supergenes at an ever-increasing pace. By its simple inheritance in largely homogenized genomic backgrounds, heterostyly makes it relatively easy to identify causal genes underlying natural variation in complex floral traits. Molecular biology is beginning to dissect the causal genes and their molecular functions, from which much can be learned about the sequence of events during the origin of heterostyly, and about plant development and its evolution in general.

Where can I find out more?

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DECLARATION OF INTERESTS

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Primer

Phenology

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Flowers blooming, fungi fruiting, insects biting, fish spawning, geese migrating, deer calving; our consciousness is steeped in a seasonal calendar of nature's events. Phenology is the study of these recurring, seasonal life-history events, though nowadays this term is widely applied to the events themselves. From Shakespeare's sonnet 98, "*From you I have been absent in the spring*", to the appearance of seasonal events and migratory species in the oral traditions of Native Americans, interest in phenology is long-standing and transcends cultures. In this primer we introduce the study of phenology, trace the development of the field, and examine the prominent role phenology has played in evidencing the widespread impacts of anthropogenic climate change on life on Earth. We will consider the potential implications of climatic change for the ability of populations to persist and the stability of species interactions.

The act of systematically recording phenological events from one year to the next can be traced back to Robert Marsham. From 1736 until 1797, Marsham recorded the timings of 27 different 'indications of spring' — from the first leafing of various tree species to the first swallow — in southeast England, and then communicated his findings to the Royal Society. Following his death, the baton of phenological recording was passed from one descendent to the next, continuing until 1958, with the total record spanning some 222 years. Remarkably, this is a mere fraction of the length of the longest known phenological record; that distinction belongs to the records describing the cherry-blossom festivals in Kyoto, Japan, the annual timing of which has been carefully pieced together from court documents and diaries all the way back to 812 AD. Following on from Marsham's time we see scientific engagement with phenology and its links to meteorological variation through the 19th and early 20th centuries, including from famous naturalists such as Henry David Thoreau. However, it wasn't until the last decade of the 20th century that interest in phenology exploded; a shift that can be attributed to mounting concern about the impacts of climate change on nature, shared by professional and citizen scientists alike.

Why timing matters

Across the planet, certain times of the year are more favourable for life than others. Toward the poles we see this in the extreme, with a stark contrast between snow and ice and long nights in the winter versus warmer conditions and long days in the summer. Moving to temperate latitudes, the annual oscillation in temperature (Figure 1A) and the duration of daylight is pronounced but less extreme. Then, moving into the tropics, the major environmental axis of annual seasonality on land is between a wet and a dry season (Figure 1B), and day length varies much less, becoming invariant at the equator. Across ecosystems many primary producers time their emergence and growth to coincide with favourable abiotic conditions. This in turn has consequences that cascade from resource to consumer through food chains, with consumers timing their key life-history events, such as growth or breeding, to coincide with favourable abiotic conditions and often a seasonal peak in the availability of food.

Faced with the seasonality of abiotic conditions (Figure 1) and in the incidence of biotic interactions (including consumers, resources, mutualists, hosts, competitors, and mates), getting the timing right can matter greatly to an organism. Consider a deciduous tree in a temperate forest: as spring arrives, the best time for leaf-out may arise as a trade-off between the benefits of leafing early, to maximise opportunities to take advantage of increasing light availability and warming temperature, and the benefits of leafing later, to minimise the risk of late frosts. For other taxa within the forest, the growth of leaves alters their environment, influencing the optimal timing for their own events. For example, plant species growing on the forest floor may need to take advantage of light availability before the canopy closes, whereas for herbivores that eat the leaves, such as caterpillars, emerging in synchrony with leafing will maximise their access to a resource.

