Received: 11 November 2020 | Revised: 16 November 2021 | Accepted: 3 January 2022

DOI: 10.1002/wcc.764

OVERVIEW

WIREs CLIMATE CHANGE WILEY

Climate change and phenology

David W. Inouye[1,2]

[1]Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA

[2]Department of Biology, University of Maryland, College Park, Maryland, USA

Correspondence
David W. Inouye, RMBL, P. O. Box 519, Crested Butte, Colorado, 81224, USA.
Email: inouye@umd.edu

Funding information
National Science Foundation, Grant/Award Numbers: DEB-0922080, DEB-1354104, DEB-1912006

Edited by Brendon M.H. Larson, Domain Editor, and Mike Hulme, Editor-in-Chief

Abstract

Climate change is a defining element of the current ecological landscape, with consequences ranging from global to local environments. One of the first indices of the ecological impact of the ongoing environmental changes was measurement of their effects on phenology, the seasonal timing of recurring annual events such as the beginning of the growing season, timing of flowering, and breeding seasons of animals. Research has moved beyond simple descriptions of these temporal changes to investigations of their root causes, impacts, and consequences at both ecological and evolutionary time scales. This changing landscape, environmental, ecological, and evolutionary, makes this an exciting, albeit sometimes depressing, time to be a scientist.

This article is categorized under:

Assessing Impacts of Climate Change > Observed Impacts of Climate Change

Climate, Ecology, and Conservation > Observed Ecological Changes

KEYWORDS

climate change, flowering, hibernation, migration, phenology

1 | INTRODUCTION

Climate change is a defining element of the current ecological landscape, with consequences ranging from global to local environments. One of the first indices of the ecological impact of the ongoing environmental changes was measurement of their effects on phenology, the seasonal timing of recurring annual events such as the beginning of the growing season, timing of flowering, and breeding seasons of animals. Research has now moved beyond simple descriptions of these temporal changes to investigations of their root causes, impacts, and consequences at both ecological and evolutionary time scales. The changing landscape, environmental, ecological, and evolutionary, makes this an exciting, albeit sometimes depressing, time to be a scientist, with no shortage of pressing ecological changes to species and their interactions to investigate.

Shifts in phenology have the potential to offset negative effects of climate change, or they may create carryover effects and mismatches that decrease fitness (Cappello & Boersma, 2021). Quantifying such shifts is thus essential to understanding and predicting the consequences of climate change for ecological communities. These shifts are typically relatively slow, matching the tempo of change in climate variables driving them, and thus long-term studies of both climate and ecological variables are essential to gaining insights into how phenology is changing and what the consequences are. The interaction of spatial and temporal components of change is increasingly recognized as a significant aspect of phenological change (O'Leary et al., 2020).

 © 2022 Wiley Periodicals LLC.

2 | HOW IS THE CLIMATE CHANGING?

2.1 | Changes in temperature and precipitation (but not uniform geographically)

The ongoing changes in the climate include primarily increases in temperature from historical averages, a variety of shifts in precipitation patterns, and changes in the variability of these measures (Chan et al., 2020; Pendergrass et al., 2017), and we have a growing understanding of anthropogenic influences behind these climate changes (IPCC, 2021). Relatively little attention has been paid to the potential impacts of changes in climatic variability, which will have consequences at both ecological and evolutionary time scales (Vázquez et al., 2017), and affect species at population, community, and ecosystem scales. There are substantial spatial variations because of the impact of regional processes affecting climate (van der Wiel & Bintanja, 2021), so that large-scale generalizations will have limited applicability. For example, surprising regional differences, with local hotspots, have been identified in temperature changes across the United States (Eilperin, 2020). As we come to understand better the influence of climate variables on phenologies, and the spatial variation in climate changes, we can make more accurate predictions of how phenologies will change in the future.

2.2 | Different time scales of change: Cycles versus linear changes

In the few recent decades during which scientists have begun to observe the environment changing due to global warming, and to record the phenological consequences, many of the changes have been linear in nature, but climatological models suggest that the environmental changes will eventually plateau, and consequently, the phenological changes will at some point also approach new equilibria, or even reverse direction if the climate changes do. Some of the regional-scale climate drivers are cyclical in nature, including the Pacific Decadal Oscillation, Quasi-biennial Oscillation, Atlantic Multi-decadal Oscillation, and El Niño Southern Oscillation, and it is likely that they in turn are being affected by climate change. For example, the intensity and frequency of ENSO events are likely to change (Cai et al., 2015; Power et al., 2013). There is some evidence that regional climates in North America have developed a cyclical pattern (Ault & St. George, 2010), that can in turn produce cycles in flowering abundance and phenology. A potential major tipping point, rather than a changing cycle, is the possibility of a collapse of the Atlantic Meridional Overturning Circulation (AMOC), which would greatly change temperature regimes in a large part of the northern hemisphere (Boers, 2021).

3 | WHAT ELEMENTS OF LIFE HISTORY PHENOLOGY ARE RESPONSIVE TO CLIMATE?

Temperature is a major environmental determinant of many aspects of life histories for both plants and animals. Both invertebrate and vertebrate animals, and aquatic and terrestrial species of plants and animals, have optimal temperatures, and preferences for precipitation amount and timing, so as these environmental variables change, there are consequences for the distribution, growth, reproduction, and survival of plants and animals. Precipitation and temperature can interact in complex ways across landscapes to affect plant phenology (Jin et al., 2019), and given that both of these variables are changing it is not surprising that phenologies are as well.Phenology is integral to so many aspects of life histories, including foraging behavior, interactions with parasites, predators and competitors, and reproductive biology, that it is not surprising that there can be significant fitness consequences for not optimizing the seasonal timing of these activities. In this section, I will address some life history attributes, how they are changing in response to climate change, and how fitness is being affected.

