Phenology

Climate change is shifting the rhythm of nature

Author

Marcel E. Visser, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

Reviewers

Elsa Cleland, University of California San Diego, USA
Gary Tabor, Center for Large Landscape Conservation, Montana, USA
Geetha Ramaswami, Nature Conservation Foundation, India
Jan van Gils, Royal Netherlands Institute for Sea Research, 't Horntje, The Netherlands
Kelly Ortega-Cisneros, University of Cape Town, South Africa
Leonor Patricia Cerdeira Morellato, Institute of Biosciences, São Paulo State University, Brazil
Rebecca Asch, Department of Biology, East Carolina University, USA
Shoko Sakai, Center for Ecological Research, Kyoto University, Japan
Yann Vitasse, Swiss Federal Research Institute, Switzerland

1.
Timing is everything for ecosystem harmony

Timing is critical in the natural world. Birds' chicks must be hatched when there is food to nourish them, pollinators must be active when their host plants flower, and snow hares must change their colour from white to brown as the snow disappears. Phenology examines the timing of recurring life-cycle stages, driven by environmental forces, and how interacting species respond to changes in timing within an ecosystem.[1,2] Plants and animals often use temperature, daylength, the arrival of rains, or other physical changes as cues for the next stage in their seasonal cycle. When spring arrives earlier, many birds react by breeding sooner, matching the advanced emergence of food for their nestlings as temperatures warm. Because temperature is such a strong influence on these cues, phenological shifts over the past decades are among the most visible consequences of global climate change, at least in temperate and polar regions of the world.

Temperature is not the only environmental variable that affects phenology. At higher latitudes, another critical variable is photoperiod, or daylength, varying at different times of year.[3-5] While photoperiod itself is not affected by climate change, the degree to which temperature affects phenology can depend on it: in some systems, high temperatures will cue the next stage during a long photoperiod, but not during a shorter one.[3,6,7] At higher latitudes, some plants and insects also need a spell of low temperature, called winter chilling, to respond well to warmer temperatures once they arrive.[8-10] Some species depend on fire to cue life-cycle stages, such as fire-stimulated seed release from cones and seed germination.[11,12] An aquatic example is the influence of rain on river discharges that in turn influence the timing and duration of the migration of fishes, along with water temperature and photoperiod factors.[13-15]

Understanding phenology in tropical regions is more complicated than in regions that have clear annual seasonal cycles, due to less variations in temperature and daylight.[16-18] Tropical species show diverse phenological strategies, individuals within a population may not synchronize, and cycles can be shorter than 12 months. Different factors, including rain, drought, moisture availability and abundant exposure to sunlight, can trigger the next life-cycle stage in tropical regions.[17-21]

A major concern with phenological changes in response to climate change is that not all interdependent species in a particular ecosystem shift in the same direction or at the same rate.[16,22-26] The reason for varying shifts is that each organism is sensitive to different environmental drivers, or shows different levels of sensitivity to a single environmental driver.[5,17,27,28] Within food chains, plants may shift their development more quickly than animals that feed on them, leading to phenological mismatches. Detailed studies on various life-cycle stages across a wide range of plant and animal species have detected significant phenological mismatches.[16,22,30-34] These mismatches between predator and food source within a food web will affect individuals' growth, reproduction and survival rates, with eventual repercussions for whole populations and ecosystems.

Image credit: Meyers Lexicon book from 1908 and Nicku / Shutterstock.com.

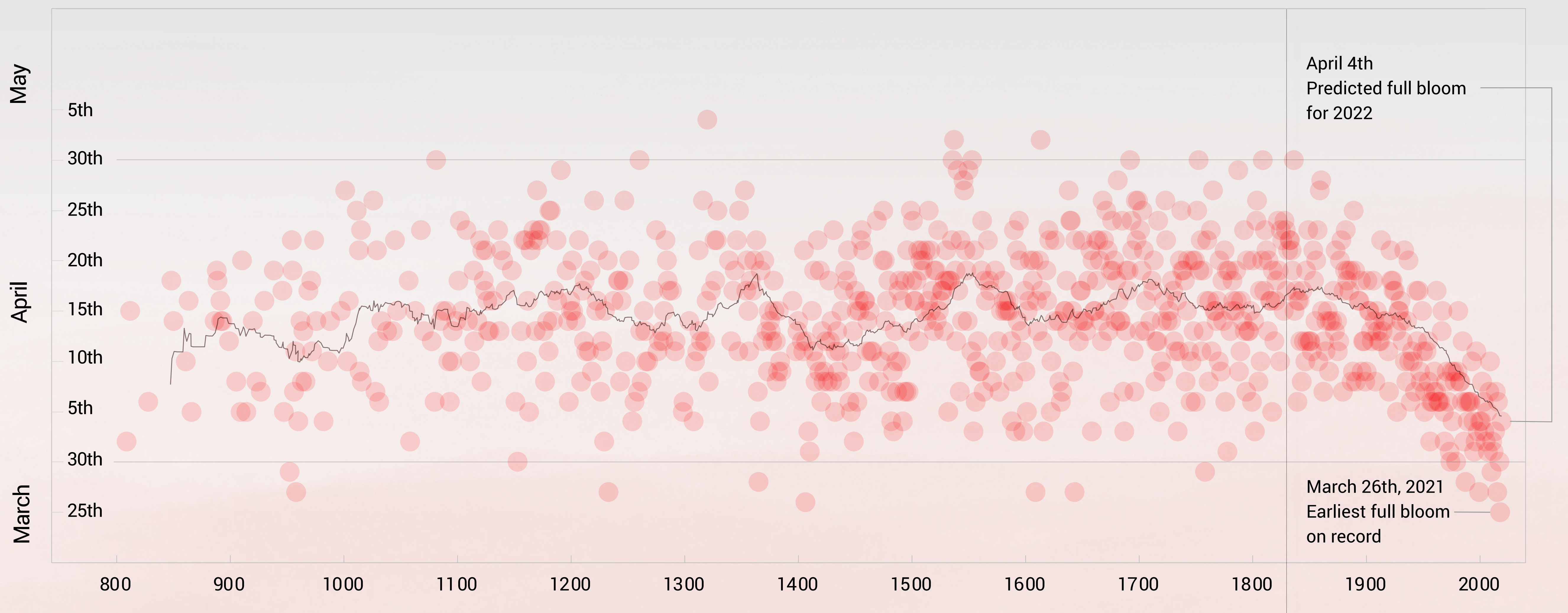
Phenology in the tropics

A key feature of tropical climates is the lack of distinct seasonal temperature variations.[18] In contrast, changes in rainfall and the switch between dry and wet seasons define clearer phases within annual cycles of the tropics.[16,18] The frequency and intensity of rainfall, or its absence, is a crucial driver of phenological changes in tropical plants, as well as sunlight, humidity, and the subtle temperature changes.[16-21] Given the high species diversity in tropical ecosystems, phenological responses to those drivers are various and complex, within species and communities.[19,35]

Rainfall patterns in tropical regions are highly influenced by the El Niño/La Niña Southern Oscillation (ENSO), characterized by its alternating warm and cool phases of sea surface temperature in the equatorial Pacific Ocean.[36] These anomalies occur every 2-7 years and typically last for 9-12 months.[36] Tropical plant communities respond to ENSO events, such as El Niño-induced mass flowering or drought-affected fruiting.[17,18,20,37] More frequent and more intense extreme weather events, delivered by ENSO and climate change, are likely to further disrupt the timing of leafing, flowering and fruit production.[17,18] Such phenological changes will have cascading effects on dependent herbivores, nectarivores and frugivores, as well as other functional groups within the ecosystems.[17,19] Long-term observations of phenological change in the tropics are still scarce, and predicting the magnitude of phenological shifts and mismatches remains a challenge.[18]

Blooming of cherry blossom over 1,200 years

Trendline is 50-year moving average



Data source:
Historical data courtesy of Dr. Yasuyuki Aono, Osaka Prefecture University, Japan, available at http://atmenv.envi.osakafu-u.ac.jp/aono/kyophenotemp4/

Data from 1950 courtesy of Japan Meteorological Agency, available at http://www.data.jma.go.jp/sakura/data/index.html

The blooming of cherry blossom (*Prunus jamasakura*) marks the arrival of springtime in Japan and is central to Japanese culture. Celebration of cherry blossom has been traced back to around 712 A.D.[38] Phenological observations in Kyoto have been historically recorded in old diaries and chronicles.[39-41] Researchers have assembled a phenological data series of full-flowering dates of cherry blossom from these documents, dating back as early as 812 A.D.[39-41]

Over 1,200 years, the full-flowering dates started as early as late March and as late as early May.[42]

Blossoming has advanced progressively to earlier dates since 1830s, which also coincided with rising temperatures based on meteorological observations, with the bias effects of urban heat already eliminated.[41,42]

2.
Disruption in ecosystem harmony

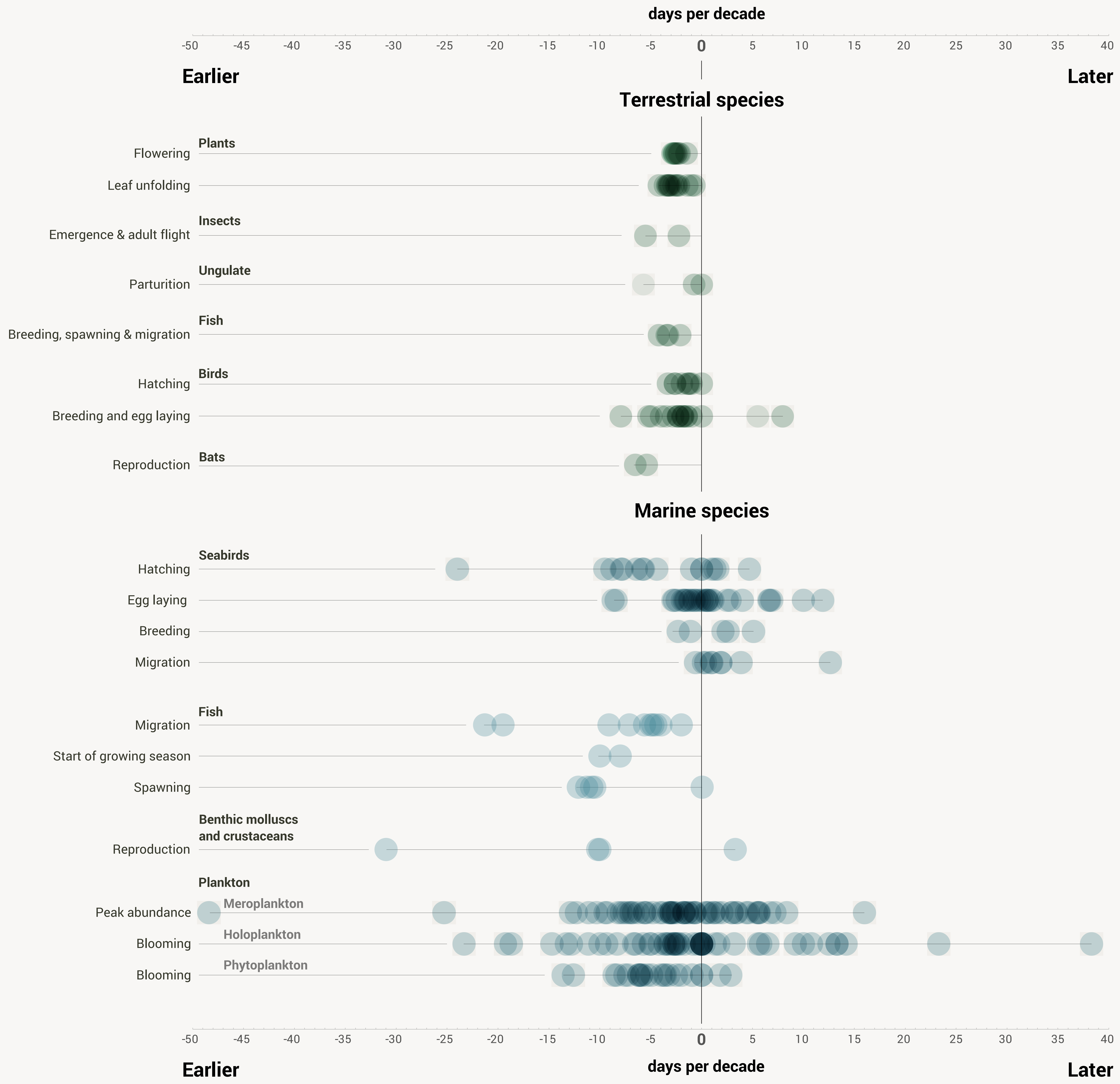
Shifts in phenology due to climate change have been detected at a variety of stages: reproduction, flowering, leaf-out, onset of larval development, moult, hibernation, migration, and others. Supporting data come from studies comparing phenological shifts among large sets of species – plants, insects, fish, amphibians, birds and mammals, for which phenological events have been recorded over the long term through observations in both hemispheres.[16,23,29-33,43-51] Researchers have also tracked an increasing probability of phenological mismatches across multiple regions, including through 10,000 data sets on plants and animals across the United Kingdom, terrestrial species in the Alps, over 1,200 time series of phenological trends in the southern hemisphere, and marine species across different oceans, among others.[16,19,23,32,43,51]

Identifying shifts, tracking trends

In the early 2000s, researchers published a few pioneering broad-scale assessments of phenological shifts that became models for ongoing work.[22,29,30] A synthesis of those databases indicate that the life stages of 203 plant and animal species advanced by about 2.8 days per decade.[30] Since then, additional ecosystems and biomes have been assessed for phenological trends. The visualization below presents the observed phenological shifts within taxonomic groups tracked in recent assessments.[31-33,49]

Each circle represents a quantified rate of phenological response of a particular species as it shifts a life-cycle stage to earlier or later by a number of days per decade. Circles appear as overlapping when two or more species in the same taxonomic group shift at similar rates.