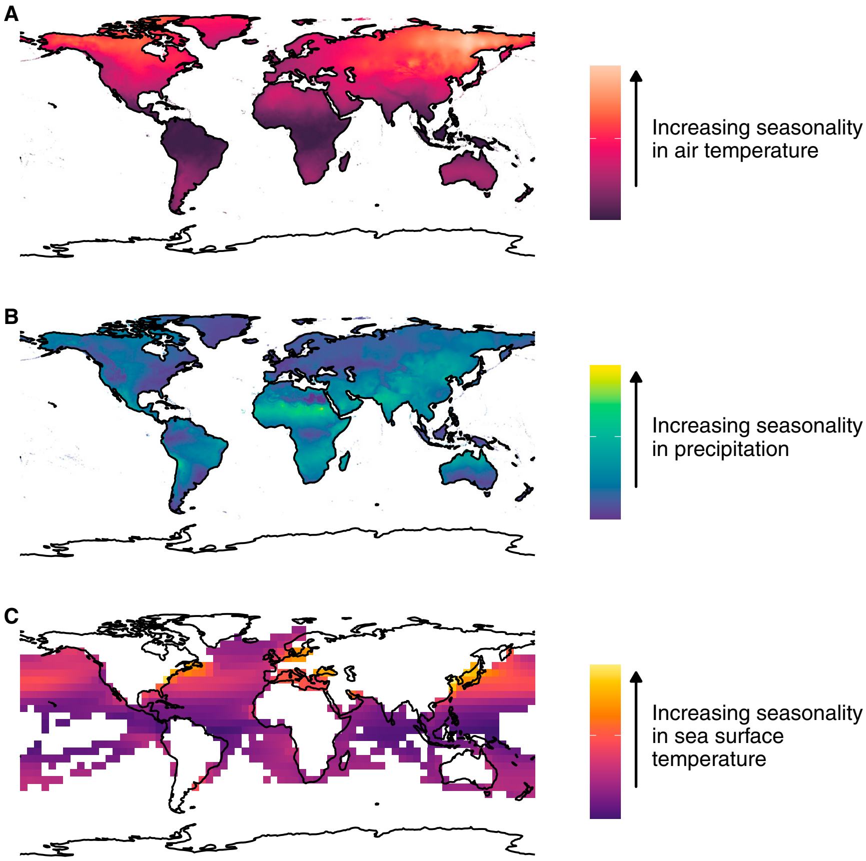

Figure 1. Global patterns of seasonality across land and sea.
Maps of global patterns in the annual seasonality of (A) air temperature, (B) precipitation, and (C) sea-surface temperature. Variation in colour represents the standard deviation of the monthly means. Maps reveal that the tropics experience the lowest temperature seasonality (A,C) and the greatest precipitation seasonality (B). Air temperature and precipitation data were taken from WorldClim bioclimatic variables (Fick and Hijmans, 2017) at a spatial resolution of 10 minutes (A = BIO4, B = BIO15). Sea-surface temperature seasonality was derived from HADSST 4 baseline temperatures from 1961–1990 (Kennedy *et al.,* 2019). (Coastlines © rnaturalearth.)

Whether due to the abiotic conditions experienced or the relative timing of biotic interactions, phenology will often have important implications for fitness, with individuals that get the timing wrong often facing a cost in terms of lower survival and/or reduced reproductive output.

Environmental cues and constraints

As timing often affects fitness, many populations have evolved to use information, or cues, from their environment to schedule phenological events, whether that be to initiate hatching, migration, growth, or reproduction in time for favourable conditions, or to cease activity before the arrival of harsh conditions. Species can be sensitive to cues that indicate absolute timing within the year cycle. For instance, outside the tropics, photoperiod follows a predictable annual cycle, with day length increasing in the spring and decreasing in the autumn, and many species are reliant on photoperiod as a cue. Generally, however, the timing of favourable conditions will not occur on a fixed day of the year, and instead this timing may differ by a month or more from one year to the next. Therefore, many organisms use other information from their environment as supplemental or alternative phenological cues. In some cases, the environment may also act as a constraint on phenology. Below we briefly examine some of the ways in which the environment acts as a cue constraint on the phenology of different taxa inhabiting different environments and regions.

Towards the poles, warmer temperatures, earlier snowmelt, and reduction of ice cover correlate with an earlier onset of activity for terrestrial plants and animals. For instance, Columbian ground squirrels in Alberta, Canada, advance their emergence from hibernation when spring is warmer and snowmelt is earlier. There are cases where sea ice appears to act as a direct constraint on phenology, for instance, some colonies of polar seabird are unable to breed until the sea ice has melted, providing access to food. The timing of sea-ice melting has also been shown to influence the phenology of phytoplankton blooms and bowhead whale migration through the Bering Strait.

