T. merula*. On young coral islands, only the white-eye *Zosterops* was observed. The biomass of the "terrestrial" birds was between 10 and 20 g ha^{-1}.

The most characteristic shore birds, which nest in forest ecosystems, were *Anous, Gygis, Sula* and *Fregata*. On the atolls, the numbers of these birds are greatest in *Pisonia* forests numbering between 1,000 and 2,000 ha^{-1} and weighing up to 600 kg ha^{-1}. Colonial nesting of *Anous, Gygis* and *Sula* in *Pisonia* trees, combined with the *Pisonia* litter, leads to the formation bog soils in moist habitats.

On average there were about 50 kg of sea bird biomass per hectare in the forested areas of atolls, of which *Gygis alba* formed 10%. In addition to feeding on fish, this species also feeds on skinks.

Only skinks (between 2 and 4 species) and gekkos (1 or 2 species) were found on small islands. Their maximum abundance was in *Pisonia* forests - up to 600 ha^{-1} (1.0 through 1.2 kg ha^{-1}). Among palm trees on atolls the abundance was around 0.1 kg ha^{-1}, while in the tropical forests of Niuafo'ou it was 0.25 kg ha^{-1}. Reptiles have not been found at all on the islands of the Kermadec Archipelago (Watt, 1974).

Table 36 presents a summary of the animal communities of typical ecosystems in the islands. Regardless of latitude (tropical, subtropical) or origin (volcanoes, atolls), the ecosystems of ancient islands were characterized by a similar total animal biomass (about 100 kg ha^{-1}, dry weight). This similarity in the biomass suggests that climatic factors have little impact on the animal biomass of ancient islands.

Animal communities on old islands have a similar structure: the fauna is very diverse although the biomass is concentrated in the worms (Megascolecidae) which inhabit the soil down to a depth of 10 cm. Another feature is the importance of invertebrates, as vertebrates accounted for only 0.1 through 1.3% of the total animal biomass. In some places between 2 and 4%, and up to 15%, of the total animal biomass was concentrated in the tree canopy and in epiphytic microhabitats.

The trophic structure of the ecosystems of ancient islands was characterized by the predominance of saprophytic animals, a comparatively high proportion of predatory species (2 through 5%), and a low proportion of herbivores. The relatively high proportion of herbivores on Norfolk Island (11.3%) is explained by the presence of numerous Scarabeid larvae.

These features of the animal communities on ancient islands are shared with tropical rain forests of continental areas (see Odum, 1971; Medina and Golley, 1974; Fittkau and Klinge, 1973). Of particular interest is the low total animal biomass which in tropical rain forest on continents and islands is 2 or 3 times as low as in the forest ecosystems of the temperate belt. In contrast primary production in the tropics is several times as high as in the temperate latitudes. In the temperate belt a number of ecosystems show a strong positive correlation between the amounts of the total animal biomass and primary production (Zlotin and Khodashova, 1976; Zlotin, 1977). The tropical data however do not appear to fit this correlation.

The disproportionate relationship between plant and animal biomass in the tropics may be related to the importance of the decomposer food chain (microscopic fungi-invertebrates) compared with the plant-herbivore food chain. Moreover, tropical herbivores are mainly suctorial or fruit-eating species of vertebrates and invertebrates; leave-eating forms, typical of most herbivore food chains are generally not abundant in tropical ecosystem.

Table 36. The structure of animal communities in island ecosystems. Data in mg m^{-2}, dry weight.

	Ancient			Young		
Climate	Tropical		Subtropical	Tropical		Subtropical
Substrate	Volcanic	Coral	Volcanic	Volcanic	Coral	Volcanic
Island	Viti Levu	Pio	Norfolk	Niuafo'ou	Suwarrow	Raoul
Arthropods						
Meso	10,010	9,510	9,880	18,435	3,170	56,650
Micro	1,120	845	no data	no data	670	no data
Nematodes	30	580	210	300	70	330
Subtotal Of Soil Fauna	11,160	10,935	10,090	18,735	3,910	56,970
Surface Forms	20	25	35	20	1,070	10
Leaf Eating	400	365	135	165	20	70
SubTotal Surface Active	420	390	170	185	1,090	80
Total	11,580	11,325	10,260	18,920	5,000	57,050
Mammals	3	3	3	7	50	170 *
Birds	2	2	7	7	170 **	5
Reptiles & Amphibians	3	30	–	8	30	–
Subtotal	8	35	10	22	250	175
Total	11,588	11,360	10,270	18,942	5,250	57,225
			Proportions			
Invertebrates	99.7	99.7	99.9	99.9	95.3	99.7
Vertebrates	<0.1	0.3	0.1	0.1	4.7	0.3
Soil Forms	96.2	96.2	98.2	99.0	74.5	99.5
Surface	3.8	3.8	1.8	1.0	25.5	0.5
Saprophytes	93.5	96.6	86.3	98.1	94.2	99.8
Herbivores	1.8	1.0	11.3	1.4	1.5	<0.1
Predators	4.7	2.4	2.0	0.5	4.3	0.1

* Predominantly feral goats; ** If all shore birds nesting on the island are included the biomass reaches 1,700 mg m^{-2}.

Tropical rain forests serve as nutrient reservoirs or "filtering" ecosystems (Fittkau and Klinge, 1973). In such nutrient poor environments, mechanisms are developed to retain nutrients in the community, as for example in well developed mycorhiza, which "clothe" the roots and leaf litter. Epiphytic plants also intercept nutrients from rain water which course down the trunks and the branches of trees.

The ecosystems on young tropical and subtropical islands have a simpler animal community which displays the dominance of single taxa and division of the community into vertical strata by canopy layer.

Unlike old islands, where the animal biotas display similar features, on young islands geology plays an important role in determining animal community structure and total animal biomass. On young coral islands the biomass was between 3 and 10 times lower than on volcanic islands of similar age. The lithology of volcanic islands is such that the soils are rich in nutrients. Moisture retention is also high and results in high primary and secondary production. In the high altitude ecosystems of Raoul the total animal biomass was between 80 and 110 g m^{-2} (dry weight), which is one of the highest values recorded anywhere in the world.

When compared with volcanic islands, young coral islands have an unusual community structure: the biomass of vertebrates is relatively high (about 5%) as is the biomass of surface active forms (25%). In addition the biomass of predators is also high and saprophytic forms are relatively less important. On young volcanic islands there is a dominance of invertebrates (99.9%) mostly consisting of soil inhabitants (99.0%) and saprophytic forms (98.1%) (see Table 36).

Despite considerable differences in total animal biomass, the ecosystems of young islands have some general features in common: simplified community structure; and accumulation of organic matter in the form of semi-decomposed plant remains (litter, amorphous semi-peaty soil organics). These functional peculiarities are also characteristic of many "immature" ecosystems in temperate latitudes.

The high populations of herbivores may be seen as a consequence of either the dynamics of natural ecosystems or of those in an early stage of succession (Zlotin, 1977; Zlotin and Khodashova, 1974; Raspopov and Rafes, 1978).

In young island ecosystems of the tropics, as well as in many ecosystems in temperate latitudes, the interactions between the primary and secondary producers are less directly linked than in older, more complex systems. Ecosystems of ancient islands (as well as those of mature tropical forests on the continent) on the other hand are characterized by more complex linkages between the biotic components of the ecosystem. Regulation of heterotrophic processes occurs at a population level, through direct trophic relationships, thus decreasing the losses of matter and energy to the decomposer food chain. This results in greater complexity and stability of the community structure.

In conclusion it would appear that one of the important determining factors in the organization of island ecosystems and their biotic complexes is the age of the island. Ecosystem age is also important in determining the maturity of ecosystems in the temperate belt, but in the tropics, ecosystem maturity seems to be achieved more rapidly.

CHAPTER IX. NOTES ON THE FAUNA AND ZOOGEOGRAPHY OF THE LEAF BEETLES (COLEOPTERA; CHRYSOMELIDAE) OF OCEANIA

L. MEDVEDEV

INTRODUCTION

During the sixth voyage of the Research Vessel "Callisto" Yu. I. Chernov[1] collected interesting observations and specimens of the leaf beetles of Oceania. Although only a limited number of species (eight) were collected on this expedition, two genera and four species turned out to be new to science, and one species was found on Kermadec Island for the first time. The study of the material naturally stimulated the author to present some general characteristics of the leaf beetle fauna in Oceania and to analyze their zoogeography. Descriptions of the new forms are given elsewhere (Medvedev, 1979).

RESULTS

SPECIES OF CHRYSOMELIDAE COLLECTED DURING THE "CALLISTO" VOYAGE

Subfamily: Eumolpinae.
Phyparida dispar Bryant, 1925.
Locality: Fiji, Viti Levu island, 20 January 1977, 1 female.

This species is an endemic of Fiji found on the islands of Viti Levu and Vanua Levu. The genus is widespread in the Indo-Malayan and Australian regions, where it is very diverse, particularly in Indonesia, New Guinea and Australia, although other species are widespread in Oceania. On Fiji the genus is represented by ten endemic species.

Demotina vitiensis Bryant, 1931.
Locality: Fiji, Viti Levu, Suva district, January 1977, 1 female.

An endemic of Fiji known on the islands of Viti Levu, Ovalau, Vanua Levu, and Lau. This Indo-Malayan genus is represented by numerous species in East, South and Southeast Asia (India having about 10 species; China about 12; Japan, 5; Indonesia, 11); it has not been recorded from New Guinea and Australia. Within Oceania 19 species are known on Fiji and one from Christmas Island in Central Polynesia.

Scelodontina suvensis Medvedev, 1979.
Locality: Fiji, Viti Levu, Suva district, January 1977, 1 female.

This genus is closely related to the Indo-Malayan genus, *Scelodonta*, and to the Fijian endemic genus, *Epinodostoma*.

Subfamily: Galerucinae.
Metrioidea signatipennis signatipennis Fairmaire.
Locality: Fiji, Viti Levu, Suva district, January 1977, 1 female.

An endemic Fijian species with three recognizable subspecies of which the nominative one is known from Viti Levu and Ovalau. The genus, which is sometimes considered as a subgenus of

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[1] I take this chance to express my sincere thanks to Yu. I. Chernov for making available to me the material that served as a basis for this work.

Monolepta, includes two other species (one found in Ceylon and one in Malacca and Sumatra), and may be considered to be an Indo-Malayan derivative.

Monolepta *bagamanica* Medvedev, 1979.
Locality: Louisiade Archipelago, Bagaman Island, December 1976, 2 females.

This species differs from all the New Guinea and North Australian species in coloration and is an endemic of the Louisiade Archipelago. The large genus, *Monolepta,* has radiated widely forming about 500 species, and representatives are common in the Old World including many forms with limited distribution.

Subfamily: New Species, Medvedev, 1979.
Locality: Louisiade Archipelago.

The discovery of a new endemic genus on the archipelago, which adjoins New Guinea, but does not have an analog on it, is remarkable. The morphological features of this genus are also unique. The most distinctive feature is the structure of the male's pronotum, having at its base a high saddle shaped protuberance. Unfortunately, the morphology of the female is unknown, but one can be quite positive that this protuberance is a secondary sexual character characteristic of males. Among the representatives of the sub-family there are many forms with very distinctive secondary sexual structures, which serve as important taxonomic characters for distinguishing species and genera. In all other genera, secondary sexual structures are confined to the head, including differences in antennae, elytra or the abdomen. In respect of these pronontal structures the new genus is quite different. The biological function and significance of this protuberance remains unclear. It cannot be considered as part of a scent producing apparatus since it lacks the ducts and lubricating apparatus of odoriferous glands.

Subfamily: Alticinae.
Chaetocnema luisiadae L.Medvedev, 1979.
Locality: Louisiade Archipelago, Bagaman Island, 12 December 1976, 16 specimens.

This new species seems to be endemic to the Louisiade Archipelago and is quite distinct from the two other species in the genus known from New Guinea, and from the North-Australian species. The characteristic metallic coloration brings it close to the species from South Australia, but morphologically it cannot be a derivative of the Australian fauna. It differs from representatives of the genus in New Guinea and Australia by a considerable reduction of elytra and the humeral protuberances. These features suggest that this species has an insular origin.

The genus is practically world-wide in distribution, and elsewhere in Oceania one species is known from New Caledonia. A North American species has recently been recorded from Hawaii and Guam.

Psylliodes solanae Brown, 1910.
Locality: Kermadec Archipelago, Raoul Island, 29 January 1977, 14 specimens.

This species was previously known only from New Zealand, but was discovered on Kermadec by the expedition, and may be a recent, accidental introduction to the island, as many species in this genus are agricultural pests.

This genus is also found worldwide, and seven species are known from Oceania. They are distributed as follows: Micronesia, one endemic species closely related to the common Japanese species; New Caledonia, one endemic species and one species in common with Vanuatu; Fiji, two endemic species; one Australian species has been found on Lord Howe and Norfolk islands, where it forms different varieties on each island possibly, of subspecific rank.