See page 57 for complete references.



Studies on birds provide ample evidence of mismatches affecting successful breeding. Species such as pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*) need their chicks to hatch when their normal food supply of caterpillars is most abundant.[52-55] This peak food-supply period is short, covering only a few weeks, so the correct timing is crucial. Other birds, like the common murres (*Uria aalge*), need to precisely time their reproduction to the inshore migration of their main prey, small forage fish.[56]

Within the annual cycle, different life stages need to synchronize. For migratory species, annual cycles involve stages of moving to breeding grounds, reproducing, moulting and returning to wintering grounds. Some life-cycle stages, like reproduction, are highly temperature-sensitive. With warming temperatures, reproductive phenology is shifting, while other stages, like moult, are more sensitive to photoperiods, so they are not occurring in synchrony.[57,58]

Phenological responses differ throughout marine ecosystems and seasonal cycles, leading to mismatches between species and among groups in the food web.[31,32,43,59] Research shows that phenological responses to climate change happen faster in marine environments than on land.[31,32] The different marine groups, from plankton to higher-up predators, all shift their phenology at different rates, indicating that climate change can cause mismatches in whole oceanic communities as well.[31,32,60,61]

Differences in the rates of phenological responses to warming across terrestrial, freshwater and marine ecosystems could ultimately affect species that depend on different ecosystems to host phenological transitions to the next life-cycle stage. Examples include fish that migrate between marine and freshwater ecosystems, and many insects, amphibians and birds whose life-cycle stages depend on both terrestrial and aquatic ecosystems.[24,62-64] Mismatched phenological shifts could cause widespread food-web disruptions and ecological consequences.[26]

While phenological responses to climate change are well-documented, remaining questions about links to populations and consequences for ecosystems deserve greater attention.[34,51] In the Arctic, after snowmelt, the vegetation that caribou (*Rangifer tarandus*) mothers and calves depend on has advanced significantly due to higher temperatures. Now caribou calves are born too late, leading to a 75 per cent decrease in offspring.[65] In roe deer (*Capreolus capreolus*), the increased mismatch between birth date and food availability also decreases calves' survival chances.[66]

Asynchronous changes in the phenology of a broad range of interacting species have the potential to disrupt the functioning of whole ecosystems and the provision of ecosystem services on which human systems depend.[34,61] Shifts in the phenology of commercially important marine species and their prey have significant consequences for all aspects of fisheries.[47,67-69] Phenological responses in crops to seasonal variations will be challenging food production in the face of climate change. For example, fruit trees that bloom early and then experience late-season frosts result in large economic losses for orchards.[70] Phenological shifts are already complicating climate-smart agricultural adaptation for major crops around the world.[71]

Hungry birds and early caterpillars

A long-standing, well-known example of phenological mismatch is between the great tit (*Parus major*) and its caterpillar food.[54,55] This small hole-nesting songbird is found across Asia and Europe and produces unusually large broods. The parents must provide large amounts of nourishment for fast-growing nestlings in the 18 days it takes for their full development. Adults may deliver caterpillars at the rate of almost one per minute during that period.[72] To ensure this level of food supply, the birds use temperature as a cue to time their breeding so the nestlings arrive at the peak abundance of caterpillars on oak trees. For similar reasons, the hatching of caterpillar eggs is timed with the emergence of oak trees' young foliage.[73]

Field observations show varying phenological responses in these two interacting species across different sites.[54,55,74,75] The great tit population in the Netherlands has advanced its egg-laying in response to warming trends, but the shift is not enough to match the peak of the caterpillar population.[54,55,74] Forecasts indicate that the caterpillars' phenology will continue to advance faster than the birds' in the coming decades, further increasing the mismatch.[76] In contrast, a 47-year population study in the United Kingdom found that both birds and caterpillars shift their timing at approximately the same rate, keeping the interaction in synchrony.[75] Similar results were found in Belgium and the Czech Republic.[77,78] These findings demonstrate the complexity in phenological responses among species and populations in different environments.[27,80]

Incredible journeys:

The challenge of mistimed migration

Migration is a behavioural adaptation to seasonality.[81] Periodic movements of animals between habitats allows them to optimize resources in multiple locations at different times of year. Migration is also necessary when seasonal air or water temperatures become unfavourable for breeding or rearing offspring. Most migratory species are therefore from high-latitude regions where changes in season and available resources are most marked.[81] Diverse species of insects, crustaceans, reptiles, fish and mammals migrate, and many cover remarkable distances. Some avian migrants nest in the high Arctic and escape its winter to lower latitudes; cetaceans migrate between the equator and polar feeding grounds; and migrating herbivorous mammals follow seasonal changes in vegetation across continents.[81,82]

Long-distance migrants are particularly vulnerable to phenological change caused by climate warming effects, which are not uniform across regions. Local climatic cues that normally trigger migration may no longer accurately predict conditions at both destination and stopover sites along the route. The challenge is even greater for migrants returning to polar regions where the speed and magnitude of climate change are greatest.[83,84] Consequently, many migratory species struggle to arrive when quality food is still abundant, weather is suitable for specific life-cycle stages, predation or competition pressure is lower, or parasites and pathogens are fewer.[34,81,85,86] Advancing spring phenology in high latitudes has caused increasing degrees of ecological mismatch for migratory species, with potential demographic consequences.[81,86,87]

Species have demonstrated the ability to modify their migratory behaviour, from adjusting the timing to changing routes and locations.[81,85,88,89] But their adaptive capacity in response to climate change is already compromised by other ongoing threats. Ecological degradation, fragmentation and loss of feeding, breeding and resting habitats, hunting, pollution, plus other hazards on long journeys, are threatening migratory species with increasing pressure to adapt to rapid environmental changes.[88,90]

Provisions to maximize adaptive potential and build resilience in species populations require a reduction in conventional threats and modification of existing conservation policies and strategies in light of climate change.[81,91] An extensive network of diverse critical sites and protected habitats could maximize the adaptation potential of migratory species.[88] It is also imperative to ensure and enhance the connectivity of land and marine habitats critical for dispersal, now and in the future.[88,92] Increasing habitat connectivity will help maintain adaptive genetic variation and population viability needed for species survival.

European migratory birds

Analysis of spring arrival times of 117 European migratory bird species over 5 decades suggests increasing levels of phenological mismatch to spring events. This has contributed to population decline in some migrants, particularly those wintering in sub-Saharan Africa.[87]

White stork *(Ciconia ciconia)*

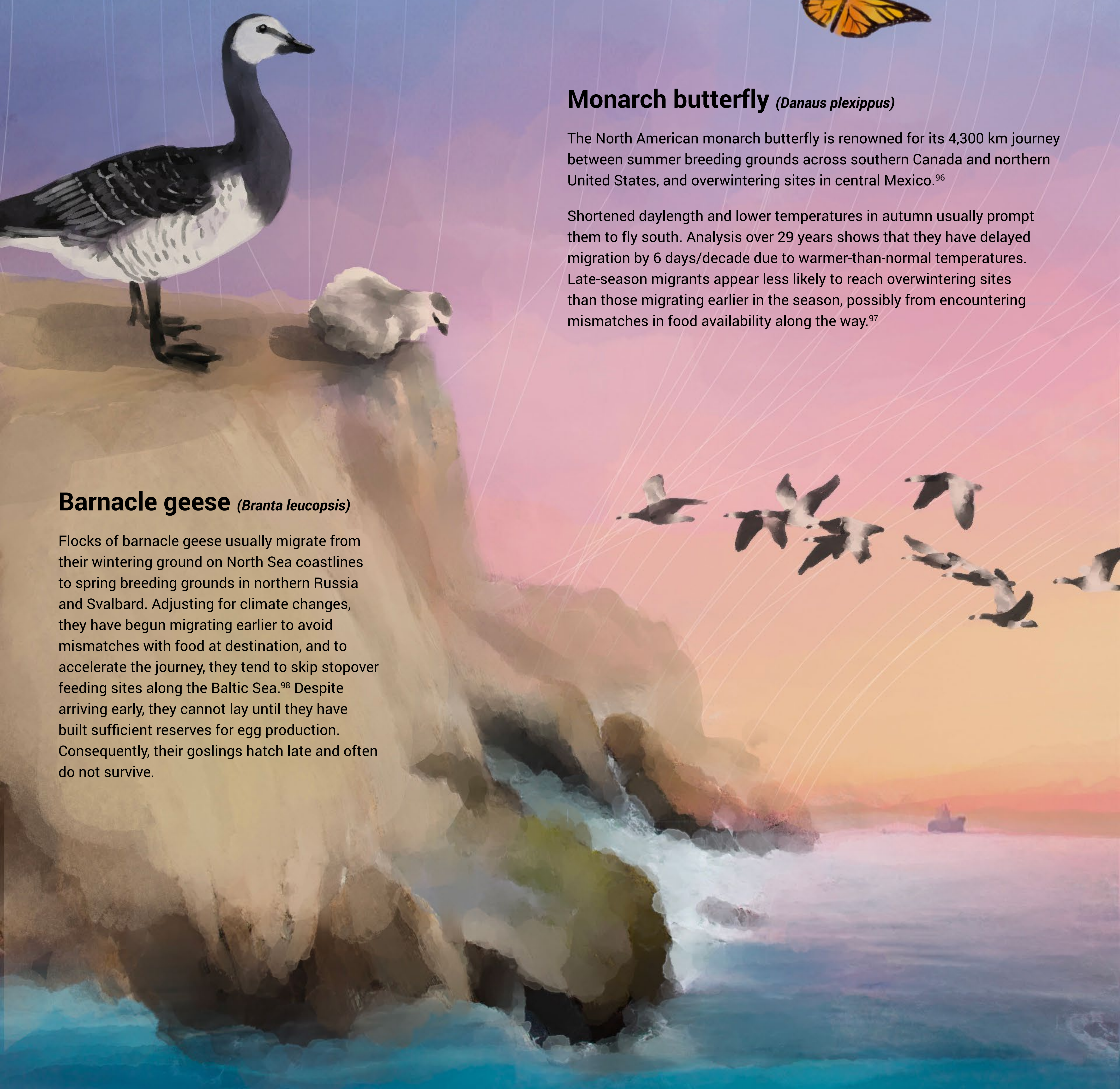
The white stork is a long-lived migratory bird that overwinters throughout Africa.[93] They adapt their migratory timing to advance arrival at breeding grounds in different parts of Europe and nest early to avoid mismatch with food supply.