In more temperate climes, where snow cover is less predictable in winter and where water is rarely limited due to regular precipitation throughout the year (Figure 1B), temperature is often the main climatic driver of phenology. Observational studies and experiments have revealed substantial sensitivity of spring and summer events to temperatures over the preceding weeks. An extensive comparative analysis across over 10,000 phenological time series collected in the UK found a clear tendency for earlier phenology in response to warmer (air and water) temperatures across a breadth of taxa including insects, birds, mammals, phytoplankton, crustaceans, and fishes. Alongside an accelerating effect of spring temperatures on phenology, for some plant and insect species, cool (rather than warm) temperatures during the autumn and winter can lead to an advance in the phenology of events occurring the following spring. As we move from temperate toward polar environments we see this effect of cool winter temperatures (termed chilling) largely replacing photoperiod as a seasonal cue, though why this should be the case remains a little unclear.

In freshwater and marine systems, temperature is again a common phenological cue, influencing planktonic blooms, macroinvertebrate emergence, and fish spawning and migration, but factors such as seasonal pulses in nutrient levels and hydrology are also often important.

Common to both temperate and polar regions, autumn brings a shift to colder conditions and shorter days, often leading to a cessation of activities (for example, abscission of leaves, insect diapause, and mammalian hibernation) or migration to warmer climes. For many deciduous trees, the timing of leaf senescence is partially determined by shortening days but may also be affected by summer precipitation and late summer temperatures. In colder environments, where early frosts occur with greater regularity, there is a tendency for day length to assume greater importance as a cue, potentially reducing the risk of leaf damage.

Closer to the equator, seasonal variation in environmental conditions is less bound to the strict circannual routines and thermal seasons found further north and south (Figure 1). Where water is limiting, phenology is more likely to respond to seasonality in precipitation (Figure 1), although temperature can still play a role. For example, rainfall is a driver of the breeding phenology for purple-crowned fairy wrens, *Malurus coronatus*, in Australia and for a range of passerines in the tropical dry forests of Brazil. In the savannas of Kenya, rainfall is important in driving the breeding phenology of seasonally breeding ungulates but has no effect on other ungulate species that breed throughout the year. Although rainfall serves as a key driver of phenology throughout lower latitude terrestrial environments, there are cases, such as the flowering times of *Protea* in subtropical Africa, where temperature is the primary driver. In tropical seas, variation in water temperature and solar insulation (partially affected by cloud cover) throughout the year influences the month in which some coral species show highly synchronised spawning; however, it is still the lunar and diurnal cycles that form the proximate cues for the day and hour at which the event occurs.

Those species that migrate long distances between wintering grounds close to the tropics and breeding grounds at higher latitudes face a particular challenge because interannual variation in conditions (for example, temperature) at their wintering grounds or along their migration route may be entirely uncorrelated with conditions at the breeding grounds. Under these circumstances, cues at the wintering ground are uninformative, meaning that an adaptive plastic response cued by wintering-ground conditions cannot evolve.

For plants and ectotherms, there is compelling evidence that the abiotic conditions described here serve as proximate cues for phenology. However, for endotherms, such as birds and mammals, the extent to which the effects of abiotic conditions are direct or indirect remains something of a mystery. Examples of potential indirect effects include responding to the phenology of another taxonomic group, such as the arrival of an ephemeral prey, or via the steady accumulation of resources over longer time periods.

A weathervane for biotic impacts of a changing climate

A consequence of weather (or weather-related) variables such as temperature, rainfall, and snowmelt being among the most common cues and drivers of phenology is that anthropogenic climate change has left a clear imprint on phenological schedules. Over the past four decades we have seen pronounced phenological shifts, which have served as an early warning of the biotic impacts of climate change. Against this climate-change backdrop, the extensive phenological datasets compiled by citizen scientists via schemes such as the USA National Phenology Network (https://www.usanpn.org/) and the UK's Nature's Calendar (https://naturescalendar.woodlandtrust.org.uk) have proven especially valuable, both as sources of data and as a channel for engaging the public with the impacts of climate change.