DISCUSSION

Chrysomelidae are poorly represented in Oceania and have patchy distributions in the region. They were completely absent from the islands of Hawaii until recently introduced. There are a few archipelagoes with over a hundred species, but on most, the number of species is limited to several dozen. The low species diversity on atolls is likely due to the harsh environment with high salinity, as is also true of the coastal strips of some of the high islands. Many chrysomelids are highly host specific and the impoverished flora of the islands may also contribute to the difficulty chrysomelids have in establishing populations on isolated islands (Gressitt, 1955).

Another characteristic of the Oceanian Chrysomelidae is the limited number of subfamilies characteristic of the region (Table 37). Of 17 subfamilies in the Indo-Malay fauna, only 7 are found in Oceania, and only 5 are widespread having a considerable number of species. In contrast, in Japan 16 subfamilies are known; in South China, 15; in New Guinea, 14; in Australia, 11; and even in the insular fauna of the Ryukyu Islands, there are 13.

Table 37. Percentage of species in the principal subfamilies of Chrysomelidae.

Subfamilies	Micronesia	Fiji	Samoa	Japan	Ryukyu	South China	New Guinea	Australia
Cricerinae	-	-	-	6	3	6	1	1
Cryptocephalinae	10	12	15	8	3	13	3	30
Eumolpinae	20	50	36	8	16	16	36	15
Chryaomelidae	-	1	5	9	3	6	2	35
Galerucinae	15	12	20	18	15	22	19	10
Alticinae	35	21	15	29	42	19	24	5
Hispinae	20	1.5	10	2	2	8	8	1
Cassidinae	-	-	-	6	8	4	4	1.5

The predominantly tropical subfamilies, the Sagrinae, Megalopodinae, Chlamisinae, and Lamprosomatnae are absent, as is the Holarctic hygrophilous Donaciinae which penetrates far into tropical Asia.

The subfamily Criocerinae, which is a very significant element of the tropical Asian fauna and includes many serious pests, is represented in Oceania by only four species. Of these, two belong to the large genus, *Lema*; one, in New Caledonia, one in the Bismarck Archipelago. The remaining two species from New Caledonia belong to the relic genus, *Stethopathys*, which includes one additional species from New Guinea and one from Australia. In the Philippines there are 12 species of *Lema* (Medvedev, 1975). The Indo-Malay subfamily Clytrinae is also absent in Oceania. In the Philippines it is represented by 4 genera and 16 species, of which 15 are endemic. This subfamily is taxonomically very closely related to the Cryptocephalinae, a subfamily which is widespread in Oceania; thus its absence from Oceania may be explained in terms of ecological/geographical replacement.

Except for two species, the subfamily Cassidinae is absent from the region. One is present only on Guam, in the western part of Oceania, and the second is a pest of sweet potatoes, which has been spread to most of Oceania by people in recent decades. The subfamily Chrysomelinae includes only two species from a regionally widespread genera, although the diversity of this group is high in the Indo-Malay region with several dozen endemic genera in New Guinea and Australia.

The following subfamilies are truly typical of Oceanian leaf beetle faunas: Cryptocephalinae, Eumolpinae, Galerucinae, Alticinae, and Hispinae. Species from these groups comprise more than 90% of the chrysomelid fauna of three oceanian archipelagoes (Table 38). In comparison the continental areas of South China and Australia have only 60-65% of their fauna in these subfamilies, a proportion that increases to 70-75% in Japan, the Ryukyus and New Guinea. The fauna of the Ryukyus is structurally quite similar to that of Japan, even though the environment of the Ryukyus is more similar to that of the oceanic islands. This would appear to indicate that the lack of certain groups in Oceania is due more to poor dispersal abilities rather than to unsuitable environments.

Table 38. Geographical distribution of the Chrysomelidae subfamilies and the number of species in Oceania and the adjoining territories (after Kimoto, 1966 with some changes).

Subfamilies	Micronesia	Fiji	Samoa	Japan	Ryukyu	South China	New Guinea	Australia
Sagrinae	-	-	-	-	-	11	8	63
Orsodacninae	-	-	-	1	-	-	-	-
Zeugophorinae	-	-	-	7	2	5	-	-
Megalopodinae	-	-	-	1	-	23	8	-
Donaciinae	-	-	-	14	1	8	4	8
Criocerinae	-	-	-	25	4	70	40	46
Synetinae	-	-	-	1	-	-	-	-
Clytrinae	-	-	-	7	3	31	20	4
Cryptocephalinae	3	17	3	33	4	92	120	1200
Chlamisinae	-	-	-	9	2	38	40	-
Lamprosomatinae	-	-	-	5	2	5	9	-
Eumolpinae	9	69	9	32	20	188	1440	590
Chrysomelinae	-	1	1	34	4	76	72	1390
Galerucinae	7	19	4	71	19	269	760	408
Alticinae	11	29	3	113	55	228	960	190
Hispinae	6	2	2	9	3	97	320	38
Cassidinae	2	-	1	21	10	63	200	63
Total	38	137	22	383	129	1,194	400	4,000

Of the five subfamilies characteristic of Oceania only the Hispinae and Alticinae have been well studied, and are considered below in greater detail.

The Hispinae in Oceania are represented by 5 tribes, 21 genera and 62 species (Table 39). In comparison, the Philippines has 138 species representing 10 tribes, and 20 genera. Of the species in Oceania over half of the genera (11 of 21) and 83% of the species (52 of 62) are endemic. The majority of the endemic species (46) occur only on one island. One species, endemic to Oceania, is found in Fiji, Samoa, and Tonga, but it is possible that it has been accidentally introduced from one island to the other two. Of 10 non-endemic species, 9 are in common with New Guinea, while in Oceania they are mainly met with on the Bismarck Archipelago (seven species) and on the Solomon Islands (two species). Only one species, *Brontispa longissimia* which damages coconut palms, has an extensive distribution covering Java, Sulawesi (Celebes), Moluccas, New Guinea, the Cape York Peninsula of Australia, and in Oceania, the Bismarck Archipelago, Solomon Islands, Vanuatu, and New Caledonia. In recent years this species has also spread to Tahiti and Samoa. The Hispinae of Oceania are characterized by clear Indo-Malay generic relations, including even those of southern islands such as Norfolk and Lord Howe. Australian elements are completely absent, although the Indo-Malayan genera also penetrates northern Australia. Typical Australian genera are of low diversity, are primitive and, apparently, cannot compete with the more competitive Indo-Malay species.

Table 39. Distribution of Genera and Number of Species of Hispinae in Oceania (after Gressitt, 1957, Uman, 1966, 1966, with changes).

Islands[1]	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Genera														
Octodonta		1								+	+		+	
Bronthispa	3	1	1	1	2	1	1		1			+	+	+
Caledonispa					2									
Plesispa		1								+	+		+	+
Oxycephala		2												
Aulostyrax			3											
Calamispa			1											
Callistola	3	3	2								+		+	
Isopedispa					2									
Torquispa					2									
Stephanispa					2									
Teretrispa					2									
Cyperispa			2											
Enischnispa		1												
Pharangispa		3												
Promecotheca		2	10	1	2			2	+	+	+	+	+	
Gonophora		1				+	+	+	+					
Aspidispa		1					+		+					
Dactylispa		1	1	1				+	+	+	+			
Dicladispa		1	1					+	+	+	+			
Hispellinus		1				+	+	+	+	+				
Total Genera	2	12	9	3	6	1	1	1	2					
Endemic Genera	-	2	4	-	5	-	-	-	-					
Species	6	16	24	3	12	2	1	1	2					
Endemic Species	6	8	21	2	11	1	1	1	1					

[1] Key to Symbols: A. Micronesia; B. Bismarck Archipelago; C. Solomon Islands; D. Vanuatu-Santa Cruz; E. New Caledonia; F. Fiji; G. Norfolk; H. Lord Howe; I. Central Polynesia; J. SE Asia; K. Indonesia; L. Philippines; M. New Guinea; N. Australia.

Individual subregions of Oceania differ from each other in generic diversity and in the degree of endemism. The Bismarck Archipelago, for instance, has a substantial set of species and genera in common with New Guinea. The Solomon Islands are richer with a higher percentage of endemics, while the comparatively impoverished fauna of New Caledonia is characterized by a high rate of endemism and may be considered to be an ancient faunal grouping. The fauna of Polynesia is poor and lacks endemics. In Hawaii, the only species present was introduced from Micronesia no more than five years ago, and in southeastern Polynesia and New Zealand there are no representatives of this subfamily. Still older zoogeographic links are displayed by this group, as mentioned by Gressitt (1957). The genus *Brontispa* is absent on the Asian continent, but it is known on the islands of Mauritius and Rodriges in the Indian Ocean. *Enischnispa* is taxonomically very close to the genus *Rhabdotohispa* from the Seychelles.

The New Guinea and the Australian leaf beetle faunas are mainly related to those of Madagascar, and thus they may represent relics of an ancient Gondwanaland fauna. Members of the subfamily Hispinae are almost exclusively associated with monocotyledons, but in Oceania and New Guinea in particular, no species have been found on bamboo, unlike the situation in Southeast Asia, where numerous species are associated with these plants.

The biogeography of the Alticinae in Oceania is somewhat different from that of the Hispinae, although comparisons between these subfamilies cannot be fully made because the Alticinae of New Guinea and Western Melanesia have not been completely detailed. For the portion of Oceania which has been reviewed (Samuelson 1973), only 6 out of 26 genera (23%) in this subfamily are endemic to Oceania, but 83 of 97 species (85%) were endemic. Of the endemic species, 53 are confined to single islands.

The Oceanian Alticinae are predominantly Oriental in origin, and many of the species in Oceania can be directly related to Oriental elements. In other cases, lineages seem to have differentiated in the Papuan subregion before spreading further. Only the faunas of the Solomons and New Caledonia seem to contain species of Australian derivation.

The fauna of New Zealand, Norfolk and Lord Howe islands appear to be relicts of long duration. The New Caledonian fauna is most clearly related to Australo-Papuan lineages. Most species seem to have reached Oceania in steps from the Orient to New Guinea, outwards towards the Solomons, then to Fiji and beyond. Considerable filtering has taken place at each step, and radiation has occurred on the larger islands. The fauna of Western Micronesia has elements which seem to have arrived in the region directly from Asia, without passing through the filter of the Papuan region. Several species have obviously been dispersed around the Pacific since the advent of man. These include 2 species of New World origin, which have arrived in Hawaii only since World War II.

THE CHRYSOMELIDAE OF MICRONESIA

As well as considering individual subfamilies of Chrysomelidae, it is worthwhile discussing the fauna of individual sub-regions, in particular, those of Micronesia and Fiji which have been well studied. The Chrysomelidae of Micronesia include 38 species in 6 subfamilies (Table 40), of which Cassidinae have been introduced in historical time (Gressitt 1955). Since then several other species have been introduced to the region or moved among islands.

Of the 17 genera there is not, however, a single endemic genus, while of the 26 species endemic to the region, 16 are endemic to single islands. At least 7 species have been brought to the islands by man, and are pests of agricultural crops including sweet potatoes, Cucurbitaceae and Leguminaceae. The comparatively low generic endemism of the southern Mariana Islands is explained by the fact that since 1945 at least 5 species have been introduced to Guam. If these recent introductions are ignored then the percentage of endemism is around 60%, and thus comparable with other islands.

The introduced species in Micronesia have been brought from the Philippines and East Asia. The native species of Micronesia seem to be most closely related to species in Melanesia and the southern Philippines. Only in the Bonin Islands is the fauna derived from eastern Asia.

THE CHYRSOMELIDAE OF FIJI

The fauna of Fiji, which lies on the boundary between Melanesia and Polynesia is distinguished by an abundance of species and a high rate of endemism (Table 41). Of 137 species, 126 (92%) are endemic to the Archipelago. Generic endemism exceeds 10% (4 of 36 genera). Fiji is a link between Melanesia and the rest of Oceania, and many species do not penetrate to Oceania, east of Fiji. Most Fijian genera also occur in the Indo-Malayan region and in New Guinea; some of the genera are known only in Oceania. The proportion of New Guinea, Australian and New Zealand genera is not great and their penetration to Fiji is via Melanesia. Two genera have disjunct distributions and are found only in New Zealand and on Fiji. For example, the genus *Alema* is represented by three endemic species in New Zealand and by two species on Fiji. These are undoubtedly ancient faunal elements.

Table 40. The fauna of Chrysomelidae of Micronesia (after Gressitt, 1955, with changes).

Island	Cryotocephalinae	Eumolpinae	Galerucinae	Alticinae	Hispinae	Totals
Ogasawara (Bonin)	-	-	-	3	6	3(1)
Kadjang (Volcano)	-	-	-	1	-	1(1)
North Marianas	-	-	-	1	-	1(1)
South Marianas	-	3	4	2	1	12(4)(2)
Palau	2	3	4	4	4	18(13)(7)
Yap	-	1	2	3	1	7(5)
Caroline Atolls	2	-	2	2	1	7(5)
Truk		2	1	-	5	10(8)(41)
Pohnpei	-	1	-	2	1	4(4)(2)
Kosrae	-	1	-	1	1	3(3)(1)
Marshall	-	-	-	-	1	1(1)
Gilbert	-	-	-	-	-	-
Total In Micronesia	3(3)	9(6)	7(3)	11(8)	6(6)	38(26)

Note. In the first set of brackets, endemics of Micronesia; in the second, local endemics.