Early breeding exposes hatchlings to unfavourable conditions, such as strong wind and heavy rainfall. With extreme weather events expected to become more frequent under changing climate, white stork hatchling mortality may increase in the future.[94,95]

Monarch butterfly *(Danaus plexippus)*

The North American monarch butterfly is renowned for its 4,300 km journey between summer breeding grounds across southern Canada and northern United States, and overwintering sites in central Mexico.[96]

Shortened daylength and lower temperatures in autumn usually prompt them to fly south. Analysis over 29 years shows that they have delayed migration by 6 days/decade due to warmer-than-normal temperatures. Late-season migrants appear less likely to reach overwintering sites than those migrating earlier in the season, possibly from encountering mismatches in food availability along the way.[97]



Barnacle geese *(Branta leucopsis)*

Flocks of barnacle geese usually migrate from their wintering ground on North Sea coastlines to spring breeding grounds in northern Russia and Svalbard. Adjusting for climate changes, they have begun migrating earlier to avoid mismatches with food at destination, and to accelerate the journey, they tend to skip stopover feeding sites along the Baltic Sea.[98] Despite arriving early, they cannot lay until they have built sufficient reserves for egg production. Consequently, their goslings hatch late and often do not survive.

Sea turtles

A range of migratory sea turtles have responded to rising seawater temperatures by shifting their timing of nesting. Loggerhead sea turtles (*Caretta caretta*) are found to nest earlier, while leatherback sea turtles (*Dermochelys coriacea*) have delayed nesting.[99-102]

However, the observed shifts in nesting phenology are likely insufficient to track optimal environmental conditions.[101-103] Beach temperatures during incubation influence hatching success and directly determine the sex of hatchling – females are produced in higher temperatures. In a rapidly changing climate, hatching success and biased sex ratio will have implications for sea turtle populations.

Baleen whales

Most baleen whales migrate seasonally between low-latitude calving grounds and higher-latitude feeding grounds, where they prey on dense concentrations of krill or forage fishes.[85,104,105]

Many baleen species are known to shift migratory timings, depending on prey availability. In the past 27 years, fin and humpback whales have advanced their arrival by 1 day/year at the Gulf of St. Lawrence feeding grounds off eastern Canada. This is likely due to earlier ice break-up and rising sea surface temperature, which triggers earlier plankton bloom and influences prey abundance.[85] Shorter-distance migrants like fin whales may reduce migration due to temperature changes and less winter sea ice, but it is harder for long-distance migrants like humpback whales to correctly time their arrival for abundant prey.[85]

Colombia's Gorgona National Natural Park is an important breeding and calving ground for Eastern South Pacific humpback whales. Their arrival has shifted up to 1 month earlier over the last 3 decades. This is likely due to changes in sea ice formation in Antarctic feeding grounds affecting krill availability, and less prey being a cue to return to tropical waters.[105]

Eastern North Pacific blue whales are also known to alter migration, arriving at their feeding grounds off California approximately 42 days earlier than 10 years ago. This shift was associated with at least a 2°C increase in sea surface temperature, and the resultant krill abundance.[106]

Although phenotypic plasticity – the ability to adapt in response to changing environmental signals – allows these species to adjust migratory timings, modifying the timing of a life stage can negatively affect another within the annual life cycle. Remaining longer on feeding grounds can cut reproduction time, and vice versa.[106] Adaptation in human activities, including fisheries, maritime traffic, and exploratory seismic testing, is also needed to accommodate whales' changing sojourns within and outside protected areas.[105]

3.

Evolving toward new synchronies

Climate change attribution for observed mismatches depends upon long-term research on the phenology of interacting species within an ecosystem. Long-term studies are essential, but the major challenge is proving causality. Climate change may influence temperatures and rainfall, but other factors may simultaneously influence species responses, such as land-use change, resource overexploitation, invasive species, and other ecological stressors. Uncertainty around causality can be partly addressed by minimizing variables: observing responses either in different locations, comparing populations in areas with a lot of warming to those with a little, or in different time periods, comparing populations in years with rapidly increasing temperatures to years with slower increases.[76,107] These approaches allow a better estimate of the specific effect of temperature increase on species' phenology, although they do not solve issues involving other environmental factors influenced by temperature. For instance, in many regions, precipitation patterns change dramatically with varying climatic conditions, altering the timing, frequency and intensity of rainy seasons.[108,109] As data accumulate, researchers realize that combinations of phenological mechanisms – temperature, photoperiod and precipitation, for instance – may need to align for the phenological cue to take effect.

A strong phenological shift in a population in response to environmental change indicates a large proportion of the individuals have the ability to change timing in the same direction, known as phenological plasticity.[110] Empirical evidence suggests that this plasticity is the main source of observed climate-related phenological shifts.[111] But individual or population plasticity may not be able to keep up with the rapid environmental changes we are experiencing.[112] Species also require genetic change to adapt successfully, which is more likely in species with short generation time, like insects, than in trees that regenerate over decades.[113] There are a handful of examples where genetic change, as a response to climate change, can be recognized as microevolution, mainly in insects and some birds.[114,115] Overall, genetic changes are happening at a much slower rate than the climate is changing.

Phenological microevolution, the process of natural selection where genetic changes shift the phenology of species to better fit the changed climate, most likely played an important role in species and ecosystem adaptation to past warming periods.[113] Still, as the rate of warming is much faster now – perhaps by as much as a factor of 100 – even microevolution will likely emerge too slowly for current rates of climate change.[116]

In practice, conservation and ecosystem management measures could be taken to encourage favourable conditions for microevolution.[117] One measure is to support and nurture the genetic diversity of populations, as this is the crucial prerequisite for microevolution and natural selection. Increasing ecological connectivity through habitat corridors would enable plant colonization and movement of animal species with novel genetic material within a particular ecosystem, promoting genetic diversity and increasing the chances of successful adaptation.[118]

Out of reach

The red knot (*Calidris canutus*) is a medium-sized shorebird in the sandpiper family. The global population is in decline and considered Near Threatened. The 6 subspecies of red knot migrate remarkably long distances from the high Arctic breeding grounds to wintering grounds across different continents.[119]

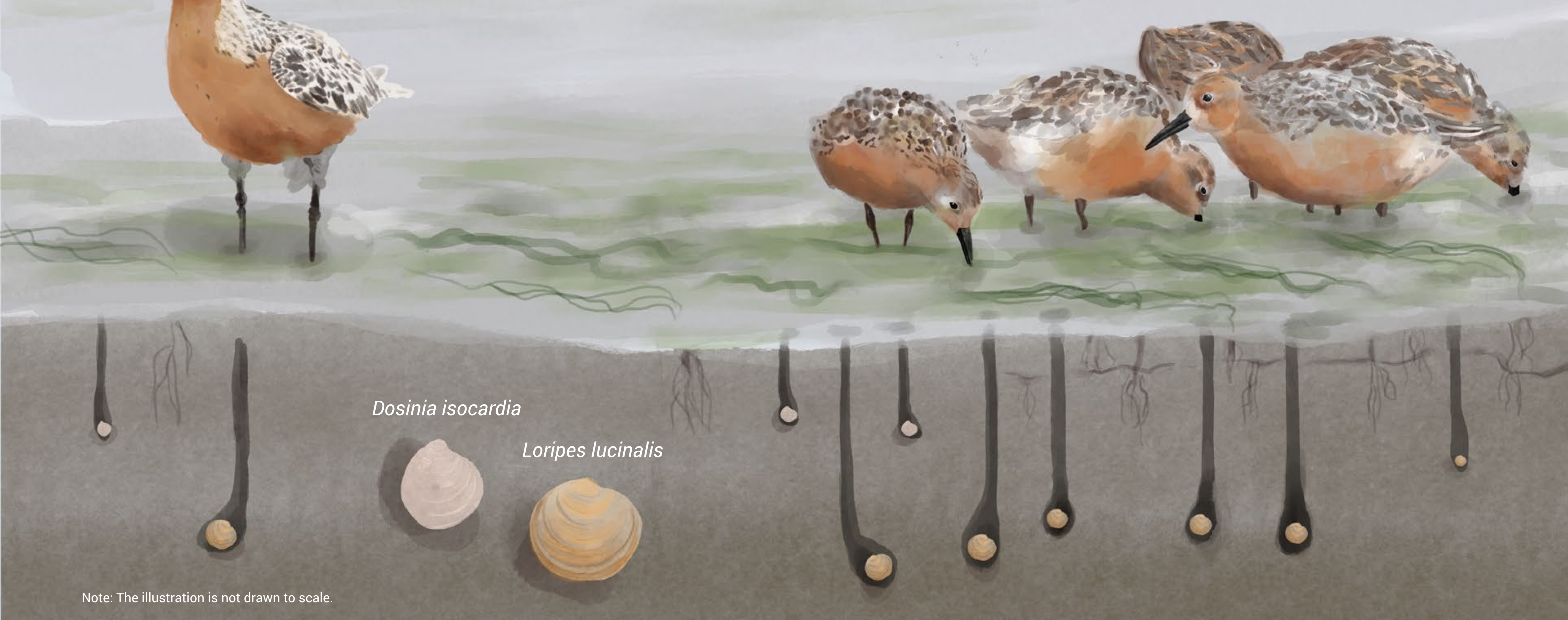
A subspecies, *Calidris canutus canutus*, breeds in central and northern Siberia, and migrates to warmer areas along the coast of Mauritania, notably Banc d'Arguin National Park. As the snow starts to melt, they mate and lay eggs. Red knot chicks feed on insects that seasonally emerge from thawing tundra permafrost, in preparation for the long voyage to Africa.[120]

In the last 3 decades, snowmelt duration in the high Arctic has progressively advanced by 0.5 days/year, resulting in the early emergence and abundance of insects. This shift in insect phenology causes a series of consequences for the red knots in later life stages.[120,121]

Since the birds have not adjusted their breeding phenology, offspring miss the peak of their food abundance. Poor food resources mean poor growth. Juvenile red knots become smaller and have shorter bills during summers with early snowmelt.[120]

Once in West Africa, their main food source changes to mollusc buried in intertidal sediments. These shorter-billed birds have less access to highly abundant bivalve species (*Loripes lucinalis*) buried deeper in the sediments. Instead, they can only consume shallowly buried rhizomes of seagrass (*Zostera noltii*) and rare species of bivalve (*Dosinia isocardia*).

This knock-on effect leads to increased mortality of the short-billed red knots, which demonstrates the complex implications of a mismatch in one location and one part of the life cycle with another part that takes place halfway across the globe.[120]



Note: The illustration is not drawn to scale.

4.
Bridges to new harmonies

Phenological shifts can only be determined from long-term records. Data collection is conducted by scientific institutions, universities, governments, and NGOs. Initiatives such as the African Phenology Network, Australia's TERN project, India's SeasonWatch, the UK Nature's Calendar, and the USA National Phenology Network include observations by citizens to track plants, insects, birds and mammals. These comprehensive data sets allow scientists to single out species and locations most at risk. They also provide data for IPCC estimates of tolerable warming rates for ecosystems, underpinning governmental objectives to reduce global warming to limits set by the Paris Agreement.[122]