In boreal and temperate environments, advancements in the timing of spring events have been especially large, with events advancing at a rate of several days per decade in some cases. Evidence for an advance in the timing of spring events has also been widespread across taxonomic groups, including fungi, algae, grasses, trees, crustaceans, insects, fish, amphibians, birds, and mammals. The extent of advance varies across taxa and regions and can be explained by a combination of variation in the rate at which temperatures have warmed for different regions and times of the year and the differing responses to temperature exhibited by different species and populations. For instance, the temporal warming experienced, thermal sensitivity of phenology, and resulting phenological advance in recent decades all vary among great tit, *Parus major*, populations across Europe. In a minority of cases the phenological shifts we observe are in the counter direction. For example, as Columbian ground squirrels advance their emergence from hibernation in response to warmer temperatures and earlier snowmelt, we might predict their emergence to have advanced in recent decades. However, over a 20-year period their emergence phenology was delayed, due to a local absence of a temporal trend in spring temperature and an increase in late winter snowstorms that delayed snowmelt. Among plant and insect species that are sensitive to winter chilling, there is potential that warmer winters may counter the accelerating effect of warmer springs on phenology and limit their ability to track spring advances in the timing of favourable conditions. For example, the spring phenology of meadow and steppe vegetation in the Tibetan Plateau has been delayed despite warmer springs, due to warmer winters delaying the fulfilment of the plants' chilling requirements.

With rising summer and autumn temperatures, many temperate autumn events have been delayed, consistent with the period of favourable environment extending at both ends, though often the magnitude of delay and variability in response appear less substantial than those of spring events (with a caveat that autumn events have also been studied less intensively). In the tropics, where rainfall seasonality is an important driver of terrestrial phenology, some regions have become substantially wetter and others have become much drier; moreover, in some regions, the magnitude and predictability of rainfall seasonality is altered. Currently, our ability to infer how changes in precipitation regimes have impacted the phenology of tropical species is impeded by a shortage of phenological time series spanning more than ten years and the fact that phenology often follows much less of a circannual cycle in tropical regions. An important facet of the effects of climate change on phenology is that we often observe substantial variation in responses among

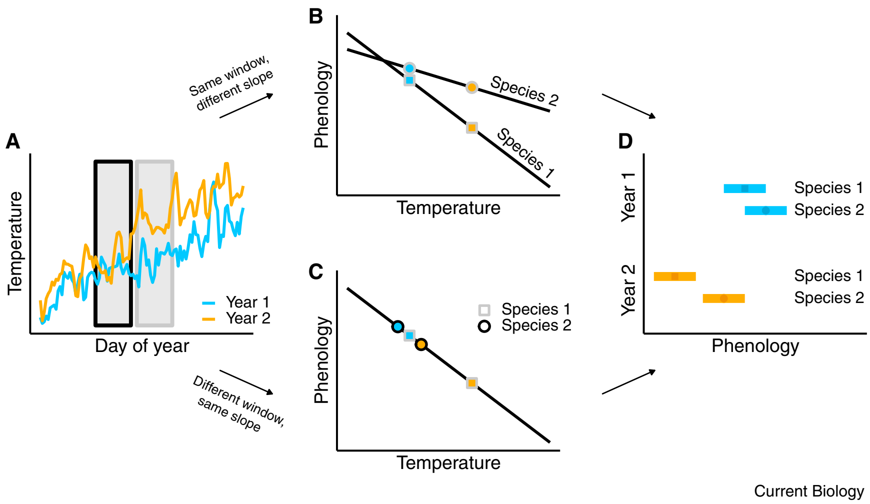

Figure 2. Processes by which phenological asynchrony between two species may occur.
(A) The pattern of daily temperature increase throughout the spring differs between two years (blue = cooler, orange = warmer), with the boxes indicating two temporal windows of temperature sensitivity. (B) Two species may respond to temperature during the same window (the grey outlined points correspond to the grey outlined window in panel (A) but differ in their phenological plasticity. (C) Two species may respond to temperatures during different windows (grey and black outlines) but with the same phenological plasticity. (D) Under both scenarios the phenology of both species is advanced in the warmer year, and we also see greater asynchrony in the warmer year.

different species and taxonomic groups. For example, multi-species analyses have found that primary producers and primary consumers are advancing at a substantially faster rate than secondary consumers, an observation that has been attributed to secondary consumers having a lower phenological sensitivity to temperature.