Of note is the poverty of the fauna of Hispinae in Polynesia as a whole, while in contrast, numerous species are present in Melanesia.

Individual islands of the Fiji Archipelago differ from each other in the number of species and in the percentage of endemic forms. The fauna of the large island of Viti Levu is much greater than that of all the other islands, including Vanua Levu, which has a similar land area. However, this information can only be considered preliminary as Viti Levu has been collected much more intensively than has Vanua Levu. Of 126 species endemic to the archipelago, 83 are endemic to one island, with 55 of these are found on Viti Levu. All the islands examined have their own endemic species, and the proportion of the total leaf beetle fauna is very high; on Viti Levu over 50%; around 30 % for the other islands (Table 41). The island of Ovalau which is only 15 km from

Viti Levu is notable for an unexpectedly low figure less than 8%. The percentage of Fiji endemics by individual island is also distinguished by fairly constant values between islands: Viti Levu, 92%; Vanua-Levu, 88%; Ovalau, 87%; Taveuni, 87%; Lau and Central Fiji, 80%; and Kadavu, only 45%. If we exclude 4 introduced pest species from the calculation, in the case of Kadavu, then the percentage of Fiji endemics rises to 80%. On the basis of current information, it appears that Viti Levu is the center of speciation for the Fijian fauna. This island has the greatest generic and specific diversity and the highest rates of endemism. The fauna of Ovalau Island is the least unique and represents a simplified and impoverished subset of the fauna of Viti Levu. The species restricted to Ovalau have either arrived in the island too recently to have speciated or are being maintained by continuous immigration from Viti Levu.

Table 41. Population of Chrysomelidae In Fiji (After Bryant and Gressitt, 1957, with changes).

Island	Cryptocephalinae	Eumolpinae	Chrysomelinae	Galerucinae	Alticinae	Hispinae	Total	Endemics Of The Islands	Endemics Of Fiji
Viti Levu	11	56	1	14	21	2	104	55	96
Ovalau	2	19	1	10	6	1	39	3	34
Vanua Levu	2	23	1	4	6	2	38	9	33
Taveuni	1	8	-	1	2	1	13	4	11
Central Fiji	-	7	-	2	-	1	10	3	8
Lau	5	8	1	3	2	1	20	7	16
Kandavu	1	4	-	3	-	1	9	2	4
Totals	17(17)	70(67)	1(1)	19(15)	129(26)	2(1)	137	83	126

Note: Numbers in brackets indicate the number of endemics.

SUBREGIONAL CHARACTERISTICS

The results of the analysis suggest that the fauna of the islands of Oceania as a whole has many common features: a constant presence of some groups and absence of others; a very high generic endemism; and a prevalence of Indo-Malayan roots over Australian ones. We have already noted the 5 subfamilies which are typical of the Oceanian fauna, and in particular those which are absent or have an impoverished representation. These groups are characterized by surface living larva and include such groups as the Criocerinae, Chrysomelinae, Cassidinae, tribe Galerucini. Among the Oceanian fauna there is a predominance of species with soil inhabiting larvae, as well as of those living in cases (Cryptocephalineae), in leaflets (Hispinae), and, to a lesser degree of miners (some Alticinae). Thus, the loss of some large groups may be explained by insular ecological factors, such as salt in the atmosphere. The three large sub-regions of Oceania differ from each other in many respects:

1. Melanesia is distinguished by an abundance of species, many endemics, radiation of the Hispinae, close links with the Papuan subregion and the Indo-Malay region, and the presence of ancient elements with links to Gondwanaland.

2. Micronesia is distinguished by an impoverished species composition, an absence of endemic

species, an abundance of Hispinae, and the strong influence of Asia, especially of the Philippines and Japan in the most northern parts of the sub-region.

3. Polynesia is distinguished by a poverty of species which increases eastward and the complete disappearance of the family, a scarcity of endemic genera (two on Samoa), a sharp impoverishment of Hispinae species, and links with Melanesia and Australia.

The Fiji Archipelago has in fact, all the features listed for Melanesia, excluding the poverty of the Hispinae fauna (the Polynesian feature) and the absence of New Zealand links.

The Chrysomelidae represent a group for which natural immigration across ocean barriers of several dozens of kilometers is difficult. Much of their dispersal in the Pacific may have been assisted by man. In post-war years introduction of species by man has been quite extensive, however, such translocation has undoubtedly been going on for many centuries, although it is much more difficult to establish both the fact of introduction and the routes of penetration. Nearly all of the non-endemic species in Oceania are pests of cultivated plants; *Aulacophora* spp. are serious pests of Cucurbitaceae; Cassidinae damages sweet potatoes; of the four Hispinae species which are not endemic to the region, three damage coconut palms and one damages rattan. Even the endemic species of Oceania that are met with on several archipelagoes are also agricultural pests, *Aulacophora quadrimaculata* F. of Melanesia, Micronesia and Samoa is a pest of the Cucurbitaceae. The coconut palm pest *Promecotheca coeruleipennis* Blanch is known on Fiji, Samoa, and Tonga. It is highly probable that these insects have also been moved by humans.

In such cases it is usually difficult to define the center of origin, but it can be assumed that introductions have generally been made from west to east. Despite the Acapulco to Manila galleon trade and hypothetically earlier human contact with the Americas, no New World species of chrysomelids have become established in the region until very recently. Gressit (1955) suggests that the fauna of Micronesia is oceanic in origin, and this viewpoint is supported by the absence of ancient elements and of endemic genera, and the sharp differences between the Micronesian fauna and that of the neighboring Ryukyu Islands.

The Bismarck Archipelago and the Solomon Islands faunas are of continental origin as they are distinguished by high species and generic diversity and by an appreciable number of endemic genera. Gressitt (1955) suggested that both of these groups separated from New Guinea prior to the latter's separation from the other neighboring landmasses; hence, faunal elements were in direct connection.

According to Gressitt (1955), the fauna of Vanuatu is also oceanic, lacking elements of the older continental faunas. This point of view seems to be not so well substantiated. New materials are needed to prove the point, as the available data (Samuelson 1973, Bryant 1936) are not sufficient to make a final conclusion.

New Caledonia, in contrast, has a continentally derived and very old fauna. Gressitt (1957) had referred it originally to New Caledonia's oceanic fauna, but later (1963) wrote "in many respects it looks continental". Geologically, New Caledonia appears to have been connected by land bridges with New Zealand and the Gondwanaland landmass in the late Jurassic and early Cretaceous. After the Cretaceous, the island was isolated and migration routes were cut off. The Chrysomelid fauna of New Caledonia has similarities to the Australian and Papuan faunas as well as more distant affinities with New Zealand. The majority of the species are apparently of Oriental origin filtered through New Guinea, and typical of the rest of Oceania.

In the case of Fiji, the opinions of entomologists diverge. Bryant and Gressitt (1957) believe the fauna to be oceanic, following the assumption by Mayr (1941) and Myers (1953) who analyzed birds and amphibians; Kaszab (1955), on the contrary, concluded that the fauna of the Archipelago's darkling beetles was continental.

The Chrysomelid fauna of Fiji appears to have reached the archipelago from New Guinea and the Solomons via the outer Melanesian arc. The disharmonic composition of the Fijian chrysomelids, particularly the presence of numerous Alticinae suggests that there was considerable filtering of the Solomons fauna as it progressed outwards, with new species being introduced over a long period of time (Samuelson 1973).

We believe the fauna of Polynesia to be of oceanic origin. Even on such a comparatively large archipelago as Samoa only 22 species are known (Maulik, 1929; Gressitt, 1955), while on the rest of the archipelagoes this figure is usually not above 10. On Lord Howe and Norfolk islands, which have a very poor fauna, there are individual Australian elements (probably introduced) and Melanesian genera which have not reached Australia. The fauna of the Kermadec Archipelago includes a single genus in common with New Zealand (most probably introduced). The other archipelagoes of Polynesia are characterized by a scanty fauna composed of genera from among the ones widespread in Melanesia but not in Australia. The only exception is the genus *Sphaerophyma* with three species, of which one is found in Samoa, one on Norfolk, and one in Australia.

All in all about 20 endemic genera of Chrysomelidae are known in Oceania. Most of them are found either on only one island, or on one archipelago; there are very few more widespread genera. Two genera are found on Fiji and Samoa; two on Vanuatu and Fiji; one in the Solomon Islands and Fiji; one on Vanuatu, Fiji and Samoa, and only the genus *Nesohaltica* with 6 species has been located on four archipelagoes (Solomon Islands, 1; Vanuatu, 1; Fiji, 3; and Samoa, 1).

The further study of these poorly known genera is of zoogeographical interest and may serve as a basis for future biogeographical analysis of the issues raised in this review.

CHAPTER X. SPATIAL PATTERNS OF NATURE ON SMALL ISLANDS

G. M. IGNAT'IEV*

INTRODUCTION

The spatial differentiation of nature is the result of independent abiotic factors, as well as the differences in age of the ecosystems. The latter factor may refer either to individual islands or to the individual parts of islands or to both. To study the spatial patterns of nature, landscape surveys were undertaken, which fixed specific features of rock lithology, topography, soils and the biotic components of landscapes. Contours and boundaries of landscape complexes and communities were plotted on maps, to permit evaluation of the extent of the various components, and on the role of certain factors in spatial differentiation of landscapes and land units[1].

Landscape studies are widely used by geographers both for theoretical research, for studying the spatial heterogeneity of an area and for applied purposes as for instance, in the study of land use and land resources. The latter trend was characteristic of studies undertaken in the 1950's to 1970's in the south-eastern part of Oceania by different research institutions from Australia and Great Britain.

Both in the USSR and elsewhere landscape studies include identifying and mapping landscape complexes or, as they are often called, natural-territorial complexes (NTC), i.e. the parts of an area, within which there is a certain congruence of rocks, relief, soils and vegetation, i.e. of the principal components of landscape, systematically arranged in space.

Natural-territorial complexes may contain categories of different rank. Categories of low rank tend to occupy small areas, those of high rank, large ones. Naturally, the degree of diversity within a complex increases from low to high category. A unit of the lowest hierarchical rank, a facies, is practically homogenous, and has within its boundaries similar soils, relief, and one plant association. The following landscape categories are generally distinguished (from low to the highest): facies, urotshistshe, locality, and landscape. Some geographers introduce intermediate categories (sub-urotshistshe, etc. See for example, Vinogradov in Appendix II). The use of such categories depends on the complexity of an area's landscape pattern.

Within any area one may distinguish the principal, spatially dominant categories and secondary ones. Thus, the landscape pattern of a territory may be determined by the dominant category (facies-dominated, urotshistshes-dominated, etc.); subdominant and secondary categories, may not be shown on generalized maps.

In studies of islands of the Southwestern Pacific by scholars from abroad the principal category used in the past is "a land system". The land system concept takes into account the properties of the components, the complexity of spatial differentiation and the size of the territory, corresponds to the category of "landscape" in Soviet physical-geographical studies. Usually only one category - a "land unit", corresponding to a "facies", is distinguished within land systems. Within the latter, only facies-dominants, subdominants and some of the most important secondary categories are shown, as a rule.

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* Deceased

[1] We use both terms, ecosystems and landscapes as they are not synonymous. The concept of a landscape is broader since abiotic components are integral parts of it, while in an ecosystem they function as external factors. Second, some landscape complexes consist only of abiotic elements. Please refer to the Appendix I and II for an explanation of the landscape concept.

In the Pacific, landscape studies have been undertaken by expeditions of the Land Division of the Scientific and Industrial Research Organization of Australia (CSIRO), as well as by Great Britain's Department of Land Resources of the Ministry of Overseas Development. The former agency has studied a considerable portion of Papua New Guinea, including Bougainville and Buka Islands for example, Haantjens, 1970). The latter agency has completed its investigations of the land resources of the Solomon Islands. Data on similar studies in Fiji (Twyford and Wright, 1965) and Nauru (Viviani, 1970) are also available. All these investigations are mainly concerned with large islands of the Pacific and the results of such investigations of natural-territorial complexes on large islands may be applied to some extent to similar complexes on small islands. Comparisons may then provide ideas concerning the role of area and age of the island in determining landscape pattern.

Of the small islands only the atoll islands were previously studied from the point of view of landscape research and some results of these studies have been presented in various issues of the *Atoll Research Bulletin* and *Atoll Environment And Ecology* (Wiens, 1962).

Landscape studies were carried out on islands of the Southwest Pacific during sixth the voyage of R/V "Dmitriy Mendeleyev" in 1971, including the islands of Nauru, Lord Howe, Upolu, Funafuti (Tuvalu) and Marakei (Kiribati) (Kaplin and Medvediev, 1973).

UNITS OF RANK IN NATURAL-TERRITORIAL COMPLEXES

As described in Chapter II, the islands of the south-west Pacific are of different origins and differ considerably in age and in area. Therefore it is not surprising that they should differ in the complexity of their ecosystems as well.