Phenological monitoring and citizen science

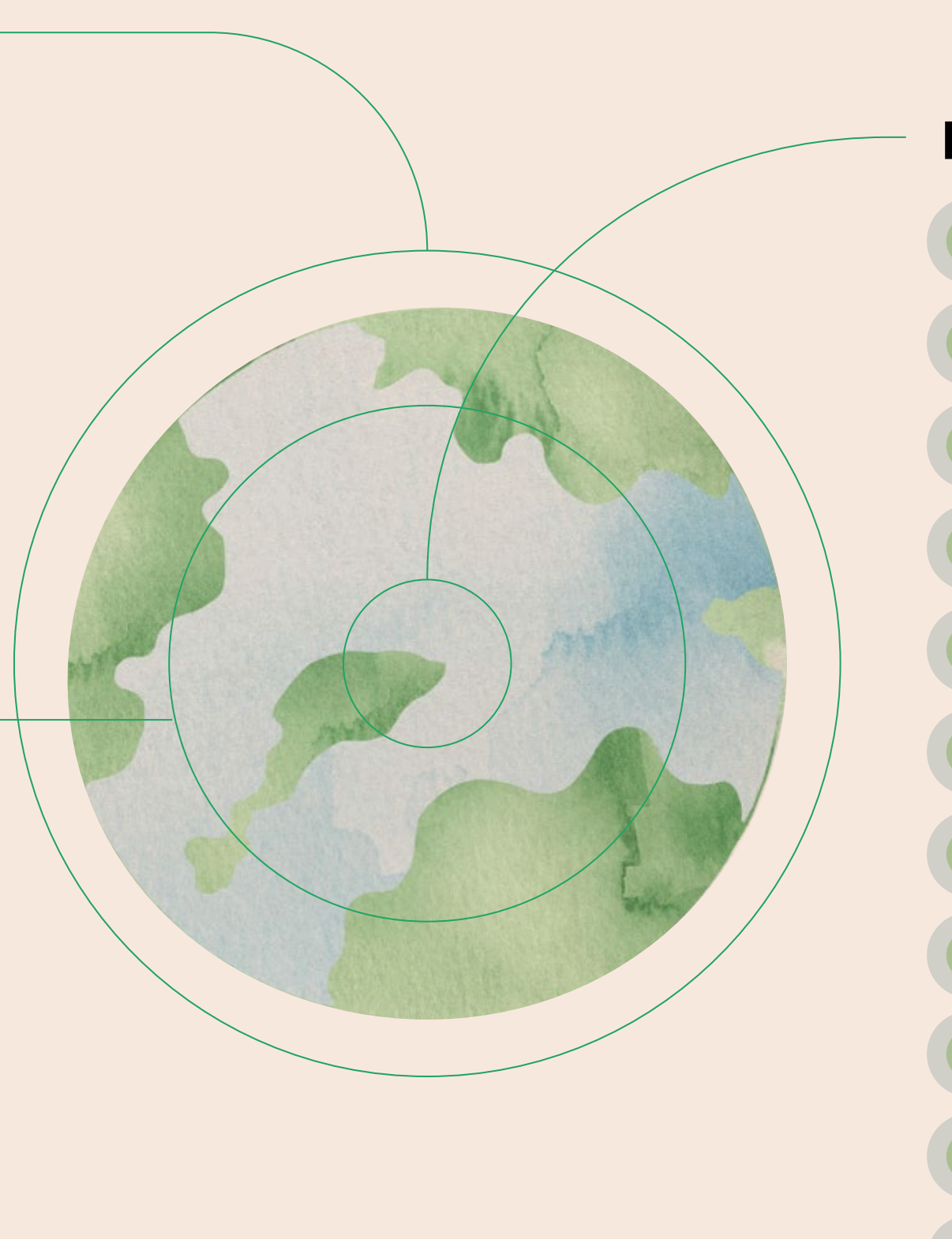
Farmers, gardeners and nature-lovers have been applying their understanding of phenological stages all around the world, for centuries. Regional and local networks allow participants to exchange knowledge and advice on diverse environments and ecosystems. With modern communication tools, identifying and tracking the development of plants and animals has become a common pastime in many countries.[123]

Formal phenological gardens contain a selected array of plants to monitor their responses to changing local conditions. Scientists working with national botanical gardens and other long-established efforts set up areas within those confines to grow the same selection of plants across different latitudes, longitudes and elevations, and collect data to compare phenological responses over time. These large-scale plant-behaviour observation systems offer data sets for other researchers to establish baselines and track trends for their own work.[124]

By studying the phenology and adaptive changes of keystone species, the collected data provide solid biological evidence of climate changes and adaptive responses from living collections that supports long-term monitoring of climate change biology.[125]

Less formal phenological gardens are an important teaching tool about the crucial timing in the life cycles of species, but they too must follow certain protocols for data quality. The Global Learning and Observations to Benefit the Environment (GLOBE) Program offers guidelines for thousands of participating schools in 125 countries.[126] After three decades, the GLOBE Program is now expanding its methods, protocols, and databases to also include citizen scientists' observations.[127] Citizen science contributions to phenological knowledge span from noting flowering dates in their gardens to observations of migrating herds for verifying aerial and satellite images.[128] An enduring citizen science project, the Christmas Bird Count initiated by the US National Audubon Society in 1900, covers most of North America and has provided solid data on the decline of bird populations over more than a century.[129]

A selection of phenology citizen science projects and activities



Global coverage

- Earthdive
- Global Phenological Monitoring Programme
- GLOBE Program Phenology Protocols
- International Waterbird Census
- WorldBirds

Regional coverage

- The African Phenology Network
- e-Butterfly
- Hummingbird Conservation Network
- International Phenological Gardens of Europe
- MonarchWatch
- Pan European Phenology Project

National coverage

- Centro de Informação en Saúde Silvestre
- Chinese Phenological Observation Network
- ClimateWatch, Australia
- Farmers' Wildlife Calendar, Ireland
- Nature Today, Netherlands
- NatureWatch, Canada
- Phaenonet, Switzerland
- PhenoRangers, Switzerland
- SeasonWatch, India
- UK Environmental Change Network
- USA National Phenology Network

Phenological shifts and mismatches, attributed to climate change, have been affecting agricultural ecosystem services for decades.[1,71,130-132] To ameliorate problems of advanced growing seasons, growing stages curtailed by heat or drought, and other climate-change repercussions, farmers have been selecting more climate-resilient cultivars.[133] Adopting new techniques, trying new seeds, sharing seed banks, and exploiting extension services are all aspects of climate-smart agriculture, promoted by the Food and Agriculture Organization of the United Nations, many NGOs, and national and sub-national agencies.[134]

Limited research has studied how phenological shifts and mismatches affect natural resource management and biodiversity conservation, with managers often unclear on how to incorporate the data into practice.[135,136] Phenological data could inform climate response, optimize implementation of monitoring, and support climate change vulnerability assessment.[135] This is especially important in less-studied areas, such as many southern hemisphere locations.[18,19] Managers need to consider how phenological changes affect their current strategies. For example, fisheries managers typically survey fish populations annually, targeting dates when populations were most abundant in an area historically. Phenological shifts could result in surveys conducted at the wrong time of the year, which would skew population estimates and catch allowances.[60]

Recent reviews of multiple specific case studies have mapped out examples of phenology, phenological shifts, and phenological mismatches in extended coverage.[27,32,33,49] This wider perspective considering larger numbers of species, ecosystems and regions and diverse phenological mechanisms at work can inform the approaches needed to help human communities and ecosystems adapt to climate-changed conditions.

Larger-scale efforts to strengthen the integrity of biological diversity will build resilience and adaptability throughout ecosystems.[137] Rehabilitating habitats, building habitat corridors to enhance ecological connectivity and genetic diversity, adjusting protected-area boundaries as species' ranges shift, and conserving biodiversity in productive landscapes are all necessary immediate management interventions.[138,139]

In conclusion, anthropogenic climate change leads to phenological shifts in both terrestrial and aquatic ecosystems. These shifts can lead to mismatches, with major consequences for individuals, populations, communities and whole ecosystems. Climate change is accelerating too quickly for many species to adapt through their natural phenological capacity.[140] Preserving the integrity of functioning biological diversity, ending habitat destruction, and pursuing ecosystem restoration will bolster the natural systems upon which we depend. However, without continued efforts to drastically reduce greenhouse gas emissions, these conservation measures will only delay the loss of those essential ecosystem services. For species and ecosystems to match accelerated rhythms set by climate change, time and opportunity to achieve new harmonies will be needed.

Food production and phenology

All season-dependent activities are inherently risky, from hot spells causing a poor wheat harvest or marine heatwaves affecting local fish stocks, to unseasonal weather impinging on travel and tourism. But food production is the most critical socioeconomic activity affected by phenological shifts as climate change accelerates.[2]

Warming trends have shifted the phenological stages of a variety of staple crops over decades and across continents.[71,141-145] The change in growth stages has consequences on crop yields and quality.[144-147] The shifts have been observed in crops ranging from cereals such as barley, maize, rice, rye, sorghum, soybean and wheat, to cotton, grapevines, and fruit trees such as apple, cherry, pear and mango.[71,143,148-154] At the same time, crop management decisions on sowing date and cultivar choice have direct effects on crop phenology.[71,155] They are often used as adaptation strategies to counteract climate-induced phenological changes.[71]

With the constant introduction of new varieties and variations in the sowing calendar, farming practices and climate have a combined influence on diverse changes in crop phenology.[71,151,155-160]

Many highly productive regions suffer more frequent, extreme climate-related events that also interfere with critical growth stages.[161] Climate-scenario crop models project that many global regions will experience reductions in yields, with additional challenges from soil degradation, unsustainable farming, pests, and water scarcity.[162]

Adaptation practices focus on implementing sustainable management, including organic fertilizer use, combining legumes with grasses, optimizing irrigation, breeding plants selectively, and choosing more resilient cultivars.[71] Projections of agricultural productivity often incorporate adaptation to climate change in their predictions, with the call for more observational evidence on the effectiveness of adaptation practices.[161]

Fisheries

Successful growth to maturity and production of fish stocks is strongly affected by any climate-induced changes to the phenology and distribution of both fish and prey.[67] For many marine fish species, spawning phenology is sensitive to temperature cues.[69,163] Spawning time, subsequent transport of fish larvae during the planktonic stage, and abundance of suitable food are critical factors for early development and survival.[43,67,164,165] Reduced survival at early life stages leads to fewer additions to the adult stock.[59] Changes in the timing of reproduction and migration and resulting phenological mismatches with prey availability have been observed in and projected for species that are important to inland and marine fisheries in some regions.[166]

Shifting species' phenologies and environmental conditions under climate change present challenges for fisheries management.[166] With observed shifts in timing of critical life stages and geographic distribution, common practices used by fisheries authorities, such as closed fishing seasons and areas, may not provide adequate protection.[59,163,166] Management measures and restrictions should consider existing and emergent critical habitats, and changes in spawning sites, nursery grounds and migratory corridors. An ecosystem-wide approach that is adaptive to both climate and environmental changes is essential for sustainable fisheries management within resilient ecosystems.[166]

Inland fisheries

Patterns of rainfall and snowfall altered by climate change affect the availability, quality and flow regime of fresh water. These are important phenological cues for species in freshwater habitats, and modifications in water flow and levels, as well as flood events, affect the timing of migration and spawning.[166-168]

Marine heatwaves

The 2012 intense marine heatwave warmed north Atlantic waters by 1-3°C, inducing a phenological response in lobsters and majorly affecting fisheries in the Gulf of Maine. Cued by rising temperatures, lobsters migrated inshore earlier, moulted faster, and reached legal fishing size sooner. The longer fishing season, overharvesting, and unmet market demand led to a price collapse.[169]

The Sardine Run

A seasonal mass migration of sardines (*Sardinops sagax*) from the temperate waters of the Agulhas Bank towards the sub-tropical waters off the northern coast of KwaZulu-Natal, South Africa, occurs annually. From May to July, the phenomenon attracts many opportunistic marine predators, as well as fishing activities and tourism.[170]

Records over 60 years show a progressive delay in arrival of sardines off Durban by 1.3 days/decade. This delay coincided with a change in the threshold thermal range for sardines as the 21°C isotherm shifted south.[170] If the shifting trends continue, the sardine run may no longer extend as far north, or the run may collapse in the long term, with implications for predators, fisheries and tourism.[170,171]