Disrupting interactions?

In many cases the optimum timing for a population (that is, the timing that maximises fitness) will be sensitive to the degree of (a)synchrony with other species or, in other words, the timing of one species relative to other(s). For example, in temperate deciduous forests, growth and flowering for many plant species, including the bluebell (*Hyacinthoides non-scripta*), is timed to begin in early spring prior to the complete leafing of the canopy above, after which much of the sunlight is blocked out.

Of all the many types of species interactions, the trophic interaction between a consumer and its resource has received particular attention and is the focus of the ‘match/mismatch hypothesis’, which was first developed by fisheries biologist David Cushing. Cushing’s observation was that spawning of several marine fish species was timed to approximately coincide with a seasonal, short-lived peak in zooplankton biomass. He noted that although the phenology of zooplankton biomass was highly sensitive to spring temperatures, the timing of fish spawning appeared to be much less so. With varying sea temperatures, this could then lead to years where fish fry are matched with their resources, resulting in high levels of fish recruitment to the adult population, and years where the fish fry are mismatched with resources, leading to low recruitment.

With climate change, the match/mismatch hypothesis has been presented as a cause for concern. Rising temperature, combined with evidence that the phenology of secondary consumers is often less temperature sensitive than the phenology of the resources they rely on, provides the necessary conditions to generate widespread mismatch at higher trophic levels. A textbook example of climate-mediated trophic mismatch involves work on the breeding phenology of European great tits in relation to the timing of the peak abundance of woodland caterpillars. In warmer years, great tit chicks hatch too late to fully benefit from the peak biomass of caterpillars, with some evidence that lower synchrony to the resource can lead to lower fledging success and decreased survival of the parent birds.

Where different species shift their phenology by different amounts (Figure 2), there is potential for climate change to perturb all manner of phenology-mediated interactions. For instance, the relative timing between seasonal infection vulnerability and pathogenic trematode infection risk influences infection load and risk of developmental malformations in the Pacific tree frog, *Pseudacris regilla*. In mutualistic plant–pollinator networks, warmer temperatures may disrupt previously synchronous pairwise interactions; for more generalist species, uncoupled timing with a few heterospecifics within a larger network may not have particularly detrimental effects, whereas more specialist species remain more vulnerable. Alternatively, shifts in climate may alter the synchrony between two species that compete for a single resource, such as plants competing for light and space, or birds competing for nest holes.

Although climate impacts on phenological interactions certainly have the potential to be extremely disruptive, cascading through interaction networks, the magnitude and frequency of such impacts will only become evident in the coming decade or two. Returning to the great tits, although mismatch has severe negative consequences for individuals, populations have not declined, and this appears to be due to density dependence of over-winter survival. The lack of evidence that mismatch impacts negatively on population sizes of great tits largely mirrors what we see so far on a broader scale across species interactions. Though it is unclear why evidence is lacking, one potential explanation is that phenological interactions and their demographic impacts are more buffered in the short term than has been appreciated. For example, many consumers are generalists, and if they become mismatched with one resource, they may simply switch to another. A further consideration is that the relative timing between two or more species may become either more or less synchronous. Indeed, a study that analysed multiple species interactions found that increases and decreases in asynchrony were about equally common. Unless the interaction is mutualistic, altered synchrony is likely to involve both positive and negative impacts.

Phenology and adaptation

Weather's impacts on ecosystems vary from one year to the next, in turn generating inter-annual variation in organisms' optimum timings. Over generations, a combination of natural selection on phenology and heritable genetic variation for the traits that underlie phenology has seen the adaptive evolution of phenological schedules that are approximately synchronous with the optimum timings. In many cases, species are also able to partially track year-to-year variation in the timing of the optimum through adaptive phenotypic plasticity (Figure 3A). For instance, a single English oak tree (*Quercus robur*) may advance its leaf-out time by as much as 28 days in a year that is 4°C warmer. Fortunately, much of the phenological plasticity we see in response to temperature is likely to be adaptive in the face of anthropogenic climate change, particularly in taxonomic groups for which temperature is a direct cue. Nonetheless, across many systems the plastic response will often be insufficient to track the optimum (Figure 3B) and there may be limits beyond which plasticity is exhausted (Figure 3C).