The least differentiated ecosystems in spatial terms are found on islands of biogenic (coral limestone) origin, such as the ecosystems on the seven motus of Suwarrow Atoll. The main elements of the island are: the beach, the central part of the island, and the transitional zones. For the central part of the island, a closed tree canopy composed of coconut trees, with participation of *Pandanus, Pisonia* and some other trees, is the characteristic plant community. The composition of the vegetation varies very little within this community, and these variations are not associated either with relief, rocks, or soils.

At the same time, differences in the other elements of the island display a rather well-developed landscape pattern in terms of their different relief features and vegetation. This landscape pattern is accounted for by two factors:

1. The natural-territorial complexes of the islands are in different stages of development and the "ecosystems" of transitional zones are younger than "ecosystems" of the central part of the island.,

2. The communities are formed under different levels of marine influence: the beach having the highest level, the central part the lowest impact. Impacts are felt in terms of different wind strengths, distribution of salt spray, and other effects.

The elements of the atoll motus discussed above should be referred to as facies, and the island itself - to an urotshistshe. All, in turn, are elements of a larger landscape structure - or an atoll, which represents an essentially subaquatic complex, with only a small proportion of the complex above high tide level.

More complicated landscape systems are found on raised coral islands, such as Niue, Nauru, and Tongatapu, which may include several urotshistshes. Thus, on Niue one can clearly observe two terraces, representing elements of different ages. Each of these includes complexes differing in exposure to the ocean, or in proximity to neighboring territories. Thus, each of the two terraces represents a separate urotshistshe. Another system is formed by the urotshistshes of the inner parts of raised coral islands; the plateau, within which there may be specific facies differentiation. Therefore, these islands represent landscape categories of a higher rank than atolls; they are classified as localities.

Volcanic islands have a wide range of ages and factors affecting the origin of surfaces. A typical volcanic island includes several localities. Thus, on Niuafo'ou and Raoul one can clearly define the caldera localities and those of craters and slopes of volcanic massifs, each consisting of an urotshistshe and facies. Older islands, for example Rarotonga, include, in addition the coastal terraces of coral limestone, urotshistshes which are similar to the terraces of raised coral islands.

Even more complex structures are represented by large islands which are elements of island arcs, such as Guadalcanal Island. These islands include at least two types of natural-territorial complexes: marine accumulative terrace plains, which are sometimes quite extensive with forest and savannah complexes; and mountain, with predominantly forest complexes. Some islands also have active volcanoes, and in general, such islands have groups of landscapes.

SPECIFIC FEATURES AND SPATIAL PATTERNS OF LANDSCAPE

Legends to landscape maps are constructed according to the principle of landscape-forming factors. The number of steps shows the number of factors (or groups of factors), which are important in determining the spatial differentiation of nature.

These maps do not indicate the factors, but rather their effects. Thus, with lowland and montane landscapes, the principal landscape forming role belongs to the factor which produces this division -in this case, a tectonic regime or some other geomorphological process. Thus, there cannot be a single succession of landscape differentiating factors for different islands and different landscapes. In some islands geomorphological factors are more important, in others climatic ones. The objective of the study was to identify the causes of the spatial differentiation of ecological and landscape complexes in the islands.

Depending on the role of the various factors, three types of island landscape complexes can be differentiated:

1. Geomorphogenic; complexes where geomorphological processes are the most important determinant factors.

2. Climatogenic; complexes which are determined by the macro-climatic regime.

3. Biogenic; complexes which owe their form to the biotic components of the community.

The first type of landscape complexes reflects the relationship of biocomplexes with different types of relief, phase of development, and the transformation of rock and soil through chemical weathering. It is for this reason that some forms of relief are associated with certain soils and vegetation, for example, lava surfaces of different age; ancient and recent terraces; or the elements of montane erosional relief.

Climatogenic differentiation of natural-territorial complexes results from both elevational changes, and the different precipitation regimes associated with slopes of various exposures. High humidity and stable tradewinds produce different spatial gradients of rainfall. The data for mean annual rainfall in Hawaii illustrates this; rainfall ranges from 190 mm in the Kawaihae Valley to 14,400 mm in the Waioli Mountains (Carlquist, 1970). These areas are, naturally, characterized by different and specific vegetation and soil patterns, as well as the products of weathering and forms of relief. Although climatogenic differentiation is associated with orographic effects, the boundaries of natural complexes do not coincide with geomorphological divides, but are a product of the atmospheric circulation and its transformation over the islands.

Biogenic differentiation is a reflection of the specific role of the biota in natural complexes. Atolls and other biogenic islands are good examples for demonstrating the role of biological organisms in the creation of surface forms, and is comparable to geological processes.

It should be noted, that factors of landscape differentiation for an area are interdependent, producing natural-territorial complexes of different magnitudes or hierarchical ranks. Island land surfaces are, in general, more differentiated than continental land surfaces of the same area. Furthermore, island complexes are smaller.

Individual factors produce different contours of natural forms which show different patterns on maps. These patterns allow one to assess the horizontal structure of landscapes, namely the patterns of contours, their diversity, number per unit area, etc. Together with the hierarchy of the system of factors producing natural-territorial complexes they allow the establishment of the general principles of spatial differentiation of island landscapes.

As demonstrated by landscape maps, the landscape patterns of islands differ from those of other land areas by their concentric distribution of the landscape elements. This is accounted for by the formation of special coastal complexes on the margins of islands. On island coasts, geomorphological processes, produce specific elements of relief around the basement rock. These processes are most clearly pronounced on raised islands, which may be surrounded by sequences of different aged terraces. In addition, coastal land areas are exposed to winds which bring salt particles from the ocean, and affect vegetation. Therefore, even on those islands where coastal accumulative forms are not so widespread, the specific type of natural-territorial complexes can be rather clearly traced along the coast.

The elements of a concentric pattern are most clearly expressed on biogenic islands (Pio, Niue, and other islands), where they reflect the main processes of island formation.

Complicated and variegated natural-territorial complexes, are formed on volcanic islands. In areas with recent volcanic relief, the aerial patterns depend on rock type. Lava rocks are characterized by a mosaic, zonal configuration; volcanic sands and ash, are characterized by a mosaic patterns.

Such patterns (Table 42) are defined by contours on maps of 1:10 000 and 1:25 000 scales. Their forms depend on the distribution of volcanic products; oval-shaped massif (in the form of hills) in the case of ashfall; by linear streams in the case of lava. These forms are preserved for a long time, even following establishment of vegetation on their surface, and anthropogenic modification of natural-territorial complexes.

However, with time the primary-volcanic forms undergo a transformation. Natural-territorial complexes of old volcanic islands often develop linear patterns of bands, or dendritic branches due to the development of erosional relief forms. Broad band patterns are characteristic of lacustrine-volcanic formations in craters or on the outer slopes of volcanoes.

Replacement of primary-volcanic complexes by fluvial ones may require different time periods. According to observations on Raoul and Niuafo'ou Islands, this process is rather rapid in volcanic ash areas, involving tens or hundreds of years, and even slower on lavas.

A peculiar mosaic type of pattern is found in natural-territorial complexes of limestone plateaus on raised coral islands. It is associated with karstic processes, which produce a specific undulating relief and affects plant composition and the thickness of soils. On Pio Island, karst processes are combined with eolian action, and the selective felling of large trees by storms produces small mosaic patterns.

Table 42. Landscape Spatial Pattern Types.

Principal Landscapeforming Processes	Types Of Spatial Patterns (Contours)	Examples (Islands)
Coastal	Concentric belts	Suwarrow & Pukapuka Atolls Bagaman, Pio Islands
Volcanic ash	Mosaic	Niuafo'ou, Raoul Islands
Volcanic lava	Mosaic, Zones	Niuafo'ou Island
Fluvial	Dendritic strips	Raoul, Norfolk Islands
Lacustrine-volcanic	Zones	Raoul Island
Karst	Mosaic	Niue Island
Climatogenic	Mosaic	Bagaman, Raoul Islands
Biogenic	Mosaic	Suwarrow & Pukapuka Atolls

Climatic differentiation of natural-territorial complexes is expressed through the formation of mosaic and zoned patterns, as a result of vertical zonation and different precipitation regimes on slopes of different aspect. High air moisture content and stable direction of water vapor drift by trade winds promotes the formation of steep spatial gradients of moisture. Thus, there are areas with humid or dry climates, which are characterized by a specific vegetation, as well as different products of weathering and exogenic forms of relief. Although climatic differentiation is associated with orographic effects, the boundaries of such complexes do not coincide with geomorphological boundaries. These boundaries are produced by the circulation and transformation of air masses over the islands.

Biogenic differentiation, signifying the role of the biota in the formation of natural-territorial complexes, produces a very specific pattern of contours. Among the different biogenic factors, mention should be made of bird transportation of matter from the ocean to islands. These "ornithocomplexes" are found on considerable portions of island areas, for example on Pukapuka Atoll. Such complexes not only have special soils and vegetation, but characteristic rocks as well (phosphorites). In this case, vegetation plays the role of a determinant factor, since trees are the main attraction for birds on islands. From this point of view *Pisonia grandis* is important, since its large branches are suitable for nesting birds. It is natural, therefore, that the boundaries of these complexes coincide with areas of certain plants.

STAGES OF EVOLUTION ON NATURAL-TERRITORIAL COMPLEXES

The above data suggest that the islands and their areas studied have been formed over a wide range of time intervals, from several thousands to millions of years. Specific features of the geological-geomorphological base of landscapes, of soils and vegetation on islands of different age have revealed that in the process of their evolution, the landscapes of tropical islands move through a number of stages, each having a special pattern of relationships between the geological-geomorphological and biogenic components. These stages have different levels of complexity in landscape patterns.

In the first stage of evolution are areas with practically no living organisms (for example, depositional areas on atolls, sand bars, and recent lava and ash surfaces). Such landforms are numerous on Suwarrow and Pukapuka atolls (coral reefs, beaches) and on Niuafo'ou Island (fresh lava surfaces of recent eruptions). On atolls, such areas quickly become an arena of active biotic processes, while in contrast, the fresh lava surfaces are practically lifeless. In both cases, relief features have only a very weak influence on the distribution of organisms. At the same time this initial stage establishes certain preconditions for further differentiation of natural communities. Thus, the elements of beach surfaces have different moisture regimes, and are subject to different levels of salt transportation from the ocean by winds. Differentiation on the lava surfaces includes fissures in the lava with quite different regimes of moisture and temperature, compared to the lava surface. In general, newly formed land areas on islands have a rather complicated micro-relief. Later, after they become populated by plants and other organisms, precipitation, temperature and geochemistry and other factors then play important roles in differentiation of natural-territorial complexes.

The second stage is characterized by primary colonization of an area by organisms. Given the fact that only a few species are able to colonize lifeless areas, the primary colonizers are fairly varied because of the complicated primary micro-relief of the surfaces. Thus, the first species on lava surfaces of Niuafo'ou Island are: *Casuarina* on the lava surfaces; *Asplenium* ferns along fissures; grass associations along erosional furrows; scrub of *Guettarda, Scaevola,* and *Tournefortia* along the sea coast. On each element of relief there develops a specific micro-community; below the *Casuarina* growth, a thick litter layer is immediately formed, since the dead leaves and branches of the tree decay slowly. Under the litter, fungi develop rapidly, and ants and other insects appear. Grasses trap silt, and under ferns, organic matter accumulates in fissures providing the micro-habitat for colonization by moisture loving plant species, earthworms and other organisms. Therefore, the lava surfaces which have aged several decades have developed a rather complicated landscape structure.

In the third stage there is some simplification of surface relief and reduction in variability of the biotic community. This is associated with a smoothing of surfaces, and the formation of a continuous, although young soil cover. The initial mosaic patterns of plant associations give way to unbroken vegetation dominated by one or two, but rarely three or four species. Unlike the plants dominating the second stage, all these species are characterized by a broad range of ecological tolerances and are rather weakly interrelated. At this stage, plant communities are still in a state of open association.

An illustration of these complexes in the third stage of evolution is provided by ancient lava fields having scoria-ash soils, well-developed humus horizon, and herbaceous-shrub vegetation, partially replaced by food gardens and plantations on Niuafo'ou Island (Figure 16. 2a-2c). The most mature complexes on typical atoll islands belong to this stage.

The fourth stage is characterized by the secondary differentiation of relief due to the tectonic instability of most of the islands and their gradual uplift[1]; to rapid processes of relief formation resulting from high precipitation, high temperatures, underdeveloped vegetation cover, and the negative impact of human activities in terms of vegetation clearance.

In most cases a specific feature of this stage is the development of fluvial processes resulting in the production of dendritic-band patterns of natural-territorial complexes.

Occurring in parallel with this process is the increasing complexity of species composition and the development of interrelations within the biological community. These processes occur independently of the physical processes described earlier.

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[1] Many islands are apparently sinking, but in these cases their continued existence is not prolonged. Most of the Pacific islands represent subaerial elements of geological sturctures rising from the Pacific Ocean floor and are subject in general to uplift.

Observations on the volcanic islands suggest that the erosional dissection of laminated ash-scoria strata does not require much time. The surface of Raoul Island, which emerged about 2000 years ago through the piling up of ash and scoria, is well dissected by run-off channels. A high level of erosional dissection may also be observed on the ash hills within the crater of Niuafo'ou Island. In these cases, vegetational development was not apparently important for this process, except that in areas where the vegetation was destroyed by human action, erosional dissection was more intensive.