References

1. Lieth, H. (1974). Purposes of a Phenology Book. In *Phenology and Seasonality Modeling. Ecological Studies (Analysis and Synthesis)*. Lieth H. (ed.). Springer, Berlin, Heidelberg. Vol. 8. https://doi.org/10.1007/978-3-642-51863-8_1
2. Liang, L. (2019). Phenology. *Reference Module in Earth Systems and Environmental Sciences*. https://doi.org/10.1016/B978-0-12-409548-9.11739-7
3. Flynn, D.F.B. and Wolkovich, E.M. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 219(4), 1353-1362. https://doi.org/10.1111/nph.15232
4. Adole, T., Dash, J., Rodriguez-Galiano, V. and Atkinson, P.M. (2019). Photoperiod controls vegetation phenology across Africa. *Communications Biology,* 2, 391. https://doi.org/10.1038/s42003-019-0636-7
5. Ren, S., Vitasse, Y., Chen, X., Peichl, M. and An, S. (2022). Assessing the relative importance of sunshine, temperature, precipitation, and spring phenology in regulating leaf senescence timing of herbaceous species in China. *Agricultural and Forest Meteorology* 313, 108770. https://doi.org/10.1016/j.agrformet.2021.108770
6. Gienapp, P., Hemerik, L. and Visser, M.E. (2005). A new statistical tool to predict phenology under climate change scenarios. *Global Change Biology* 11(4), 600–606. https://doi.org/10.1111/j.1365-2486.2005.00925.x
7. Way, D.A. and Montgomery, R.A. (2014). Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment* 38(9), 1725-1736. https://doi.org/10.1111/pce.12431
8. Forrest, J.R.K. (2016). Complex responses of insect phenology to climate change. *Current Opinion in Insect Science* 17, 49-54. https://doi.org/10.1016/j.cois.2016.07.002
9. Marshall, K.E., Gotthard,K. and Williams, C.M. (2020). Evolutionary impacts of winter climate change on insects. *Current Opinion in Insect Science* 41, 54-62. https://doi.org/10.1016/j.cois.2020.06.003
10. Wang, H., Wang, H., Ge, Q. and Dai, J. (2020) The Interactive Effects of Chilling, Photoperiod, and Forcing Temperature on Flowering Phenology of Temperate Woody Plants. *Frontiers in Plant Science* 11(443), 1-12. https://doi.org/10.3389/fpls.2020.00443
11. Bowman, D.M.J.S., Kolden, C.A., Abatzoglou, J.T., Johnston, F.H., van der Werf, G.R., Flannigan, M. (2020). Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment* 1, 500–515. https://doi.org/10.1038/s43017-020-0085-3
12. Keeley, J.E. and Fotheringham, C.J. (2000). Role of fire in regeneration from seed. In *Seeds: the ecology of regeneration in plant communities*. Fenner, M. (Eds.). CABI. Chapter 14. 311-330. https://doi.org/10.1079/9780851994321.0311
13. Bailly, D., Agostinho, A.A. and Suzuki, H.I. (2008). Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Research and Applications* 24(9), 1218-1219. https://doi.org/10.1002/rra.1147
14. Arevalo, E., Maire, A., Tétard, S., Prévost, E., Lange, F., Marchand, F. *et al.* (2021). Does global change increase the risk of maladaptation of Atlantic salmon migration through joint modifications of river temperature and discharge? *Proceedings of the Royal Society B* 288(1964), 20211882. http://doi.org/10.1098/rspb.2021.1882
15. Teichert, N., Benitez, J.P., Dierckx, A., Tétard, S., De Oliveira, E., Trancart, T., Feunteun, E. and Ovidio, M. (2020). Development of an accurate model to predict the phenology of Atlantic salmon smolt spring migration. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30(8), 1552-1565. https://doi.org/10.1002/aqc.3382
16. Chambers, L.E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L.J. *et al*. (2013) Phenological Changes in the Southern Hemisphere. *PLOS ONE* 8(10), e75514. https://doi.org/10.1371/journal.pone.0075514
17. Butt, N., Seabrook, L., Maron, M., Law, B.S., Dawson, T.P., Syktus, J. *et al*. (2015). Cascading effects of climate extremes on vertebrate fauna through changes to low-latitude tree flowering and fruiting phenology. *Global Change Biology* 21(9), 3267-3277. https://doi.org/10.1111/gcb.12869
18. Sheldon, K.S. (2019). Climate Change in the Tropics: Ecological and Evolutionary Responses at Low Latitudes. *Annual Review of Ecology, Evolution, and Systematics* 50, 303–33. https://doi.org/10.1146/annurev-ecolsys-110218-025005

19. Morellato, L.P.C., Alberton, B., Alvarado, S.T., Borges, B., Buisson, E., Camargo, M.G.G. *et al.* (2016). Linking plant phenology to conservation biology. *Biological Conservation* 195, 60-72. https://doi.org/10.1016/j.biocon.2015.12.033

20. Ramaswami, G., Datta, A., Reddy, A., and Quader, S. (2018). Tracking phenology in the tropics and in India: the impacts of climate change. In *Biodiversity and Climate Change: An Indian Perspective*. Bhatt, J.R., Das, A. and Shanker, K. (eds.). 45-69. New Delhi: Ministry of Environment, Forest and Climate Change, Government of India. https://www.ncf-india.org/other/1116

21. Sakai, S. and Kitajima, K. (2019). Tropical phenology: Recent advances and perspectives. *Ecological Research*, 34(1), 50-54. https://doi.org/10.1111/1440-1703.1131

22. Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918), 37-42. https://doi.org/10.1038/nature01286

23. Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R. *et al.* (2010). Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16(12), 3304-3313. https://doi.org/10.1111/j.1365-2486.2010.02165.x

24. Donnelly, A., Caffarra, A. and O'Neill, B.F. (2011). A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. *International Journal of Biometerology* 55(6), 805-817. https://doi.org/10.1007/s00484-011-0426-5

25. Stevenson, T.J., Visser, M.E., Arnold, W., Barrett, P., Biello, S., Dawson, A. *et al*. (2015). Disrupted seasonal biology impacts health, food security and ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 282(1817), 20151453. https://doi.org/10.1098/rspb.2015.1453

26. Kharouba, H.M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E. and Wolkovich, E.M. (2018). Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences of the United States of America* 115(20), 5211–5216. https://doi.org/10.1073/pnas.1714511115

27. Chmura, H.E., Kharouba, H.M., Ashander, J., Ehlman, S.M., Rivest, E.B. and Yang, L.H. (2019). The mechanisms of phenology: the patterns and processes of phenological shifts. *Ecological Monographs* 89(1), e01337. https://doi.org/10.1002/ecm.1337

28. Stemkovski, M., Pearse, W.D., Griffin, S.R., Pardee, G.L., Gibbs, J., Griswold, T. *et al.* (2020). Bee phenology is predicted by climatic variation and functional traits. *Ecology Letters* 23(11), 1589-1598. https://doi.org/10.1111/ele.13583

29. Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* 421(6918), 57-60. https://doi.org/10.1038/nature01333

30. Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13(9), 1860–1872. https://doi.org/10.1111/j.1365-2486.2007.01404.x

31. Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J. *et al.* (2013). Global imprint of climate change on marine life. *Nature Climate Change* 3(10), 919-925. https://doi.org/10.1038/nclimate1958

32. Poloczanska, E.S., Burrows, M.T., Brown, C.J., Molinos, J.G., Halpern, B.S., Hoegh-Guldberg, O. *et al.* (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science* 3(62). https://doi.org/10.3389/fmars.2016.00062

33. Renner, S.S. and Zohner, C.M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49, 165-182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

34. Visser, M.E. and Gienapp, P. (2019). Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution* 3(6), 879-885. https://doi.org/10.1038/s41559-019-0880-8

35. Staggemeier, V.G.,Camargo, M.G.G., Diniz-Filho, J.A.F., Freckleton, R., Jardim, L. and Morellato, L.P.C. (2019). The circular nature of recurrent life cycle events: a test comparing tropical and temperate phenology. *Journal of Ecology* 108(2), 393-404. https://doi.org/10.1111/1365-2745.13266

36. World Meteorological Organization (2021). FAQs - El Niño/La Niña. https://public.wmo.int/en/about-us/frequently-asked-questions/el-niño-la-niña. Accessed 22 January 2021.
37. Detto, M., Wright, S.J., Calderón, O. and Muller-Landau, H.C. (2018). Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation. *Nature Communications* 9, 913. https://doi.org/10.1038/s41467-018-03306-9
38. Moriuchi E. and Basil, M. (2019). The Sustainability of Ohanami Cherry Blossom Festivals as a Cultural Icon. *Sustainability* 11(6), 1820. https://doi.org/10.3390/su11061820
39. Aono, Y. and Kazui, K. (2008). Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. *International Journal of Climatology* 28(7), 905-914. https://doi.org/10.1002/joc.1594
40. Aono, Y. and Saito, S. (2010). Clarifying springtime temperature reconstructions of the medieval period by gap-filling the cherry blossom phenological data series at Kyoto, Japan. *International Journal of Biometeorology* 54, 211-219. https://doi.org/10.1007/s00484-009-0272-x
41. Aono, Y. (2015). Cherry blossom phenological data since the seventeenth century for Edo (Tokyo), Japan, and their application to estimation of March temperatures. *International Journal of Biometeorology* 59, 427–434. https://doi.org/10.1007/s00484-014-0854-0
42. Primack, R.B., Higuchi, H. and Miller-Rushing, A.J. (2009). The impact of climate change on cherry trees and other species in Japan. *Biological Conservation* 142(9),1943-1949. https://doi.org/10.1016/j.biocon.2009.03.016
43. Edwards, M. and Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430, 881–84. https://doi.org/10.1038/nature02808
44. Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. and Schwartz, M.D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22(7), 357-365. https://doi.org/10.1016/j.tree.2007.04.003
45. Morellato, L.P.C., Camargo, M.G.G. and Gressler, E. (2013). A review of plant phenology in South and Central America. In *Phenology: an integrative environmental science*. Schwartz, M.D. (eds.). Chapter 6. 91–113. Dordrecht: Springer. https://doi.org/10.1007/978-94-007-6925-0_6
46. Vitasse, Y., Signarbieux, C. and Fu, Y.H. (2018). More uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences of the United States of America* 115(5), 1004-1008. https://doi.org/10.1073/pnas.1717342115
47. Staudinger, M.D., Mills, K.E., Stamieszkin, K., Record, N.R., Hudak, C.A. *et al.* (2019). It’s about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fisheries Oceanography* 28(5), 532–566. https://doi.org/10.1111/fog.12429
48. Gérard, M., Vanderplanck, M., Wood, T. and Michez, D. (2020). Global warming and plant–pollinator mismatches. *Emerging Topics in Life Sciences* 4(1), 77–86. https://doi.org/10.1042/ETLS20190139
49. Iler, A.M., CaraDonna, P.J., Forrest, J.R.K. and Post, E. (2021). Demographic Consequences of Phenological Shifts in Response to Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 52, 221–245. https://doi.org/10.1146/annurev-ecolsys-011921-032939
50. Lima, D.F., Mello, J.H.F., Lopes, I.T., Forzza, R.C., Goldenberg, R. and Freitas, L. (2021). Phenological responses to climate change based on a hundred years of herbarium collections of tropical Melastomataceae. *PLOS ONE* 16(5), e0251360. https://doi.org/10.1371/journal.pone.0251360
51. Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A. *et al.* (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews* 96(5),1816–1835. https://doi.org/10.1111/brv.12727
52. Visser, M.E., Noordwijk, A.V., Tinbergen, J.M. and Lessells, C.M. (1998). Warmer springs lead to mistimed reproduction in great tits (Parus major). *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265(1408), 1867-1870. https://doi.org/10.1098/rspb.1998.0514

53. Both, C. and Visser, M.E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411(6835), 296–298. https://doi.org/10.1038/35077063

54. Visser, M.E., Holleman, L.J.M. and Gienapp, P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147, 164–172. https://doi.org/10.1007/s00442-005-0299-6

55. Visser, M.E., te Marvelde, L. and Lof, M.E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153(1), 75–84. https://doi.org/10.1007/s10336-011-0770-6

56. Regular, P.M., Hedd, A., Montevecchi, W.A., Robertson, G.J., Storey, A.E. and Walsh, C.J. (2014). Why timing is everything: Energetic costs and reproductive consequences of resource mismatch for a chick rearing seabird. *Ecosphere* 5(12), 1-13. https://doi.org/10.1890/es14-00182.1

57. Moyes, K., Nussey, D.H., Clements, M.N., Guinness, F.E., Morris, A., Morris, S. *et al.* (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology* 17(7), 2455–2469. https://doi.org/10.1111/j.1365-2486.2010.02382.x

58. Tomotani, B.M., van der Jeugd, H., Gienapp, P., de la Hera, I., Pilzecker, J., Teichmann, C. and Visser, M.E. (2018). Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. *Global Change Biology* 24(2), 823-835. https://doi.org/10.1111/gcb.14006

59. Asch, R.G., Stock, C.A. and Sarmiento, J.L. (2019). Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Global Change Biology* 25(8), 2544–2559. https://doi.org/10.1111/gcb.14650

60. Asch, R.G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America* 112(30), E4065-E4074. https://doi.org/10.1073/pnas.1421946112

61. Asch, R.G. (2019). Changing seasonality of the sea: past, present, and future. In *Predicting Future Oceans, Sustainability of Ocean and Human Systems Amidst Global Environmental Change*. Cisneros-Montemayor, A.M., Cheung, W.W.L. and Ota, Y. (eds.). Chapter 4. 39-51. https://doi.org/10.1016/B978-0-12-817945-1.00004-6

62. Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Löf, A. and Ragnarsson, B. (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology* 82(12), 1864–1870. https://doi.org/10.1139/z04-184

63. Li, Y., Cohen, J.M. and Rohr, J.R. (2013). Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology* 8(2), 145-161. https://doi.org/10.1111/1749-4877.12001