Contemporary genetic adaptation in response to selection favouring individuals that are closer to the optimum timing provides a means of making up the shortfall between phenology and the optimum timing (Figure 3A). Consequently, phenological traits have attracted a lot of interest from evolutionary biologists working on global climate change. For an evolutionary response to occur, there must be a heritable component to phenology and there must be directional selection on phenology in response to the changing environment. From transplant experiments and resurrection studies on plant species (where seeds are stored and then plants are grown from seed at a later date), it is apparent that phenological traits can evolve very rapidly when placed under strong selection by shifts in temperature or drought. For instance, population differences in the flowering times of range-expanding populations of the annual plant *Dittrichia graveolens* grown

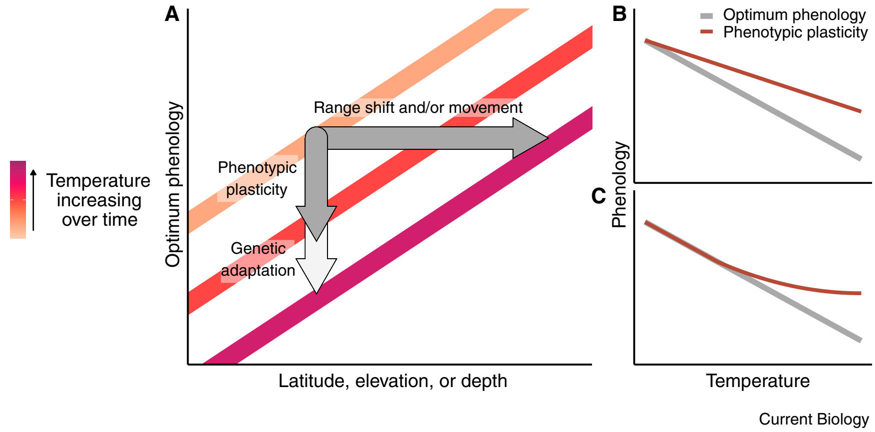

Figure 3. Mechanisms to track shifts in optimum phenology.
(A) When conditions are colder, the optimum phenology is delayed, as seen with increasing latitude, elevation, and depth (the optimum slope could be reversed for depth in some areas depending on conditions, but the principles remain the same). If temperature increases (for example, under anthropogenic climate warming), the optimum timing advances. To match this advance in the optimum, a population may advance their phenology via phenotypic plasticity and genetic adaptation (vertical arrow) and/or physically move to a location where the optimum phenology matches that of the population (horizontal arrow). As the temperature increases, phenotypic plasticity may not be able to accurately track the changing optimum if the thermal sensitivity of phenology is (B) insufficient, whereby the slope is shallower than the optimum, or (C) exhausted, where the plastic response cannot be maintained beyond some threshold condition.

in a common-garden environment are consistent with an advance by 4 weeks in just 50 years. Similarly, common-garden experiments replicated over time reveal a substantial capacity for phenology to evolve in some insect species, including the timing of pupation and diapause in pitcher-plant mosquitoes (*Wyeomyia smithii*) and the hatching reaction norm of winter moths (*Operophtera brumata*).