A different kind of regularity is found on some lava surfaces. Where permeability is high, surface streams are not formed until a clayey layer associated with weathering and soil formation has been established. The latter is a product of weathering under high temperatures and high precipitation. Another precondition is a relatively dense forest vegetation capable of protecting soils from erosion. Thus, it turns out that the reconstruction of landscape patterns through fluvial processes is dependent on evolution of their vegetation cover.

According to Wright (1963), the processes of ferrallitization, argillization of soil strata and dissection of the surface by streams on Upolu Island (W. Samoa) take place simultaneously and are rather slow. Thus the surface of the Aopo lava formation which was laid down in the 18th and 19th centuries is covered by a shallow, sandy, loam soil, and is practically uneroded by streams; lavas of the Puapua formation (Upper Holocene) are covered by a shallow, loamy soil with a total percentage of ferric and aluminium oxides up to 25%. One can observe only some traces of weak erosional dissection on this surface. Lavas of the Mulifanua formation (Upper Pleistocene) are covered by medium-deep, medium-loamy soils with 50 % of ferric and aluminium oxides. The surfaces are weakly eroded, and the hollows are only filled with water immediately after rainfall. Considerable dissection as evidenced by the formation of deep valleys is observed only in those parts of the island, which are built of lavas erupted in the Middle Pleistocene (Salani formation). These territories have medium to deep, heavy, loamy, low permeable soils with up to 80 % of ferric and aluminium oxides. Still more ancient lava surfaces were transformed into erosional mountains.

During the long period of soil development, complex plant communities with rich floristic compositions, were established and differentiated by the surfaces found on the island. Thus, large and ancient islands that have many different habitats may have more than 600 species of vascular plants, which differ according to the surfaces found on the island.

In cases when secondary differentiation of surfaces takes place before the establishment of well-developed plant communities, habitat conditions may be reflected in different ecotypes of the same plant species. This is illustrated by the variety of *Metrosideros* forms discussed elsewhere in this volume. It may be suggested that geological-geomorphological differentiation plays an important role in the establishment of specific features of island biota as well, providing favourable conditions for the processes of variability and species formation, which are especially active on isolated islands.

The fifth and final stage is the polydominant, tropical forest communities with a rich and varied flora and fauna, which represent complicated, interrelated systems with balanced matter and energy cycles. Owing to this interdependence, these communities are comparatively weakly influenced by geological-geomorphological features, and forests of similar composition may be formed on very different elements of relief and rocks.

The specific features of natural complexes are most fully pronounced on biotically rich, ancient and large islands. Establishment of such complexes requires a high diversity of species, and the combination of different biological lifeforms adapted to the habitat conditions of a humid tropical forest.

Comparatively little affected by geological-geomorphological factors, the tropical forest biocenoses are more "sensitive" to climatogenic factors, including those associated with relief or even determined by it. This is due to the intensive moisture exchange between the vegetation and the atmosphere, and accounts for the pronounced differentiation of the windward and leeward slopes of islands of different age, especially on ancient islands.

Complexes of the fifth stage are found on New Guinea and to a certain extent, on islands such as Bagaman. On oceanic islands, biotic resources are as a rule, insufficient for the evolution of natural-territorial complexes to this final stage.

Each stage has its own particular types of anthropogenic modifications of the ecological community that result mainly from agricultural activity. In turn, agriculture depends on soil characteristics. Young soils of communities in the initial stages of development do not have the high productivity necessary to provide nutrients required for food gardens and plantations.

This specific feature is very clear on biogenic islands; there, the soils under natural complexes in the first and second stage are not used for agriculture; those in the third stage are largely used for single crop coconut plantations or food gardens of simple composition. Plantations and vegetable gardens of complex crop patterns, including mixed cropping, are found in complexes of the fourth and fifth stages. Intensive use of land, followed by the withdrawal of large amounts of biomass and removal of mobile nutrients from soils, often produces degradation of the agrosystem and the development of savannah which represents an anthropogenic disclimax. Regeneration of the community on such savannah is rather rare, because of repeated burning which favors grassland maintenance.

The evolution of biocenoses, and in a broader sense of landscapes, which conserve the above features, takes place in different ways on islands of different origin. Highly developed biocenoses are, in general, developed more rapidly on volcanic islands, than on biogenic ones, where specific soils provide the conditions favorable for only calcicole flora, at least in the initial stages of development. One can trace differences not only in vegetational composition, but in the developmental levels of biocenoses, between biogenic and vulcanogenic islands over a long time span. Thus, a very recent volcanic island, such as the Niuafo'ou Island, has many more complicated complexes, than Nauru, a raised coral island (Kaplin and Medvediev, 1973). On biogenic islands the stage of mature biocenoses (the fourth stage) is possible only when they reach an age of several hundred thousand years.

On Nauru and Niue islands there is a rather clear differentiation of biocenoses in accordance with relief, mostly associated with karst depressions, which allows development of the forest complexes to the fourth stage. At the same time, the impoverished plant species composition on Nauru compared to Niue, and the weak specialization of species in respect to the types of habitat and other specific features, suggest that the Nauruan landscapes have only just entered the fourth stage of development. The more ancient biocomplexes of Niue, of about 600,000 years old (Schofield, 1959) are clearly differentiated by relief forms. The wide distribution of grassy waste lands is also characteristic for Niue, where they have replaced forest complexes.

Most of the tropical islands of the Pacific consist of several parts, which originated at different times and therefore, have landscape patterns of many different origins. The volcanic islands include land areas of biogenic origin, raised reefs and aggradational-abrasion limestone terraces. Using symbols for complexes of different genesis (A - biogenic, B - volcanic, C - continental), and numerals for stages (1-5, from early to mature) it is possible to give a formalized representation of the landscape patterns of typical oceanic islands of the Pacific (Table 43).

The table demonstrates that the complexity of landscape patterns correlates with the age of the islands, becoming greater when an island passes the boundary in terms of hundreds of thousands of years. In this case, the islands include highly differentiated complexes of the fourth stage.

Complexes of different hierarchical rank pass through different stages of evolution; aggradational terraces of islands are, as a rule, represented by urotshistshes or localities; volcanic surfaces of different age are of the same rank. In cases where volcanic activity is spread over a considerable area, a complex of the rank of an entire landscape representing the evolution of each stage, is possible.

In the table, the complexes of different evolutionary stages are conventionally linked by a + sign. Actually, the independent combination of different complexes is demonstrated by only very recent islands, since during the course of their development, the interaction of complexes becomes more intensive. Besides the usual relationships associated with the hydrological cycle, movements of air and rock debris products, and biota are important factors in the exchanges between the complexes. Thus, young complexes on ancient islands differ considerably in vegetation from those of more recent islands. Ancient islands are much richer in species and their plant communities are, in general, more developed. Aggradational terraces of ancient islands are characterized by specific associations of "strand forests", which include, in addition to the characteristic atoll plants, large trees of *Barringtonia* sp. and others.

Table 43. Type, age, and landscape patterns of some tropical islands of the Pacific.

Locality	Island Type	Age in years	Landscape pattern
Suwarrow (Cook Islands)	Atoll	Thousands	A1 + A2 + A3
Funafuti (Tuvalu)	Atoll	Thousands	A1 + A2 + A3
Marakei (Kiribati)	Atoll	Thousands	A1 + A2 + A3
Pukapuka (Cook Islands)	Atoll	Thousands	A1 + A2 + A3
Pio (Solomon Islands)	Raised Coral	Tens of Thousands	A1 + A2 + A3
Nauru	Raised Coral	Hundreds of Thousands	A1 + A2 + A3
Niue	Raised Coral	Hundreds of Thousands	A1 + A2 + A3
Niuafo'ou (Tonga)	Volcanic	Thousands	B1 + B2 + B3
Raoul (Kermadec Islands)	Volcanic	Thousands	B1 + B2 + B3
Lord Howe	Volcanic	Millions	B4 + A1 + A2 + A3
Rarotonga (Cook Islands)	Volcanic	Millions	B4 + A1 + A2 + A3 + A4
Norfolk	Volcanic	Millions	B3 + B4 + A1 + A2 + A3 + A4
Efate (Vanuatu)	Volcanic	Millions	B3 + B4 + A1 + A2 + A3 + A4
Upolu (W. Samoa)	Volcanic	Millions	B3 + B4 + A1 + A2 + A3
Bagaman (Louisiades)	Continental	Millions	A1 + C1 + C2 + C3 + C4 + C5

COMBINATION OF DIFFERENT FACTORS OF LANDSCAPE DIFFERENTIATION

Above we have discussed only those cases of natural-territorial complexes evolution where the spatial pattern of these complexes is principally a product of the interaction between geological-geomorphological and biogenic factors. It was noted that on many islands, the factors of climatogenic differentiation are also important. Each of the factors is, essentially, a combination of several more specific factors, some of which act within larger parts of islands; others, in only isolated, small areas. Due to this fact, each island represents a complicated differentiated system of complexes of different hierarchical rank. Table 44 presents a scheme for the spatial differentiation of nature on the islands visited.

The most complicated structures (natural-territorial complexes) are those island elements which include complexes in the second and fourth stages of evolution. On all islands, geomorphological factors of differentiation and coastal processes are important. Vertical zonation and barrier effects due to climatogenic factors on the differentiation of natural-territorial complexes are characteristic of high

Table 44. The scheme of differentiation of natural-territorial complexes (NTC) on some Pacific Islands. Factors of differentiation are underlined, and the descriptions of the complexes are abbreviated; origin and stages of evolution are shown in parentheses.

Anchorage Motu (Suwarrow Atoll)

Differentiation in effects of coastal processes

Beach (A1) | Seaward Platform (A2) | Seaward Platform With Thin Cover (A3) | Depositional Bar (A3) | Intra-island Depression (A3) | Lagoonal Platform (A3)

Pio Island

Differentiation in effects of coastal processes

First Terrace | Intra-island NTC | Second and Third Terraces

Geomorphological Processes | Differences In Relief Elements

Beach (A1) | Supra-littoral Zone (A2) | High Areas (A3) | Low Areas (A3)

Bagaman Island

Differentiation in effects of coastal processes

Coastal NTC | Intra-island NTC

Geomorphological Differences | Climatic Differences Accentuated By Anthropogenic Factors

Aggradational Terraces | Abrasion Benches (C1 + C2 + C3) | Forest NTC | Savannah NTC (C4)

Climatic Differences

Differences In Effects Of Coastal Processes

Surface Slopes (C4) | Windward Slopes (C4)

Beach (C1), Beach Ridge (C2), Supra-littoral Zone (C3)

Niuafo'ou Island

Types Of Relief

Coastal Ash-lava Plain | Slopes Of The Stratovolcano | Crater Floor

Age of Surface | Vertical Zonation | Types Of Relief

Recent Lava Fields (B1 + B2) | Old Lava Fields (B3) | Middle Level Slopes (B3) | Upper Level Slopes (B3) | Inner Crater Slopes (B3) | Volcanic Cones (B3) | Lacustrine Volcanic Plains (B3)

Type Of Volcanic Products | Level Of Human Modification Of Vegetation

Table 44. (Continued).

Raoul Island

Types of relief

Coastal Lowlands
Slopes Of Stratovolcano
Crater Plain

Differences In Effects Coastal Processes
Development Of Fluvial Processes
Types Of Relief

Beaches (B1)
Storm Bars (B2)
Slopes & Valleys (B3 - B4)
Inner Crater Slopes (B3)
Deluvial Trains (B3)
Lacustrine-Volcanic Plains (B1+B2+B3)

Terraces (B3)
Vertical Zonation
Stages Of NTC Evolution

Watershed Slopes (B3 - B4)
Mid-level Slopes (B3-B4)
Low Level Slopes (B3-B4)

Anthropogenic Impact On Vegetation

Forest NTC
Herbaceous NTC

Norfolk Island

Types of relief

Mountain
Plateau (not studied)

Climatic Differences

Windward Slope
Leeward Slope

Forms Of Erosional Relief

Convex Slopes (B4)
Concave Slopes (B4)
Crest-like Slopes (B4)

Gentle Convex Slopes (B4)
Gentle Concave Slopes (B4)

islands.

The non-homogeneity of spatial differentiation in the various elements of islands presents certain difficulties in defining categories for individual complexes. In all cases the lowest hierarchical rank is a facies; however, the structure of facies is not equally or clearly pronounced in different stages of evolution. In the third stage the former surfaces display less differentiation effects that can be attributed to soils, vegetation, and habitat in general. Therefore, landscape maps show these complexes as non-differentiated ones.

The non-homogeneity of spatial differentiation of elements on islands may also be a result of the reduction in rank of natural-territorial complexes (as for example, when an urotshistshe is represented by only one facies, the abrasion benches on the Bagaman Islands; or by only one urotshistshe, the coastal lowlands on Raoul Island). In addition, climatogenic differentiation on the slopes of montane islands allows the subdivision of urotshistshes into zonal types of facies; slopes of high, middle, and low inclination (as on Raoul Island); and also the differentiation of facies dependent on anthropogenic factors (also seen on Raoul Island).