64. Nash, L.N., Antiqueira, P.A.P., Romero, G.Q., de Omena, P.M. and Kratina, P. (2021). Warming of aquatic ecosystems disrupts aquatic–terrestrial linkages in the tropics. *Journal of Animal Ecology* 90(7), 1623-1634. https://doi.org/10.1111/1365-2656.13505

65. Post, E. and Forchhammer, M.C. (2008). Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363(1501), 2367-2373. https://doi.org/10.1098/rstb.2007.2207

66. Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.M., Delorme, D., Warnant, C. and Bonenfant, C. (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biology* 12(4), e1001828. https://doi.org/10.1371/journal.pbio.1001828

67. Brander, K. (2010). Impacts of climate change on fisheries. *Journal of Marine Systems* 79(3-4), 389-402. https://doi.org/10.1016/j.jmarsys.2008.12.015

68. The Food and Agriculture Organization of the United Nations (FAO) (2018). *Impacts of climate change on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options*. http://www.fao.org/3/i9705en/I9705EN.pdf

69. Rogers, L.A. and Dougherty, A.B. (2019). Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biology* 25(2), 708-720. https://doi.org/10.1111/gcb.14483

70. Vitasse, Y., Schneider, L., Rixen, C., Christen, D. and Rebetez, M. (2018). Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. *Agricultural and Forest Meteorology* 248, 60-69. https://doi.org/10.1016/j.agrformet.2017.09.005

71. Fatima, Z., Ahmed, M., Hussain, M., Abbas, G., Ul-Allah, S., Ahmad, S. *et al.* (2020). The fingerprints of climate warming on cereal crops phenology and adaptation options. *Scientific Reports* 10(1), 18013. https://doi.org/10.1038/s41598-020-74740-3

72. Perrins, C.M. (1991). Tits and their caterpillar food supply. *Ibis* 133(1), 49-54. https://doi.org/10.1111/j.1474-919X.1991.tb07668.x

73. Van Asch, M., Tienderen, P.H., Holleman, L.J.M. and Visser, M.E. (2007). Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology* 13(8), 1596–1604. https://doi.org/10.1111/j.1365-2486.2007.01400.x

74. Visser, M.E., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F. *et al.* (2015). Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biology* 13(4), e1002120. https://doi.org/10.1371/journal.pbio.1002120

75. Charmantier, A., Mccleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. and Sheldon, B.C. (2008). Adaptive Phenotypic Plasticity in Response to Climate Change in a Wild Bird Population. *Science* 320(5877), 800-803. https://doi.org/10.1126/science.1157174

76. Visser, M.E., Lindner, M., Gienapp, P., Long, M.C. and Jenouvrier, S. (2021). Recent natural variability in global warming weakened phenological mismatch and selection on seasonal timing in great tits (*Parus major*). *Proceedings of the Royal Society B* 288(1963), 20211337. https://doi.org/10.1098/rspb.2021.1337

77. Bauer, Z., Trnka, M., Bauerová, J., Možný, M., Štěpánek, P., Bartošová, L. *et al.* (2010). Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. *International Journal of Biometeorology* 54, 99–111. https://doi.org/10.1007/s00484-009-0259-7

78. Matthysen, E., Adriaensen, F. and Dhondt, A.A. (2010). Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus, Parus major*). *Global Change Biology* 17(1), 1-16. https://doi.org/10.1111/j.1365-2486.2010.02213.x

79. Bonamour, S. (2021). Great tit response to climate change. *Nature Climate Change* 11, 802-807. https://doi.org/10.1038/s41558-021-01160-0

80. Cole, E.F., Regan, C.E. and Sheldon, B.C. (2021). Spatial variation in avian phenological response to climate change linked to tree health. *Nature Climate Change* 11, 872–878. https://doi.org/10.1038/s41558-021-01140-4

81. Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F. *et al.* (2009). Travelling through a warming world: climate change and migratory species. *Endangered Species Research* 7(2), 87-99. https://doi.org/10.3354/esr00095

82. Joly, K., Gurarie, E., Sorum, M.S., Kaczensky, P., Cameron, M.D., Jakes, A.F. *et al.* (2019). Longest terrestrial migrations and movements around the world. *Scientific Reports* 9, 15333. https://doi.org/10.1038/s41598-019-51884-5

83. Intergovernmental Panel on Climate Change (2019). Summary for Policymakers. In: *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. https://www.ipcc.ch/srocc/chapter/summary-for-policymakers/

84. Intergovernmental Panel on Climate Change (2021). Summary for Policymakers. In: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* https://www.ipcc.ch/report/ar6/wg1/

85. Ramp, C., Delarue, J., Palsbøll, P.J., Sears, R. and Hammond, P.S. (2015). Adapting to a Warmer Ocean—Seasonal Shift of Baleen Whale Movements over Three Decades. *PLOS ONE* 10(3), e0121374. https://doi.org/10.1371/journal.pone.0121374

86. Kubelka, V., Sandercock, B.K., Székely, R. and Freckleton, R.P. (2022). Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology & Evolution* 37(1), 30-41. https://doi.org/10.1016/j.tree.2021.08.010

87. Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Hüppop, K. *et al.* (2011). Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B: Biological Sciences* 278(1707), 835–842. https://doi.org/10.1098/rspb.2010.1778

88. Secretariat of the Convention on the Conservation of Migratory Species of Wild Animals (2014). *A Review of Migratory Bird Flyways and Priorities for Management.* https://www.cms.int/sites/default/files/publication/CMS_Flyways_Reviews_Web.pdf

89. Lamaris, *et al*. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology* 28(15), 2467–2473. https://doi.org/10.1016/j.cub.2018.05.077

90. Bairlein, F. (2016). Migratory birds under threat. *Science* 354(6312), 547-548. https://doi.org/10.1126/science.aah6647

91. The Zoological Society of London (ZSL) (2010*). Climate change impacts on migratory species - The path ahead*. https://www.cbd.int/cop/cop-10/doc/unep-cms-cop10-cc-en.pdf.

92. Secretariat of the Convention on the Conservation of Migratory Species of Wild Animals (2022). *Ecological Connectivity*. https://www.cms.int/en/topics/ecological-connectivity

93. BirdLife International (2021*). IUCN Red List for birds*. http://datazone.birdlife.org/species/factsheet/white-stork-ciconia-ciconia/text

94. Jovani, R. AND Tella, J.L. (2004) Age-related environmental sensitivity and weather mediated nestling mortality in white storks *Ciconia ciconia*. *Ecography* 27(5), 611–618. https://www.jstor.org/stable/3683463

95. Tobolka, M., Zolnierowicz, K.M. and Reeve, N.F. (2015). The effect of extreme weather events on breeding parameters of the White Stork *Ciconia ciconia. Bird Study* 62(3), 377-385. https://doi.org/10.1080/00063657.2015.1058745

96. Culbertson, K.A., Garland, M.S., Walton, R.K., Zemaitis, L. and Pocius, V.M. (2021). Long-term monitoring indicates shifting fall migration timing in monarch butterflies (*Danaus plexippus*). *Global Change Biology* 28(3), 727-738. https://doi.org/10.1111/gcb.15957

97. Taylor, O.R., Lovett, J.P., Gibo, D.L., Weiser, E.L., Thogmartin, W.E., Semmens, D.J. *et al.* (2019). Is the timing, pace, and success of the monarch migration associated with sun angle? *Frontiers in Ecology and Evolution*, 7, 442. https://doi.org/10.3389/fevo.2019.00442

98. Lameris, T.K., van der Jeugd, H.P., Eichhorn, G., Dokter, A.M., Bouten, W., Boom, M.P. *et al*. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, *28*(15), 2467-2473. https://doi.org/10.1016/j.cub.2018.05.077

99. Robinson, N.J., Valentine, S.E., Tomillo, P.S., Saba, V.S., Spotila, J.R. and Paladino, F.V. (2014). Multidecadal trends in the nesting phenology of Pacific and Atlantic leatherback turtles are associated with population demography. *Endangered Species Research*, 24(3), 197-206. https://doi.org/10.3354/esr00604

100. Patrício, A.R., Hawkes, L.A., Monsinjon, J.R., Godley, B.J. and Fuentes, M.M.P.B. (2021). Climate change and marine turtles: recent advances and future directions. *Endangered Species Research* 44, 363-395. https://doi.org/10.3354/esr01110

101. Almpanidou, V., Katragkou, E. and Mazaris, A.D. (2017). The efficiency of phenological shifts as an adaptive response against climate change: a case study of loggerhead sea turtles (Caretta caretta) in the Mediterranean. *Mitigation and Adaptation Strategies for Global Change* 23(7), 1143–1158. https://doi.org/10.1007/s11027-017-9777-5

102. Butler, C.J. (2019). A Review of the Effects of Climate Change on Chelonians. *Diversity*11(8), 138. https://doi.org/10.3390/d11080138

103. Monsinjon, J., Lopez-Mendilaharsu, M., Lara, P., Santos, A., dei Marcovaldi, M.A., Girondot, M. and Fuentes, M.M. (2019). Effects of temperature and demography on the phenology of loggerhead sea turtles in Brazil. *Marine Ecology Progress Series*, *623*, 209-219. https://doi.org/10.3354/meps12988

104. Moore, S.E., Haug, T., Víkingsson, G.A. and Stenson, G.B. (2019). Baleen whale ecology in arctic and subarctic seas in an era of rapid habitat alteration. *Progress in Oceanography* 176, 102118. https://doi.org/10.1016/j.pocean.2019.05.010

105. Avila, I.C., Dormann, C.F., García, C., Payán, L.F. and Zorrilla, M.Z. (2020). Humpback whales extend their stay in a breeding ground in the Tropical Eastern Pacific. *ICES Journal of Marine Science* 77(1), 109–118. https://doi.org/10.1093/icesjms/fsz251

106. Szesciorka, A.R., Ballance, L.T., Širović, A., Rice, A., Ohman, M.D., Hildebrand, J.A. and Frank, P.J.S. (2020). Timing is everything: Drivers of interannual variability in blue whale migration. *Scientific Reports* 10, 7710. https://doi.org/10.1038/s41598-020-64855-y

107. Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T. *et al.* (2004). Large–scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271(1549), 1657–1662. https://doi.org/10.1098/rspb.2004.2770

108. Dunham, A.E., Razafindratsima, O.H., Rakotonirina, P., Wright, P.C. (2018). Fruiting phenology is linked to rainfall variability in a tropical rain forest. *Biotropica* 50(3), 396-404. https://doi.org/10.1111/btp.12564

109. Suonan, J., Classen, A.T., Sanders, N.J. and He, J.S. (2019). Plant phenological sensitivity to climate change on the Tibetan Plateau and relative to other areas of the world. *Ecosphere* 10(1), e02543. https://doi.org/10.1002/ecs2.2543

110. Bradshaw, A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13, 115–155. https://doi.org/10.1016/S0065-2660(08)60048-6

111. Charmantier, A. and Gienapp, P. (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications* 7(1), 15–28. https://doi.org/10.1111/eva.12126

112. Zettlemoyer, M.A. and Peterson, M.L. (2021). Does Phenological Plasticity Help or Hinder Range Shifts Under Climate Change? *Frontiers in Ecology and Evolution* 9, 392. https://doi.org/10.3389/fevo.2021.689192

113. Visser, M.E. (2008). Keeping up with a warming world: assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences* 275(1635), 649-659. https://doi.org/10.1098/rspb.2007.0997

114. Van Asch, M., Salis, L., Holleman, L.J., Van Lith, B. and Visser, M.E. (2013). Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change* 3(3), 244–248. https://doi.org/10.1038/nclimate1717

115. Helm, B., Van Doren, B.M., Hoffmann, D. and Hoffmann, U. (2019). Evolutionary response to climate change in migratory pied flycatchers. *Current Biology* 29(21), 3714-3719. https://doi.org/10.1016/j.cub.2019.08.072

116. Diffenbaugh, N.S. and Field, C.B. (2013). Changes in ecologically critical terrestrial climate conditions. *Science* 341(6145), 486–492. https://doi.org/10.1126/science.1237123

117. Hoffmann, A.A. and Sgrò, C.M. (2011). Climate change and evolutionary adaptation. *Nature* 470(7335), 479-85. https://doi.org/10.1038/nature09670.

118. Tabor, G. (2019). Ecological connectivity: A bridge to preserving biodiversity. In U*NEP Frontiers 2018/19 – Emerging issues of environmental concern*. United Nations Environment Programme, Nairobi. https://www.unep.org/frontiers

119. BirdLife International (2018*). Species factsheet: Calidris canutus*. http://datazone.birdlife.org/species/factsheet/red-knot-calidris-canutus. Accessed on 09 December 2021.