In comparison to plants and insects, the evidence for contemporary climate-mediated adaptive evolution of phenology in vertebrates is limited both in quantity and taxonomic breadth. Part of this scarcity of evidence is due to the logistical challenge of conducting transplant experiments on vertebrates, but in the rare instances where they have been attempted, we do see some evidence for evolution of phenology. For example, long-distance migrant pied flycatchers (*Ficedula hypoleuca*) were reared in an aviary in Germany in 1981 and then again in 2002 under identical common-garden conditions, and their phenological schedules through the annual cycle compared. Over a 20-year period there was a substantial genetic advance in spring activity and migratory behaviour combined with a delay in autumn activities. Further evidence of adaptation in bird phenology comes from a study that applied artificial selection to the breeding times of a Dutch population of great tits, though intriguingly this study succeeded in generating a response to selection for delayed timing but not for advanced timing, which may imply some constraints on evolving earlier timing. Alongside experimental studies, there have been numerous attempts to use long-term pedigree studies of vertebrates to infer evolution of phenology. Some of the strongest evidence for genetic shift comes from a 45-year study of red deer (*Cervus elaphus*) on the Scottish island of Rum, which reported a 2-week advance in female calving dates with a substantial genetic component.

In cases where climate change shifts the optimum timing, there is a further mechanism that may allow tracking of optimal timing whilst maintaining a constant phenology, and this is through dispersal. For example, when temperature is the primary determinant of optimal phenology, then dispersal to higher latitudes, higher elevations, or cooler depths could allow an organism to maintain a constant environment and phenology (Figure 3). Consistent with this mechanism, a comparative study of flowering plant species in the UK found that annual species that advanced their phenology less in response to temperature exhibited a greater average northwards shift of their northern range boundary, though this trend was less apparent in perennial plants. Across 289 Lepidopteran species in Finland, many were found to advance their flight times and/or move their northward range boundary northwards, with species that made both adjustments showing a greater tendency for population increase. In the marine environment, a global meta-analysis including 115 fish taxa showed that populations utilise the three-dimensional environment to track cooler waters — with evidence for shifts in both latitude and depth — and that species that changed depth generally moved smaller distances latitudinally. There is also evidence that movement could facilitate the evolutionary adaptation of migrant bird species, with pied flycatchers transplanted from the northern areas of the Netherlands to Sweden found to breed earlier and have higher fitness than the local Swedish birds. Long-distance dispersals do occur in nature, and although it is clear that this could provide a source of genetic variation that enables a population to adapt to an earlier optimum phenology, the extent to which the direction of dispersal is adaptive or random is unclear.

Changing face of phenology

To close, we briefly summarise some of the major recent research directions that have emerged in phenology.

Big data

A field that has its foundations in the careful recording of observations in the notebooks and diaries of Japanese courts and naturalists is now experiencing a technological revolution. For the past few decades, satellite-mounted sensors have provided global data of increasingly high spatial resolution on the phenology of green-up and senescence of primary productivity across terrestrial and aquatic biomes. Data arising from these sensors and those attached to drones are even being used to try to distinguish the phenologies of different functional groups that comprise a community. There has also been a proliferation of earth-based technology for monitoring phenology, including cameras that have been deployed to monitor the phenology of plants and penguins, to acoustic sensors that can be used to collect high-resolution data on any species that generates a distinct sound. Alongside the deployment of sensors, we have seen rapid development of machine-learning tools that can automate detection of bat or bird species from acoustic data, moth species from photographs in traps, and pollinator taxa photographed while visiting flowers. These new sensors, alongside additional emerging approaches such as metabarcoding and environmental DNA, mean that vast quantities of high-resolution phenology data can now be obtained for regions, environments, and species that have been neglected in the past.

Shifting emphasis

From 1990–2000, interest in phenology focused primarily on the impacts of climate on phenology, whereas from 2000–2020 attention shifted to the effects of different cues and drivers, and the impacts of changing phenology on individual species interactions. We now expect to see further shifts in emphasis as a consequence of the availability of ever larger multi-taxa phenology datasets resolved at finer taxonomic resolution. One change that is already evident is an increase in synthetic analyses examining how and why the contributions of different drivers vary across many taxa and/or regions. We also expect to see a further shift towards framing the impacts of climate change on phenological interactions in the broader context of interaction networks, rather than the narrow context of an interaction chain. It remains to be seen whether taking a broader ecological context will reveal phenological impacts to be more buffered and resilient than previously thought, or more fragile.

To conclude, we have seen that over the last 250 years phenology has moved from being mainly the preserve of amateur naturalists and horticulturalists to a fast-moving frontier of applied research, benefiting from the latest technological innovations and serving as a testing ground for state-of-the-art evolutionary and community ecology.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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