Analysis of landscape patterns on islands examined during this cruise leads to the following conclusions:

1. The level of complexity of a landscape pattern depends primarily on the type of island: low islands such as coral islands having simpler patterns; high islands, more complicated ones.

2. In landscape differentiation the primary role belongs to geomorphological factors; however, on high islands climatogenic factors may be equally important, and their influence increases with development of the island landscape.

3. Ancient islands have natural-territorial complexes which are heterogeneous in age; along with mature complexes, they include young ones as well. However, these complexes are not identical to those of similar age found on recent islands; they are related to more ancient complexes spread in other parts of the island. As a rule, this is reflected in the composition of their biota, in the screening role of relief, and in other locality specific features.

CHAPTER XI. CONCLUSION

Y. G. PUZACHENKO

The results of this cruise and the ideas suggested by them concerning the structure and functioning of ecosystems and of their individual components on small islands of the southwestern Pacific permit the formulation of some general hypotheses concerning island communities and ecosystems.

One of the fundamental ideas discussed in this monograph, the notion of physical space as a specific environmental resource, was clearly formulated by Y. I. Chernov and analysed in the case of animal populations. Space or area was understood here as not only the arena of different factors and required for transformation of an ecosystem and of its individual components in the course of time, but also as an environmental factor which puts constraints on all other factors and on the possible successional pathways of the ecosystems. Data for vegetation and animal populations suggest that, in contrast to large islands and continents, small islands undergo simplification of the ecosystem and of its individual components, as demonstrated through lower species diversity, a more clearly pronounced dominance of some species, and in higher species density. In general, individual species in these ecosystems are characterised by small size; the subdivisions of communities are also of smaller size with more clearly pronounced boundaries than in other areas.

Thus, the simplified ecosystems of small islands are not only a product of reduced species diversity and habitat types, but the impacts of these characteristics on the structure and functioning of the system. One might suggest that the long-term existence of a species requires a certain minimum number of individuals, and that this minimum population size is a species characteristic which varies in different taxa. Hence, species that will survive in insular situations, have the lowest required population size, or are able to maintain higher populations per unit of area on small islands than on large ones. Such ideas explain the obvious dominance of a limited set of species in island environments, their clear spatial differentiation, and the distinct boundaries between individual ecosystems of the rank of a biogeocenosis.

Contrary to the MacArthur-Wilson (1967) model, where the area of an island defines the possible number of species and influences the probability of survival, these ideas would suggest that those species which are found on islands are selected on the basis of their ability to produce a sufficiently large population on a limited area; and on the basis of their adaption to such limited environments. This aspect of a species ecology may be combined with increased dispersal ability, although such ability is clearly not limiting in the long-term as evidenced by the insular distribution of many ground species of birds, reptiles, and insects of demonstratably poor dispersal abilities.

Survival within a limited area, apparently, may be ensured by generalised feeding, the comparatively longer life span of an individual, lower specificity in terms of micro-habitat requirements, and by overall reduction in potential mobility. The latter is, apparently, more important for animals, because a higher mobility of an island species could result in the reduction of population size. Thus, specialisation towards an isolated environment should be automatically associated with generalisation in respect to some ecological requirements.

The majority of species inhabiting small islands are usually the vicariant species of large islands and continents. On continents or large islands these species may be more specialised than in the island situation; their mobility may also be higher, but the possession of ecological plasticity and the capability of adopting a more generalised ecology and high population density are displayed by these species.

Thus, lower mobility, which was first noticed by Darwin in the case of Lepidoptera, is a adaptation to island conditions.

Obviously, plants may survive in a limited area due to their longer individual lifespans. This characteristic is apparently inherent in several pioneer species, such as *Metrosideros* and *Casuarina*, which occupy surfaces practically devoid of vegetation. Continuation of these extremely light-demanding species is ensured by permanent volcanic activity and soil erosion which cause a mosaic reversion to earlier seral stages. When compared to the generation span of such species, episodic events are rather rare phenomena, and the survival of such species may only be ensured by longer individual life spans.

The great variety of species inhabiting the coastal areas of islands have, generally, good dispersal abilities and therefore, isolation of an island is effectively non-existant for them. In plants these are the species inhabiting the motus and low aggradational terraces of high islands. Although these species are mostly specific for atolls and terraces, the majority of them are pioneer light demanding species, which are able to colonise recent ash plains as well, even those remote from the ocean, or simply well-lighted stony areas. The combination of high potential for distribution and high light requirements directly determines their pioneer character. The above features are common for practically all pioneer forms and do not represent a specific adaptation to an island environment. The same high dispersal ability is also inherent in some animal species of the coastal complex.

Thus, on islands, apparently contradictory adaptations ensuring species distribution are combined. Species with different adaptations are able to find suitable conditions in different evolutionary stages of ecosystem development. The presence of a wide variety of species on islands does not preclude the possibility of extinction of some of their representatives over time. It also does not exclude the possibility of new species introductions. Data concerning the distribution of millepedes, doves, and Lepidoptera on Pukapuka and Suwarrow atolls support this "patchiness" of distribution which results from local extinctions and, accordingly, of changes in the composition of the fauna and in the number of species as predicted by MacArthur and Wilson's equilibrium model. The process described by this model is, apparently, of low importance however, in the formation of island communities.

The equilibrium model represents the situation of the initial, and earliest stages of settlement of completely lifeless islands. On such an island in the absence of competition, different species may be potentially introduced, but even in such cases there is a higher probability that the initial stages of the successional sequence will be formed by the pioneer species adapted to these habitat conditions. On the young motus of Suwarrow Atoll one encounters only *Pemphis* and *Scaevola*, more rarely *Tournefortia*, while on the older adjacent motus, the variety of species is greater. As potential habitats, the islands have maintained conditions close to that of the Mesozoic. Even those atolls with recent surfaces have existed continuously throughout the Pleistocene. These time intervals are greater than the periods needed to achieve the equilibrium number of species according to the MacArthur-Wilson model; therefore, the fauna and flora of present islands may be considered as balanced and composed of a community of coadapted species, the composition of which is strongly determined by environmental conditions.

Simberloff (1974) has made a thorough review of the literature on these issues and notes an undoubted selectivity in island ecosystems compared to the potential inflow of migrant species from large islands and continents. However, a number of important results discussed in preceding chapters amplify these ideas:

1. Vegetation and animal populations of young islands have more uniform patterns, similar to those of the middle latitudes; uniformity is apparent in terms of the simplified vertical structure of communities, rather clear dominance of a comparatively limited number of species, relative spatial homogeneity of vegetation within similar environments, and lower species diversity of heterotrophic organisms along with their high individual population numbers.

Species composition and structure are dependant on abiotic factors, in particular, edaphic conditions. Island soils are usually underdeveloped or are represented by initial stages of soil formation, and bear all of the characteristics of the parent rock.

This combination of features indicates that the ecosystems of young islands are comparatively open, both from the point of view of functioning (in exchange of matter), and in the influence of management by external environmental factors. The plant formations provide rather high food resources for the heterotrophic food chain, but the detrital food chain is very important in most island ecosystems.

The open character of the biota results in variegated spatial patterns on the level of natural-territorial complexes and well-pronounced boundaries between individual phytocenoses. Individual plant species are rather clearly differentiated in different stages of succession, as well as in specific climax communities. Differentiation of the latter is especially pronounced in island ecosystems with low species diversity. Despite the above differentiation, the ecosystems are formed by species possessing broad ecological amplitudes, and in plants most are species with high light demands. Therefore, a simple internal structure may be consistent with high spatial differentiation of the total island system.

2. The vegetation and animal populations of old islands are characterized, above all, by much higher species diversity in each community, complicated systems of endodynamic transformations at the parcel level, low population densities of heterotrophic organisms with high species diversity, and general diversity of life-forms. Non-homogeneity of biota under homogenous environmental conditions is prominent, and in contrast, different environmental conditions do not necessarily result in different impacts on the structure of the biota. Ecological plasticity of species is less well expressed, and their co-adaptations are well developed and complicated. Under these ecological limitations the high number of species results in a very high level of utilisation of the solar energy by the entire community.

Independent of environmental conditions, old islands all tend to develop ferrallitic soils. This similarity of soils greatly accentuates the spatial uniformity of environmental conditions and reduces the spatial diversity of natural-territorial complexes. All these characteristics suggest the comparatively closed nature of mature ecosystems in reference to the processes of matter transfer and the role of environmental factors. Simple food chains and the lower singificance of heterotrophic organisms support the concept that in the course of evolution the ratio of energy losses in a system tends to be reduced. Lower gross productivity of mature ecosystems and maintenance of high plant biomass are also characteristic of these ecosystems (Odum, 1975). Thus, the simplified structure of young ecosystems corresponds to more complicated functioning and more open character, while the complicated structure of old ecosystems corresponds to simple functioning and closed character.

The above points demonstrate the importance of community evolution in the structure and functioning of ecosystems. With increasing age in an ecosystem, the volume of the ecological space becomes obviously narrower for plants. This does not necessarily result in a reduction in the number of species and phytomass reserves. For animals the volume of ecological space becomes seemingly greater, due to acumulation of phytomass and higher number of plant species; however, this does not result in the expected increase in density, although species diversity becomes definitely greater. In mature ecosystems, narower ecological niches are correlated with a reduction in population numbers as well. In terms of species survival, this can only be compensated for by a longer life span of the individuals.

Thus, the adaptation of species on young and old islands is essentially different. On young islands less specialised forms, which have increased capability for migration, or increased potential for survival within a limited area under high population density, are favored. On old island ecosystems more specialised species, which form co-adapted communities, are favored.

However, the old island ecosystems of small islands are still essentially simpler, than those of similar age on large islands and microcontinents. Given the large numbers of species inhabiting large islands and continents, small islands have, in general, the less specialised species (or the species, which are able to reduce their specialisation), thus ensuring the maintenance of a necessary number of individuals within a limited space.

Therefore, the present structure of island ecosystems, their species diversity, heterogeneity, and other features cannot be fully understood without considering age and evolutionary interactions of all the components. Just as there are old island surfaces of different age, which differ in vegetation and animal population patterns, there are islands of different geological age. As a result of long evolution, the major biotic elements of island ecosystems have become adapted to the environmental conditions, which existed at different stages of their evolution.

The potential for continued adaptation, and, obviously, the rapid development of new behavioural patterns, phenological reactions, and species characteristics in the conditions of spatially limited and isolated areas remains high. The adaptation of *Megapodius* to geothermal incubation may represent such a change while *Metrosideros* on Raoul Island has developed diverse and extensive adaptations to the habitat conditions there in rather limited time. Further detailed studies of the process of adaptation, and a search for criteria to define its stages, and the subprocesses taking place on different time scales, are of primary importance to the development of general theories of insular ecology and geography.

When compared with the structure of the biogeocenoses of islands of different age in the southwestern Pacific region, the biogeocenoses spread over the vast Eurasian territory can be characterised as extremely young and simple. They are, undoubtedly, in the very initial stages of phytocenogenesis, and one can suppose, that they are presently undergoing intensive processes of species formation and sophistication. In the USSR, the only formations, which are prossibly similar in age to the old tropical islands are the turgay ecosystems in the south of the Far East, the subtropical forests of Talysh, and, possibly, the savannah-like ecosystems of Badkhyz.

Comparison of ecosystems of the coniferous-broad-leaved forests in the south of the Soviet Far East with similar young European ecosystems reveals a situation close to the one discussed above. Although the contrasts are less clear, the trends are quite similar. Especially well-pronounced is reduction of population density of birds and soil invertebrates in old ecosystems with about the same or much higher species diversity. High species diversity of trees is another characteristic feature, which goes together with rather long individual life span and comparatively low individual productivity.

There is no doubt that appraisal of ecosystems and of individual biogeocenoses in terms of their phyllocenogenetic maturity is of major significance for optimal use of natural resources, for the selection of economic species, and for the conservation of individual landscapes and ecosystems. Finally, appreciation of the fact that the ecosystems of the European USSR are far from an equilibrium state, is very important, both for formulating the strategies of the studies of ecosystems dynamics, and for their economic use. It may be supposed that from the point of view of economics, the young age of the ecosystems is a positive, rather than a negative feature. Taking into account, that they are remote from the state of thermodynamic equilibrium, which is approached by ecosystems in the final stages of phyllocenogenesis, and their correspondingly open character from the point of view of management, one can suggest that they have potentially higher productivity and are easier to manage, and with a higher capacity for regeneration. Despite these positive features, the young age inevitably results in the explosive character of many processes, especially in the case of disturbance of low-stable equilibrium, difficulties in the prognosis of autochtonous transformations, and possible deviations from "normal" responses to the imposition of external management impacts.

The results of this scientific expedition permitted the analysis of some structural characteristics of ecosystems, which are close to the climax, and identification of their dependence on age. This was only possible through the observation of a parallel series of islands of different age and genesis, excluding any other explanation of the observed effects. Thus, data on the structural characteristics of some ecosystems were obtained, which identified the phyllocenogetic age of the systems, and of its individual components covering a wide time interval.