120. van Gils, J.A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., de Fouw, J. *et al.* (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352(6287), 819-821. https://doi.org/10.1126/science.aad6351

121. Bowden, J.J., Eskildsen, A., Hansen, R.R., Olsen, K., Kurle, C.M. and Høye, T.T. (2015). High-Arctic butterflies become smaller with rising temperatures. *Biology Letters* 11(10), 20150574. http://dx.doi.org/10.1098/rsbl.2015.0574

122. Intergovernmental Panel on Climate Change (2014). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects.* Contribution of Working Group II to the Fifth Assessment. https://www.ipcc.ch/report/ar5/wg2/

123. Mäder, P., Boho, D., Rzanny, M., Seeland, M., Wittich, H.C., Deggelmann, A. *et al.* (2021). The Flora Incognita app – Interactive plant species identification. *Methods in Ecology and Evolution* 12(7), 1335-1342. https://doi.org/10.1111/2041-210X.13611

124. Renner, S.S. and Chmielewski, F.M. (2022). The International Phenological Garden network (1959 to 2021): its 131 gardens, cloned study species, data archiving, and future. *International Journal of Biometeorology* 66(1), 35-43. https://doi.org/10.1007/s00484-021-02185-y

125. Huang, H., Liao, J., Zhang, Z. and Zhan, Q. (2017). Ex situ flora of China. *Plant Diversity* 39(6), 357-364. https://doi.org/10.1016/j.pld.2017.12.001

126. The GLOBE Program (2021). GLOBE Impact Around the World. https://www.globe.gov/about/impact-and-metrics. Accessed 24 Dec 2021.

127. Murphy, T., Riebeek Kohl, H., Ristvey Jr, J.D., Chambers, L.H., and Bourgeault, J. (2018). Global citizen science using the GLOBE Program. https://ui.adsabs.harvard.edu/abs/2018AGUFMED54A..03M/abstract

128. Dickinson, J.L., Zuckerberg, B. and Bonter, D.N. (2010). Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* 41(1), 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

129. Langham, G.M., Schuetz, J.G., Distler, T., Soykan, C.U. and Wilsey, C. (2015). Conservation Status of North American Birds in the Face of Future Climate Change. *PLOS ONE* 10(9), e0135350. https://doi.org/10.1371/journal.pone.0135350

130. Castex, V., Beniston, M., Calanca, P., Fleury, D. and Moreau, J. (2018). Pest management under climate change: The importance of understanding tritrophic relations. *Science of The Total Environment* 616-617, 397-407. https://doi.org/10.1016/j.scitotenv.2017.11.027

131. Marcinkowski, P. and Piniewski, M. (2019). Effect of climate change on sowing and harvest dates of spring barley and maize in Poland. *International Agrophysics* 32(2), 265-271. https://doi.org/10.1515/intag-2017-0015

132. Bai, H., Xiao, D., Zhang, H., Tao, F. and Hu, Y. (2019). Impact of warming climate, sowing date, and cultivar shift on rice phenology across China during 1981–2010. *International Journal of Biometeorology* 63(8), 1077–1089. https://doi.org/10.1007/s00484-019-01723-z

133. Acevedo, M., Pixley, K., Zinyengere, N., Meng, S., Tufan, H., Cichy, K. *et al.* (2020). A scoping review of adoption of climate-resilient crops by small-scale producers in low-and middle-income countries. *Nature Plants* 6(10), 1231-1241. https://doi.org/10.1038/s41477-020-00783-z

134. Zilberman, D., Lipper, L., McCarthy, N., and Gordon, B. (2018). Innovation in response to climate change. In *Climate smart agriculture*. Lipper, L., Thornton, P., Campbell, B.M., Baedeker, T., Braimoh, A., Bwalya, M. *et al.* (Eds). Springer, Cham. Vol 52. 49-74. https://doi.org/10.1007/978-3-319-61194-5

135. Enquist, C.A., Kellermann, J.L., Gerst, K.L. and Miller-Rushing, A.J. (2014). Phenology research for natural resource management in the United States. *International Journal of Biometeorology* 58(4), 579–589. https://doi.org/10.1007/s00484-013-0772-6

136. Kharouba, H.M. and Wolkovich, E.M. (2020). Disconnects between ecological theory and data in phenological mismatch research. *Nature Climate Change* 10(5), 406-415. https://doi.org/10.1038/s41558-020-0752-x.

137. Seddon, N., Turner, B., Berry, P., Chausson, A. and Girardin, C.A.J. (2019). Grounding nature-based climate solutions in sound biodiversity science. *Nature Climate Change* 9(2), 84–87. https://doi.org/10.1038/s41558-019-0405-0

138. Prober, S.M., Doerr, V.A.J., Broadhurst, L.M., Williams, K.J. and Dickson, F. (2019). Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecological Monographs* 89(1), e01333. https://doi.org/10.1002/ecm.1333

139. Bergstrom, D. M., Wienecke, B. C., van den Hoff, J., Hughes, L., Lindenmayer, D. B., Ainsworth, T. D. *et al.* (2021). Combating ecosystem collapse from the tropics to the Antarctic. *Global change Biology* 27(9), 1692-1703. https://doi.org/10.1111/gcb.15539

140. Radchuk, V., Reed, T., Teplitsky, C. Van De Pol, M., Charmantier, A., Hassall, C. *et al.* (2019). Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* 10, 3109. https://doi.org/10.1038/s41467-019-10924-4

141. Estrella, N., Sparks, T.H. and Menzel, A. (2007). Trends and temperature response in the phenology of crops in Germany. *Global Change Biology* 13(8), 1737-1747. https://doi.org/10.1111/j.1365-2486.2007.01374.x

142. Wang, Z., Chen, J., Xing, F., Han, Y., Chen, F., Zhang, L. *et al*. (2017). Response of cotton phenology to climate change on the North China Plain from 1981 to 2012. *Scientific Reports* 7, 6628. https://doi.org/10.1038/s41598-017-07056-4

143. Abed, A., Bonhomme, M., Lacointe, A., Bourgeois, G. and Baali-Cherif, D. (2019). Climate change effect on the bud break and flowering dates of the apple trees in mountainous and plain regions of Algeria. *Advances in Horticultural Science* 33 (3), 417-431. https://doi.org/10.13128/ahs-24618

144. Chmielewski, F.-M., Müller, A. and Bruns, E. (2004). Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. *Agricultural and Forest Meteorology* 121(1–2), 69-78. https://doi.org/10.1016/S0168-1923(03)00161-8

145. Tao, F., Yokozawa, M., Xu, Y., Hayashi, Y. and Zhang, Z. (2006). Climate changes and trends in phenology and yields of field crops in China, 1981–2000. *Agricultural and Forest Meteorology* 138(1-4), 82–92. https://doi.org/10.1016/j.agrformet.2006.03.014

146. Nguyen-Sy, T., Cheng, W., Tawaraya, K., Sugawara, K. and Kobayashi, K. (2019). Impacts of climatic and varietal changes on phenology and yield components in rice production in Shonai region of Yamagata Prefecture, Northeast Japan for 36 years. *Agronomy & Crop Ecology* 22(3), 382-394. https://doi.org/10.1080/1343943X.2019.1571421

147. Azmat, M., Ilyas, F., Sarwar, A., Huggel, C., Ashra, S.V., Hui, T. *et al*. (2021). Impacts of climate change on wheat phenology and yield in Indus Basin, Pakistan. *Science of The Total Environment* 790, 148221. https://doi.org/10.1016/j.scitotenv.2021.148221

148. Tomasi, D., Jones, G.V., Giust, M., Lovat, L. and Gaiotti, F. (2011). Grapevine Phenology and Climate Change: Relationships and Trends in the Veneto Region of Italy for 1964–2009. *American Journal of Enology and Viticulture* 62, 329-339. https://doi.org/10.5344/ajev.2011.10108

149. Rajan, S. (2012). Phenological Responses to Temperature and Rainfall: A Case Study of Mango. In *Tropical Fruit Tree Species and Climate Change.* Sthapit, B.R., Ramanatha Rao, V. and Sthapit, S.R. (Eds.) Bioversity International, New Delhi, India. https://cgspace.cgiar.org/handle/10568/105191

150. Xiao, D., Tao, F., Liu, Y., Shi, W., Wang, M., Liu, F. *et al*. (2013) Observed changes in winter wheat phenology in the North China Plain for 1981–2009. *International Journal of Biometeorology* 57, 275–285. https://doi.org/10.1007/s00484-012-0552-8

151. Ahmad, S., Abbas, G., Fatima, Z., Khan, R.J., Anjum, M.A., Ahmed, M. *et al*. (2017). Quantification of the impacts of climate warming and crop management on canola phenology in Punjab, Pakistan. *Journal of Agronomy and Crop Science* 203(5), 442-452. https://doi.org/10.1111/jac.12206

152. Subedi, S. (2019). Climate change effects of Nepalese fruit production. *Advances in Plants & Agriculture Research* 9(1), 141-145. https://doi.org/10.15406/apar.2019.09.00426

153. Tan, Q., Liu, Y., Dai, L. and Pan, T. (2021). Shortened key growth periods of soybean observed in China under climate change. *Scientific Reports* 11, 8197. https://doi.org/10.1038/s41598-021-87618-9

154. Kunz, A. and Blanke, M. (2022). “60 Years on”—Effects of climatic change on tree phenology—A Case Study Using Pome Fruit. *Horticulturae* 8(2), 110. https://doi.org/10.3390/horticulturae8020110

155. Rezaei, E.E., Siebert, S. and Ewert, F. (2017). Climate and management interaction cause diverse crop phenology trends. *Agricultural and Forest Meteorology* 233, 55-70. https://doi.org/10.1016/j.agrformet.2016.11.003

156. Zhang, T., Huang, Y. and Yang, X. (2012). Climate warming over the past three decades has shortened rice growth duration in China and cultivar shifts have further accelerated the process for late rice. *Global Change Biology* 19(2), 563-570. https://doi.org/10.1111/gcb.12057

157. He, L., Asseng, S., Zhao, G., Wu, D., Yang, X., Zhuang, W. *et al*. (2015). Impacts of recent climate warming, cultivar changes, and crop management on winter wheat phenology across the Loess Plateau of China. *Agricultural and Forest Meteorology* 200, 135-143. https://doi.org/10.1016/j.agrformet.2014.09.001

158. Abbas, G., Ahmad, S., Ahmad, A., Nasim, W., Fatima, Z., Hussain, S. *et al*. (2017). Quantification the impacts of climate change and crop management on phenology of maize-based cropping system in Punjab, Pakistan. *Agricultural and Forest Meteorology* 247, 42-55. https://doi.org/10.1016/j.agrformet.2017.07.012

159. Karapinar, B. and Özertan, G. (2020). Yield implications of date and cultivar adaptation to wheat phenological shifts: a survey of farmers in Turkey. *Climatic Change* 158, 453–472. https://doi.org/10.1007/s10584-019-02532-4

160. Liu, Y., Chen, Q., Ge, Q., Dai, J. and Dou, Y. (2018). Effects of climate change and agronomic practice on changes in wheat phenology. *Climatic Change* 150(3-4), 273-287. https://doi.org/10.1007/s10584-018-2264-5

161. Porter, J.R., L. Xie, A.J., Challinor, K., Cochrane, S.M., Howden, M.M., Iqbal, D.B. *et al*. (2014) Food security and food production systems. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Field, C.B. Barros, V.R., Dokken, D.J., Mach, K.J., Mastrandrea, M.D., Bilir, T.E. *et al*. (Eds.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. pp. 485-533. https://www.ipcc.ch/report/ar5/wg2/

162. Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A. C., Müller, C., Arneth, A. *et al*. (2014). Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proceedings of the National Academy of Sciences of the United States of America* 111(9), 3268-3273. https://doi.org/10.1073/pnas.1222463110

163. Peer, A.C. and Miller, T.J. (2014). Climate Change, Migration Phenology, and Fisheries Management Interact with Unanticipated Consequences. *North American Journal of Fisheries Management* 34, 94–110, 2014. https://doi.org/10.1080/02755947.2013.847877

164. Doney, S.C., Ruckelshaus, M., Emmett Duffy, J., Barry, J.P., Chan, F., English, C.A. *et al*. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science* 4(1), 11-37. https://doi.org/10.1146/annurev-marine-041911-111611

165. Thaxton, W., Taylor, J. and Asch, R. (2020). Climate-associated trends and variability in ichthyoplankton phenology from the longest continuous larval fish time series on the east coast of the United States. *Marine Ecology Progress Series* 650, 269–287. https://doi.org/10.3354/meps13404

166. The Food and Agriculture Organization of the United Nations (FAO) (2018). *Impacts of climate change on fisheries and aquaculture: Synthesis of current knowledge, adaptation and mitigation options*. http://www.fao.org/3/i9705en/I9705EN.pdf

167. Krabbenhoft, T.J., Platania, S.P. and Turner, T.F. (2014). Interannual variation in reproductive phenology in a riverine fish assemblage: implications for predicting the effects of climate change and altered flow regimes. *Freshwater Biology* 59(8), 1744-1754. https://doi.org/10.1111/fwb.12379

168. Woods, T., Kaz, A. and Giam, X. (2021). Phenology in freshwaters: a review and recommendations for future research. *Ecography*(44), 1-14. https://doi.org/10.1111/ecog.05564

169. Mills, K., Pershing, A., Brown, C., Chen, Y., Chiang, F.-S., Holland, D. *et al*. (2013). Fisheries management in a changing climate: Lessons from the 2012 ocean heat wave in the Northwest Atlantic. *Oceanography* 26(2), 191–195. https://doi.org/10.5670/oceanog.2013.27

170. Fitchett, J.M., Grab, S.W. and Portwig, H. (2019). Progressive delays in the timing of sardine migration in the southwest Indian Ocean. *South Africa Journal of Science* 115(7/8), 5887. https://doi.org/10.17159/sajs.2019/5887

171. Teske, P.R., Emami-Khoyi, A., Golla, T.R., Sandoval-Castillo, J., Lamont, T., Chiazzari, B. *et al*. (2021). The sardine run in southeastern Africa is a mass migration into an ecological trap. *Science Advances* 7(38), eabf4514. https://doi.org/10.1126/sciadv.abf4514

Graphic references

Identifying shifts, tracking trends

Plants

33. Renner and Zohner (2018)

Anderson, J.T., Inouye, D.W., McKinney, A.M., Colautti, R.I. and Mitchell-Olds, T. (2012). Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. *Proceedings of the Royal Society B: Biological Sciences* 279(1743), 3843-3852. https://doi.org/10.1098/rspb.2012.1051

Askeyev, O.V., Tischin, D., Sparks, T.H. and Askeyev, I.V. (2005). The effect of climate on the phenology, acorn crop and radial increment of pedunculate oak (*Quercus robur*) in the middle Volga region, Tatarstan, Russia. *International Journal of Biometeorology* 49(4), 262-266. https://doi.org/10.1007/s00484-004-0233-3

Ehrlén, J. and Valdés, A. (2020). Climate drives among year variation in natural selection on flowering time. *Ecology Letters 23*(4), 653-662. https://doi.org/10.1111/ele.13468

Lambert, A.M., Miller Rushing, A.J. and Inouye, D.W. (2010). Changes in snowmelt date and summer precipitation affect the flowering phenology of *Erythronium grandiflorum* (glacier lily; Liliaceae). *American Journal of Botany 97*(9), 1431-1437. https://doi.org/10.3732/ajb.1000095

Kudo, G. and Cooper, E.J. (2019). When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proceedings of the Royal Society B: Biological Sciences 286*(1904), 20190573. https://doi.org/10.1098/rspb.2019.0573

Insects

Konvicka, M., Benes, J., Cízek, O., Kuras, T. and Kleckova, I. (2016). Has the currently warming climate affected populations of the mountain ringlet butterfly, *Erebia epiphron* (Lepidoptera: Nymphalidae), in low-elevation mountains? *European Journal of Entomology* 113, 295. https://doi.org/10.14411/eje.2016.036

Macgregor, C.J., Thomas, C.D., Roy, D.B., Beaumont, M.A., Bell, J.R., Brereton, T. *et al*. (2019). Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year. *Nature Communications* 10(1), 1-10. https://doi.org/10.1038/s41467-019-12479-w

Ungulates

Froy, H., Martin, J., Stopher, K.V., Morris, A., Morris, S., Clutton Brock, T.H. *et al*. (2019). Consistent within individual plasticity is sufficient to explain temperature responses in red deer reproductive traits. *Journal of Evolutionary Biology* 32(11), 1194-1206. https://doi.org/10.1111/jeb.13521

Plard, F., Gaillard, J-M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C. *et al*. (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLOS Biology* 12, e1001828. https://doi.org/10.1371/journal.pbio.1001828

Renaud, L.A., Pigeon, G., Festa-Bianchet, M. and Pelletier, F. (2019). Phenotypic plasticity in bighorn sheep reproductive phenology: from individual to population. *Behavioral Ecology and Sociobiology* 73(4), 1-13. https://doi.org/10.1007/s00265-019-2656-1

Stopher, K.V., Bento, A.I., Clutton-Brock, T.H., Pemberton, J.M. and Kruuk, L.E. (2014). Multiple pathways mediate the effects of climate change on maternal reproductive traits in a red deer population. *Ecology 95*(11), 3124-3138. https://doi.org/10.1890/13-0967.1

Fishes

Friedland, K.D., Reddin, D.G., McMenemy, J.R. and Drinkwater, K.F. (2003). Multidecadal trends in North American Atlantic salmon (*Salmo* salar) stocks and climate trends relevant to juvenile survival. *Canadian Journal of Fisheries and Aquatic Sciences* 60(5), 563-583. https://doi.org/10.1139/f03-047

Kennedy, R.J. and Crozier, W.W. (2010). Evidence of changing migratory patterns of wild Atlantic salmon *Salmo salar* smolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology* 76(7), 1786-1805. https://doi.org/10.1111/j.1095-8649.2010.02617.x

Kovach, R.P., Joyce, J.E., Echave, J.D., Lindberg, M.S. and Tallmon, D.A. (2013). Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PloS one* 8(1), e53807. https://doi.org/10.1371/journal.pone.0053807

Ohlberger, J., Thackeray, S.J., Winfield, I.J., Maberly, S.C. and Vøllestad, L.A. (2014). When phenology matters: age–size truncation alters population response to trophic mismatch. *Proceedings of the Royal Society B: Biological Sciences* 281(1793), 20140938. https://doi.org/10.1098/rspb.2014.0938

Birds

Arlt, D. and Pärt, T. (2017). Marked reduction in demographic rates and reduced fitness advantage for early breeding is not linked to reduced thermal matching of breeding time. *Ecology and Evolution* 7(24), 10782-10796. https://doi.org/10.1002/ece3.3603

Both, C. and Visser, M.E. (2005). The effect of climate change on the correlation between avian life history traits. *Global Change Biology* 11(10), 1606-1613. https://doi.org/10.1111/j.1365-2486.2005.01038.x

D'Alba, L., Monaghan, P. and Nager, R.G. (2010). Advances in laying date and increasing population size suggest positive responses to climate change in common eiders *Somateria mollissima* in Iceland. *Ibis* 152(1), 19-28. https://doi.org/10.1111/j.1474-919X.2009.00978.x

de Villemereuil, P., Rutschmann, A., Ewen, J.G., Santure, A.W. and Brekke, P. (2019). Can threatened species adapt in a restored habitat? No expected evolutionary response in lay date for the New Zealand hihi. *Evolutionary Applications* 12(3), 482-497. https://doi.org/10.1111/eva.12727

Fletcher, K., Howarth, D., Kirby, A., Dunn, R. and Smith, A. (2013). Effect of climate change on breeding phenology, clutch size and chick survival of an upland bird. *Ibis* 155(3), 456-463. https://doi.org/10.1111/ibi.12055

Gaston, A.J., Gilchrist, H.G., Mallory, M.L. and Smith, P.A. (2009). Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: a case of progressive mismatching. *The Condor* 111(1), 111-119. https://doi.org/10.1525/cond.2009.080077

Imlay, T.L., Mills, J., Saldanha, S., Wheelwright, N.T. and Leonard, M.L. (2018). Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. *Ecosphere* 9(4), e02166. https://doi.org/10.1002/ecs2.2166

Kentie, R., Coulson, T., Hooijmeijer, J.C., Howison, R.A., Loonstra, A.J., Verhoeven, M.A. *et al.* (2018). Warming springs and habitat alteration interact to impact timing of breeding and population dynamics in a migratory bird. *Global Change Biology* 24(11), 5292-5303. https://doi.org/10.1111/gcb.14406

Ludwig, G.X., Alatalo, R.V., Helle, P., Lindén, H., Lindström, J. and Siitari, H. (2006). Short-and long-term population dynamical consequences of asymmetric climate change in black grouse. *Proceedings of the Royal Society B: Biological Sciences* 273(1597), 2009-2016. https://doi.org/10.1098/rspb.2006.3538

McDermott, M.E. and DeGroote, L.W. (2016). Long term climate impacts on breeding bird phenology in Pennsylvania, USA. *Global Change Biology* 22(10), 3304-3319. https://doi.org/10.1111/gcb.13363

McDermott, M.E. and DeGroote, L.W. (2017). Linking phenological events in migratory passerines with a changing climate: 50 years in the Laurel Highlands of Pennsylvania. *PLoS One* 12(4), e0174247. https://doi.org/10.1371/journal.pone.0174247

Moe, B., Stempniewicz, L., Jakubas, D., Angelier, F., Chastel, O., Dinessen, F. *et al.* (2009). Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Marine Ecology Progress Series* 393, 235-246. https://doi.org/10.3354/meps08222

Møller, A.P. (2008). Climate change and micro-geographic variation in laying date. *Oecologia* 155(4), 845-857. https://doi.org/10.1007/s00442-007-0944-3

Nilsson, A.L.K., Slagsvold, T., Røstad, O.W., Knudsen, E., Jerstad, K., Cadahia, L. *et al.* (2019). Territory location and quality, together with climate, affect the timing of breeding in the white-throated dipper. *Scientific Reports* 9(1), 1-11. https://doi.org/10.1038/s41598-019-43792-5

Rosenfield, R.N., Hardin, M.G., Bielefeldt, J. and Keyel, E.R. (2017). Are life history events of a northern breeding population of Cooper's Hawks influenced by changing climate? *Ecology and Evolution* 7(1), 399-408. https://doi.org/10.1002/ece3.2619

Sanz, J.J., Potti, J., Moreno, J., Merino, S. and Frias, O. (2003). Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology* 9(3), 461-472. https://doi.org/10.1046/j.1365-2486.2003.00575.x

Sauve, D., Divoky, G. and Friesen, V.L. (2019). Phenotypic plasticity or evolutionary change? An examination of the phenological response of an arctic seabird to climate change. *Functional Ecology* 33(11), 2180-2190. https://doi.org/10.1111/1365-2435.13406

Schaefer, T., Ledebur, G., Beier, J. and Leisler, B. (2006). Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. *Journal of Ornithology* 147(1), 47-56. https://doi.org/10.1007/s10336-005-0011-y

Vatka, E., Orell, M. and Rytkönen, S. (2011). Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Global Change Biology* 17(9), 3002-3009. https://doi.org/10.1111/j.1365-2486.2011.02430.x

Visser, M.E., Gienapp, P., Husby, A., Morrisey, M., de la Hera, I., Pulido, F. *et al.* (2015). Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *PLoS Biology* 13(4), e1002120. https://doi.org/10.1371/journal.pbio.1002120

Watanuki, Y., Ito, M., Deguchi, T. and Minobe, S. (2009). Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Marine Ecology Progress Series* 393, 259-271. https://doi.org/10.3354/meps08264

Weatherhead, P.J. (2005). Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia* 144(1), 168-175. https://doi.org/10.1007/s00442-005-0009-4

Wegge, P. and Rolstad, J. (2017). Climate change and bird reproduction: warmer springs benefit breeding success in boreal forest grouse. *Proceedings of the Royal Society B: Biological Sciences* 284(1866), 20171528. https://doi.org/10.1098/rspb.2017.1528

Bats

Linton, D.M. and Macdonald, D.W. (2018). Spring weather conditions influence breeding phenology and reproductive success in sympatric bat populations. *Journal of Animal Ecology* 87(4), 1080-1090. https://doi.org/10.1111/1365-2656.12832

Marine species

31. Poloczanska *et al.* (2013)

32. Poloczanska *et al.* (2016)