APPENDIX I. CONCEPTS OF SPATIAL AND TEMPORAL LAND SURFACE PATTERNS IN RUSSIAN GEOGRAPHY

Y. G. PUZACHENKO

The formation of a scientific concept is determined by the following factors: a) its scientific and methodological principles; b) the features of the object studied; and c) practical considerations. The evolution of Russian concepts of geography and in particular those concerning the spatial and temporal patterns of the earth's surface reflects these factors.

In its development, early Russian geography was greatly influenced by the German schools of geography and natural science. The basic methodological approach in the natural sciences and particulary in geography was Gestalt-stragegy, based on a discrete and closely interrelated natural system of objects and phenomena. Geographical determinism as expressed in the ideas of Alexander von Humboldt, who is considered to be the founder of modern geography, long dominated geographical thinking. Given the philosophies of science extant at the time, the vastness of Russia and the limited number of researchers, it was the only possible approach in geographical studies of Russia.

An underlying principle of Russian geography was that climate, geology and lithology determined soils, vegetation, fauna and the course of all natural historical processes. This principle provided the theoretical basis for the broad interpolation of phenomena and the solution of practical problems, i.e. inventory of natural resources and the state of the environment in vast territories.

Obviously, the scope of interpolation depended on the scale of research and the degree of generalization required. Russian geographers have always considered the map as a basis of geography. Map scale determined the size of discrete areas as well as the conditions of interpolation and extrapolation. All of these factors were considered in the development of a hierarchial classification of Russian landscapes (territories) which was completed by 1963, and generalized in a phenomenological theory within a branch of geography known as landscape science. In 1915, the Russian scientist L. Berg (1958) developed the concept of the geographical landscape: that discrete territorial units could be considered as a whole because of the specific interrelationships between objects and phenomena. Berg considered studies of the location of geographical landscapes as the principle aim of geography.

The basic concepts of classical Russian landscape studies, as expressed in the studies of the leading Soviet geographers of that period (Annenskaya, *et al*, 1963) are based on the following principles:

1. The entire planetary cover can be subdivided into a hierarchial system of discrete territorial units. These units are referred to as a natural and territorial complex, or a natural territorial unit;

2. Lower units with their individual features occur repeatedly in space and can be classified;

3. Higher units are unique, because of the individual features of their genesis, and cannot be classified. These units are regional in scale;

4. A specific unit can be isolated, and further classified, but when several units have a spatial integrity based on their geological history, they form a large atypical regional unit of a lower order. This unit is considered as basic, and is referred to as a landscape.

The criteria for isolating (defining) a landscape are as follows:

Author's Note. This Appendix is provided since many of the concepts and terms used throughout the text may be unfamiliar to non-Russian and non-European scientists.

1. A landscape occupies a considerable area of several hundred of square kilometers (scale criterion);

2. A landscape has a generally uniform geological structure. Landscapes are differentiated by transitional zones;

3. A landscape is a genetically homogeneous territory;

4. A landscape has a definite set of landforms defined by geology and a succession of uniform paleogeographic events;

5. A landscape has a uniform climate that is differentiated into several local climates and microclimates that occur regularly over space;

6. Heat and precipitation are distributed along a landscape's relief elements and result in the formation of regularly occuring habitats for its biogenic components (plant and animal communities);

7. Landforms, features of the earth's surface, and the lithological pattern of surface rocks constitute a basis for isolating smaller natural and territorial units - morphological elements of a landscape. Landforms occur regularly and form a genetically uniform system, which is referred to as a landscape morphological structure;

8. Each landscape has a unique external appearance. The greater the physiognomic differences between landscapes, the more they differ in origin and history. Landscapes with similar histories have little physiognomic differences.

Thus a landscape is a natural and territorial complex formed under the influence of a uniform geological factor, and characterized by homogeneous structural elements. An integration of geology and geological history comprises a basic criterion for isolating a landscape as an individual unit. This integration is manifested in the physiognomic features and expressed by a combination of features of the earth's surface, such as soil, plant communities, etc. The 1963 schema of landscapes is presented in Table 45.

In practice, seven (in the most simple cases) to 12 hierarchially arranged territorial units comprise the hierarchy.

Facies are considered to be the basic territorial unit and require no further classification. The facies comprise a natural and territorial complex of uniform soil forming rocks, relief, moisture, microclimate, soil type and biology. Facies are usually defined at the microrelief level. The minimum size of a facies may be dozens of meters and is mapped at scales of 1:25,000, 1:10,000 and larger.

A land subunit (podurotshitshe in Russian) is a natural and territorial complex of several genetically and locally placed facies. They have a common position and exposition on a mesorelief, i.e. several facies on a ravine slope.

A land unit (urotshitche in Russian) is a natural and territorial complex of facies or groups of facies (subland units) that forms a genetic, dynamic and local system within a single mesoform relief. Typical land units for a plain are ravines, hills, and plains of first order in mountainous areas.

Complex land units are usually found in mountainous areas and comprise a system of plains of the second or third order, provided they have a lithologically homogeneous geological base.

A locality is usually comprised of a relatively unique combination of land units and is formed on a uniform geological base. A locality can be defined within a complexly differentiated territory that represents landscape changes over time and is caused by different genetic factors or complex geological composition. For example, in fluvio-glacial plains which form a genetically uniform landscape, there are localities of waterlogged depressions, outwash plains and morainal hills.

Table 45. Taxonomic Units & Physico-geographical Characteristics In Russian Landscape Geography.

Regional Units	Country	
	↑	
	District	
	↑	
	Province	
	↑	
	Region	Typologic Units
	↑	
	Landscape ⟶	Species ⟶ Class ⟶ Type
Morphological Units	↑	
	Locality* ⟶ (Mestnost)	Species ⟶ Class ⟶ Type
	↑	
	Complex Land Unit* ⟶	Species ⟶ Class ⟶ Type
	↑	
	Land Unit ⟶ (Urotshitche)	Species ⟶ Class ⟶ Type
	↑	
	Land Subunit* ⟶	Species ⟶ Class ⟶ Type
	↑	
	Facies ⟶	Species ⟶ Class ⟶ Type

* Complementary units may not necessarily be present in an actual hierarchy.

The cartographic criteria for the natural and territorial units are presented below.

Unit	Minimum Map Scale
Landscape	1:1,000,000
Locality	1:500,000
Complex Land unit	1:250,000
Land unit	1:100,000
Land subunit	1:50,000 - 1:25,000
Facies	1:25,000 - 1:10,000

Photo and map interpretation of small-scaled images indicate a 1:3 ratio of linear sizes between neighbouring interrelated units (Vinogradov, 1976).

While the landscape concepts described above have been useful in solving practical problems in the Soviet Union, these concepts have not been adopted by all scientists. Landscape evolutionists consider the classification as useful although lacking a solid basis. Although the definitions refer to genesis and process, the criteria used to define the units are vague and informal. At present, the concept of a spatial hierarchy, the identification of landscape units, and qualitative studies of landscape structure have wide application.

The hierarchy of landscapes readily accommodates a fluctuation theory of landscape development (Puzachenko, 1986). According to this theory, landscape elements formed during fluctuation intervals that differ over 2 - 3 times will be present in the landscape. If these intervals are are shorter, they will most probably be destroyed beause of a resonance effect (Puzachenko, 1986). The theory also suggests that larger-sized hierarchial units require a longer period of development or fluctuation. For small-sized islands, the equilibrium time for communities, relief and soils will be much shorter for their establishment.

Modern methods for analyzing space imagery, when combined with field studies provide a reliable basis to further assess the above phenomenological concepts, improve the quality and content of complex maps, and apply more intricate techniques for planning experiments and observations. These methods allow a comparative study of the kinetics of objects in space and time, and allow geographers to construct comprehensive models of phenomena (objects).

A CONCEPT OF BIOGEOCOENOSIS AND ITS DYNAMICS IN RUSSIAN ECOLOGY

In the late 1930s, Tansley formulated the ecosystem concept which is now fundamental to modern ecology. This concept was a natural outgrowth of the development of ideas on the interrelationships between a bioceonosis (a concept introduced by K. Moebius in 1877) and the habitat. A similar concept of the biogeocoenosis was formulated by V. Sukachev in 1942. Accordingly, a biogeocoenosis is a bounded surface area of the earth where biocoenosis and its related atmosphere, lithosphere, hydrosphere and pedosphere are homogeneous, have uniform interrelationships, and form an internally related whole. Expressed simply:

Biogeocoenosis = Biocoenosis (Phytcoenosis + Zoocoenosis) + Biotope (Edaphotope + Climatope)

It is not known whether Sukachev (Sukachev, 1972) was familiar with Tansley's works at the time of World War II. However, in later years, Sukachev pointed out that unlike the ecosystem which has no strict territorial dimensions, a biogeocoenosis is mainly a homogeneous, small area. Sukachev's early concepts of the biogeocoenosis emphasized the importance of the exchange between matter and energy, or a turnover process, and considered the biogeocoenosis as a basic territorial unit of the biosphere. In terms of territory, a biogeocoenosis almost coincides with the landscape unit of the facies, but only under equilibrium conditions. While the facies emphasizes the homogeneity of soil-forming rocks and landforms, the biogeocoenosis also considers the homogeneity of the plant cover. According to Sukachev, the boundaries of the biogeocoenosis and phytocoenosis were the same. Thus while ecosystems were defined on the basis of their interactions between organisms and their environment, a biogeocoenosis was mainly concerned with the nature of the interrelationships, i.e., matter and energy exchange. In short, the concepts of the ecosystem and the biogeocoenosis are close, with the former having a more general notion. In the USSR today, the term ecosystem is more often used, while the biogeocoenosis is used to emphasize discrete territorial formations.

Sukachev's biogeocoenosis concept, that the dynamics of the biogeocoenosis were expressed spatially by a range of landscapes, was an original and early development in scientific thought. He was probably the first to realize that the dynamics of biogenocoesis occurred at different rates and were affected by factors dependent on scale (i.e., microscale, mesoscale) of analysis. Furthermore, Sukachev opposed the concept of a climax, but emphasized that community development never stops, but assumes subtle forms.

The classification that Sukachev (1972) proposed in 1964 is as follows:

A. Cyclic (periodic) dynamics of biogeocoenoses (reversible transformations of biogeocoenoses)

  1. Daily (24 hours)

  2. Seasonal

  3. Annual weather transformations

  4. Transformations due to renewal and growth of trees and vegetation

    a. Uniform processes of tree renewal
    b. Irregular (undulating) renewal process of tree growth
    c. Synusial dynamics, particularly parcel dynamics

B. Dynamics of the biogeocoenotic earth cover or successions in biogeocoenoses

  1. Autogenous (irreversible) successions

    a. Syngenetic successions
    b. Endogenic (endodynamic) successions
    c. Phylocoenogenetic successions

      i. Phytophylocoenogenetic successions
      ii. Zoophylocoenogenetic successions

  2. Exogenic (reversible and irreversible) successions

    a. Hologenetic irreversible successsions

      i. Climatogenic successions
      ii. Geomorphic successions
      iii. Selectocoenogenetic or areogenic successions

    b. Local (reversible and irreversible) catastrophic successions

      i. Anthropogenic
      ii. Zoogenic
      iii. Pyrogenic
      iv. Windfalls
      v. Successions caused by mudflows, landslides, sudden floods, etc

This classification is based on the following principles:

A. The driving force of a succession

  1. Autogenic (endogenic) or related to the interrelationships of biogeocoenotic components-plants and the environment, animals and plants, plant-plant, generational, etc.

  2. Exogenic or determined by external forces, including other biogoecoenoses

B. Reversibility or irreversibility of successions

C. Area occuppied by a succession

1. A single biogeocoenosis with transforming parts

2. A complex of territorially related biogeocoenoses (in some cases, a large area comparable to a biogeographic region

D. Period of succession (from 24 hours to geologic time)

For the tropical rainforests, Sukachev felt that plant renewal and regrowth was an important aspect of biogeocoenotic changes.

Syngenetic succession includes all variations of biogeocoenotic transformations that occurred primarily during interactions between various plants and animal species. The abiotic component is considered to be an inert component of the system. Early stages of primary successions are ususally syngenetic, although such successions may occur at later stages of development.

Endogenetic successions are formed under the impacts of all biogeocoenotic components, and are characterized by intensive changes in soils because of biogeochemical processes and high biotic activity. The biota may be transformed because of changes in the soil.

Phylogenetic successions are related to the evolution of species, a consequence of autochthonous, self-development of the biogeocenotic cover of large areas. The formation of new species causes a low rate of transformations in all other components. Thus, it is possible to speak of an evolution of the entire biogeocoenotic cover. During syngenesis and endogenesis, a biogeocenosis moves towards equilibrium. A phylocoenogenosis may periodically disturb this equilibrium, thus initiating a potentially continual and irreversible dynamic transformation process. While endogenesis occurs only in limited and non-isolated areas, a phylogenesis is observed in large areas such as a biogeographic region or isolated islands.

Climatogenic, exogenic successions usually occur in large areas, and hence, are in principle irreversible. Such successions are similar to successions associated with geomorphic and tectonic processes. Successions of a geological time scale and those caused by climatic changes are irreversible.

Selectocoenogenetic successions usually occur over long time periods. These successions are caused by species that undergo no genetic or morphological transformations, and are of particular interest for island biogeography.

In terms of a time frame, these successions have different rates of development. Cyclic successions may occur over fairly short intervals, ranging between hours and hundred of years. Syngenesis and some types of endogenic and climatogenic successions require short ecological intervals, while endogenesis and some types of selectogenesis need long intervals. Phylocoenogenesis and mature endogenesis require geological time scales for development.

Sukachev's schema is also a classification of basic, independent factors that affect the dynamics of change in any ecosystem. All classes and processes of change, except for local catastrophic change, are observable. Under intensive human impacts, analysis of the transformations require global study. The classification also implies time scales of biogenesis, spatial processes, equilibrium and non-equilibrium processes (reversibility and irreversibility). As various transformations may occur simultaneously, but at different rates, an understanding of how rapid changes are modified by a slowly evolving background is important. Islands have particularly favourable conditions to carry out such studies. In our work on the ecosystems of the Southwest Pacific, we used Sukachev's multidimensional concepts of independent factors as a conceptual framework.

APPENDIX II. A UNIVERSAL HIERARCHY OF LAND UNIT LEVELS

B. V. VINOGRADOV

There are a large number of local, national, personal and professional land unit classification systems throughout the world. These systems, some of which are philosophically or practically-based include: British Metropolitan (Bourne, 1931; Webster and Beckett, 1970); Australian (Christian, 1958), Canadian (Hills, 1966; Lacate, 1969; Rowe, 1980); German (Schneider, 1969; Haase, 1964); French (Long, 1969); Russian (Vinogradov, 1967, 1976, 1984); Sotchava, 1979); Dutch (Zonneveld, 1979); and American (Anderson, *et al*, 1976; Bailey, 1987). As these systems were developed in different countries, environments and for different reasons, they differ widely in terminology and the cartographic scales used. By contrast, a world-wide hierarchical system of land unit classification is needed for the purposes of integrated ecological monitoring, comparision of analogous sites, and for the common classification of global data about land units at different geographic scales.

A BRIEF HISTORY

In the British school, the hierarchy of land units is based on the study of site, which (Bourne, 1931:16) defined as "an area which appears, for all practical purposes, to provide throughout its extent similar local conditions as to climate, physiography, geology, soil, and edaphic factors in general." In Britian, this system was developed primarily for overseas military purposes, and is essentially a system for terrain analysis by aerial photo interpretation (Webster and Beckett, 1970). The system consists of the following categories: land element (individual terrain units at a scale near 1:10,000); land facet (the large portion of terrain that can be conveniently treated as on block for extensive landuse and construction at a scale up to 1:80,000); land system (recognizable at a cartographic scale from 1:250,000). This hierarchy of land units and cartographic scales was later modified for use in Australia and Canada.

Because of its extensive wildland areas, the Australian system employs a discrete hierarchy of land units and at different scales (Christian, 1958; Christian and Stewart, 1968):

Land(scape) Region	1:10,000,000 - 1:2,500,000
Land System	1:250,000 - 1:500,000
Land Unit	1:50,000 - 1:100,000
Land Site	1:10,000 - 1:25,000

Some of the Canadian land classification systems are similar to the Australian system, but with some differences (Rowe, 1980; Lacate, 1965; Hills, 1968). Forest land units are diefined as relatively small, homogeneous segments of the land surface which have a characteristic topographic form and internal geologic structure, and which are associated with distinctive types of soils and vegetation, observable on 1:12,000 - 1:16,000 aerial photos (Lacate, 1965). Land associations are aggregations of geographically associated land units, which can be mapped by 1:60,000 aerial photos. The most developed "biophysical" classification of lands in Canada utilizes 5 scale levels (Lacate, 1969):

Land Region	1:1,000,000 - 1:2,000,000
Land District	1:500,000 - 1:1,000,000
Land System	1:125,000 - 1:250,000
Land Type	1:10,000 - 1:20,000 (1:60,000)
Land Phase	1;3,000

A four level hierarchy of landuse and land cover classification is widely used in the United States, and is especially adapted for inventory by remote sensing at the the following scales (Anderson, *et al*, 1976):

Level I	1:500,000 - 1:3,000,000

Level II	1:60,000 - 1:80,000
Level III	1:20,000 - 1:60,000
Level IV	1:8,000 - 1:20,000

The first level includes 10 large units ranging in size from towns and urban areas, to tundra and glaciers. The second level consists of 100 zonal units, the third of 1000 regional units, and the fourth of 10,000 local units.

Later, a hierarchy of spatial units, based on the concept of integrating more than one system of identifying homogeneous land units, was adopted in the United States. The hierarchy was expressed in the ECOCLASS concept (Corliss, 1974) in which potential vegetation and regional land systems were linked to define ecological land units from low to high levels as follows: land unit, land type, land association, subsection, section, and province.

The most detailed hierarchial system of land units was developed in Germany during 1950-60s (Meynen and Schmithuesen, 1953; Schneider, 1969; Haase, 1964). This classification and its range of map scales is presented below:

Geographische Zone	1:100,000,000
Georegion	1:30,000,000
Naturraum 1-te Ordnungstufe, Naturraumliche Region	1:10,000,000
Naturraum 2-te Ordnungstufe, Megachore	1:3,000,000
Naturraum 3-te Ordnungstufe, Makrochore	1:1,000,000
Naturraum 4-te Ordnungstufe, Mesochore obere Stufe	1:500,000
Naturraum 5-te Ordnungstufe, Mesochore untere Stufe	1:200,000
Naturraum 6-te Ordnungstufe, Mikrochore	1:100,000
Naturraum 7-te Ordnungstufe, Oekotopkomplex	1:30,000
Fliese, Oekotop	1:10,000

The French school of chorological biogeography is based on phytoecological studies (Godron, 1968; Long, 1969). These studies utilize hierarchial levels of "perceptions ecologiques", forming a "pyramide de perception" as follows:

Zone biogeographique	1:10,000,000
Region ecologique	1:500,000 - 1:1,000,000
Secteur ecologique	1:50,000 - 1:250,000
Parcelle cadastrale, Station ecologique	1:10,000 - 1:20,000
Element ecologique	1:500

In the USSR, the landscape concept has been long used in mapping and aerial surveys, and have been specified for different landscape zones. In addition, the hierarchy of spatial units to mapping, aerial and space survey scales have been tested on the rangelands of Central Asia and Kazakhstan (Vinogradov, 1967). The relationship of levels to scales are as follows:

Landscape (landschaft) or macrocombination	1:1,000,000 and smaller
Locality (mestnost') or mesocombination	1:300,000 - 1:600,000
Simple combination (urotshitche) or microcombination	1:25,000 - 1:100,000
Elementary land unit or phytocenosis	1:5,000 - 1:10,000
Fractal land unit or fragment of phytocenosis	1:3,000 or larger

Wetlands and forests have also been subject to detailed study by the landscape approach (Mazing, 1984; Vinogradov, 1984). With respect to the latter, these efforts have been influenced by the geosystem surveys of the Siberian forests (Sotchava, 1979), and the application of aerial and space technologies. The relationship of wetlands and forested spatial units to scale are as follows:

Moor region, Forest region	1:3,000,000
Moor landscape, Forest landscape (landschaft)	1:1,000,000
Swamp system, Forest locality (mestnost')	1:300,000
Swamp body, Forest system (urotshitche)	1:100,000
Swamp type, Forest unit	1:30,000
Swamp facie, Forest stand	1:10,000
Swamp mosaic, Tree population	1:3,000

Conceptually, a hierarchial system must include a sequential description of the range of scale integration levels. Furthermore, the system must include the hierarchial levels above and below the level of analysis (Feibleman, 1954). For example, mapping of ecosystems at a scale of 1:100,100 should be accompanied by additional survey mapping at a scale of 1:300,000 and by selected mapping at a scale of 1:30,000 (Vinogradov, 1967).

The poor correspondence of the different classification systems and their scale hierarchies led to the development of a universal and integrated hierarchy of spatial units (See Table 46). This hierarchy was subjected to a wide range of verification and analytical studies, including mathematical modelling, comparative multi-scale cartography, morphometric image analysis, optical conversion, statistical generalization and information value, to name a few (Vinogradov, 1976; Puzachenko, 1976).

Table 46. A Comparision of Land Unit Hierarchies.

Scale	Australia	USSR	Canada	France	Universal
1:10,000,000				Zone ecologique	Gigachore
				↓	
1:3,000,000					Megachore
			Land region		
			↓		
1:1,000,000	Landscape	Landschaft			Macrochore
	↓				
			Land district	Region ecologique	
			↓	↓	
1:300,000		Mestnost'			Mesochore
	Land system		Land system	Secteur ecologique	
1:100,000		Slozgnoe Urotshitche		↓	Microchore
	Land unit	↓			
1:30,000		Prostoe Urotshitche			Nanochore
		↓			
	Land site				
1:10,000	↓	Faciya			Monochore
1:3,000					Picochore
				Parcelle ecologique	
1:1,000				↓	Femtochore

Sources: Australia,Christian (1958); USSR, Vinogradov (1962); Canada, Lacate (1966); France, Long (1969); Universal, Vinogradov (1976, 1984).

THE UNIVERSAL LAND UNIT CLASSIFICATION

The most obvious way to form a discrete hierarchial classification is through a statistical frequency analysis of the size of land units obtained from aerial and/or space images. This analysis revealed frequency maxima which corresponded to the range of hierarchial levels of land units at different map scales. The relationship of frequency (F) to size (L) of land units is described by a power function which incorporates a trignometric function with synusoidal waves (Vinogradov, 1984):

$$\log F = \log a - b \log L + c \sin \log L$$

where *log* a - b *log* L describes a hyperbola in coordinate F, and c *sin log* L is the sinusoidal amplitude which decreases with the increase of L. The base is near the value of *pi*, e.g. 3.1-3.2. On the basis of this approximation, a universal hierarchy of land units, with scale level differences near 3.0-3.5 is suggested below:

Scale Level	Universal Unit Name	Common Unit Name
1:300,000,000	Exochore	Biosphere
1:100,000,000	Petachore	Dominion, Zone
1:30,000,000	Terachore	Subzone, Biome
1:10,000,000	Gigachore	Ecoregion
1:3,000,000	Megachore	Province
1:1,000,000	Macrochore	Landscape
1:300,000	Mesochore	Land system
1:100,000	Microchore	Combined land unit
1:30,000	Nanochore	Simple land unit, Land type
1:10,000	Monochore	Biogeocenosis, Land site

This hierarchy has the advantage of uniform scale distances between levels and has been successfully applied in the USSR. It has also been adopted by the French (Godron, 1984) and the Dutch (Pedroli, 1987).

Analogous hierarchial systems also have been identified in other sciences. In geophysics, the interrelationship between successive organizational levels of strata varies from 2.5-5.8, and averages 3.3 (Sadvosky, *et al*, 1987). In animal ecology, the behavorial classes for rodents and lizards are smoother and correspond to the following land areas (Yablokov, *et al*, 1983):

Family, reproductive community, subcolony	0.1-1.0 ha
Dem, colony, settlement	1.0-10 ha
Population	10-100 ha
Population group	100-1,000 ha

In the 1980s, the hierarchial landscape system has been applied in a number of ways. Firstly, it was used for multi-level areospace surveys with different degrees of resolution (Botkin, *et al*, 1984):

Level I	Global AVHRR	1.1 km
Level II	Continental AVHRR	1.1-80 m
Level III	Biome Landsat MSS, TM	80-30 m
Level IV	Regional Landsat TM, High altitude aircraft	3-30 m
Level V	Plot, high and low altitude aircraft	1-3 m
Level VI	Sample site surface measurements	1 m

The International Geosphere-Biosphere Programme also requires a hierarchial system (Dyer and Vinogradov, 1990). In this organizational model, the hierarchy of Geosphere-Biosphere Stations and

Biosphere Reserves in relation to their area of coverage in m^2 is as follows:

GBO (1*), R&D, and training	10^{12} and more
GBO (2*), Co-operating Biosphere centers	10^{11} - 10^{10}
GBO (3*), Affiliated Networks, Biosphere Clusters & Reserves (1*)	10^{9} - 10^{8}
Base stations, Biosphere reserves (2*)	10^{7} - 10^{6}
Regional stations, Biosphere reserves (3*)	10^{5} - 10^{4}
Biosphere pickets, Microsite studies	10^{3} - and less

This hierarchial conception is also used in geographical information systems. Detailed studies involving ground level ecological information from various sizes of land units, remote sensing data, and a variety of hierarchial models (Haber and Schaller, 1989) revealed a hierarchial structure (HOLON) or a series of nested levels (Haigh, 1987).

A world-wide hierarchy of land units is far from complete. For such a hierarchy, all regional and national land classification systems need to be compared between each other, and subjected to a wide range of quantitative approaches for validity (statistical and geophysical, remote sensing), as they may suggest a discrete land unit classification. Lastly, the hierarchy should be multi-dimensional: chorological (as suggested here), typological and dynamic.

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