3.1 | Growth and reproduction—animals

An example of the effects of temperature on growth and reproduction is provided by a long-term study of two sympatric and closely related bird species in Belgium, the blue tit (*Cyanistes caeruleus*) and the great tit (*Parus major*; Matthysen et al., 2011). Both advanced their mean first-egg dates by 11–12 days from 1997 to 2007. Time from first

egg to fledging was reduced by 2–3 days, in large part through decreases in nestling development time. The average time until fledging advanced by 15.4 and 18.6 days for blue and great tits, respectively. Further south, Magellanic penguins (*Spheniscus magellanicus*) have shifted median hatch dates 10 days from 1983 to 2017 (Cappello & Boersma, 2021). Because median fledge dates did not shift over the 34 years, median nestling period decreased by 14%, impacting chick growth.

A mammalian example comes from a long-term study of red deer (*Cervus elaphus*) on the Isle of Rum, Scotland, which found that phenological traits of oestrus date and parturition date in females, and antler cast date, antler clean date, rut start, and end dates in males all advanced by between 5 and 12 days across a 28-year study period (Moyes et al., 2011). A more recent study found that decreases in rainfall have affected red deer rutting behavior (F. Millán et al., 2021). Another example is the increased body mass of marmots entering hibernation as a consequence of the lengthening growing season in montane meadows in Colorado, which results in a decrease in mortality during hibernation (Ozgul et al., 2010). Reproductive phenology in smaller mammals (e.g., *Peromyscus* mice) is also influenced by temperature (McLean & Guralnick, 2021), creating the potential for effects of climate change.

Almost four decades of data for Great Tits (*Parus major*) in the Netherlands found that phenological mismatch has a strong effect on individual fitness, although not in population demography (Reed et al., 2013). Study of a marine example, the guillemot (*Uria aalge*), found that females deviating significantly from the population's mean laying date each year had reduced breeding success (Reed et al., 2009). A study of host–parasite interactions found that the joint product of infection load and phenological synchrony influenced the pathological consequences of infections, pointing to the sensitivity of disease outcomes to shifts in climate (McDevitt-Galles et al., 2020).

Our understanding of these consequences of the changing climate points to the value of long-term longitudinal data, as decades of observations are often required to reach substantive conclusions about changes in growth and reproduction, two important aspects of life history, and the consequences for fitness.

3.2 | Migration

Migration is typically associated with reproduction and growth, and thus observed changes in the phenology of migration suggest that there are significant alterations ongoing in these important components of species ecology and fitness. Both terrestrial and aquatic migratory species are being influenced by climate change, resulting in changes in their phenology, with potential consequences for abundance too. Phenological changes can decouple previously synchronized interactions such as mutualisms, competition, and predation that migratory species will experience. Some of these can be local effects, but others can potentially affect interactions over large distances.

Probably the best-known migrations are those of birds, moving from breeding to overwintering grounds. They also provide some of the best data, since both scientists and naturalists have tracked bird migrations for centuries. As a generalization, migration dates are changing, typically earlier, in response to climate change. We're beginning to understand how individual behavior, generational changes, and changes in temperature are creating these new phenological patterns (Gill et al., 2019; Kolarova et al., 2017; Therrien et al., 2017). New tools, including radar, have provided insights into how nocturnal migrations have changed at continental scales (Horton et al., 2020). Long-term records show that changes are occurring in migration phenology, typically concluding that increasing temperatures are responsible (Cadahia et al., 2017; Kluen et al., 2017; Kullberg et al., 2015).

In addition to these terrestrial examples, there are also fish migrations that have historically served as phenological markers. For example, "shadbush" (*Amelanchier* species) was historically associated with anadromous shad migrations in the eastern USA because the shrubs flowered about the same time that the fish appeared. Fish migrations, and the associated spawning, are changing in response to warmer ocean and river temperatures (Kovach et al., 2012; Kuczynski et al., 2017; Sims et al., 2004). Migration phenology of adult and fry pink salmon (*Oncorhynchus gorbuscha*) has changed in response to warming water temperatures (Taylor, 2008; van Leeuwen et al., 2016), and there has been rapid microevolution of earlier adult migration timing (Kovach et al., 2012).

Many species of large mammalian herbivores that migrate do so to take advantage of changes in the phenology of their food plants (Merkle et al., 2016). Antelope, caribou, red deer, and reindeer have large-scale migrations that appear to track closely plant growth that occurs in the spring, "surfing the green wave" (Aikens et al., 2017). The green wave hypothesis is that these animals should follow high-quality forage at the leading edge of green-up in the spring; 7 of 10 populations of large herbivores were found to move in ways that supported this hypothesis (Merkle et al., 2016). In some cases, they may follow the wave, while in others (e.g., red deer) they may move rapidly from winter to summer

ranges, in effect "jumping the green wave" (Bischof et al., 2012). Snowmelt has also been shown to be a way for caribou to track vegetation phenology (Laforge et al., 2021), but green wave surfing can be modified by the effects of predation (Rivrud et al., 2018). Shorter altitudinal migrations occur as herbivores move from winter range to higher-elevation breeding grounds, for example, deer and elk in North America, are more likely to track the green wave closely. These kinds of insights have been facilitated by the use of GPS collars in concert with remote sensing to track phenological changes across landscapes (Fisher et al., 2006; O'Leary et al., 2020).

A model of how surfing the green wave affects fitness in a migratory population of elk (*Cervus elaphus*) in the Greater Yellowstone Ecosystem predicts up to a 20% decrease in pregnancy rates, a 2.5% decrease in population growth, and a 30% decrease in abundance over 50 years if green-wave surfing deteriorates by 5–15 days (Middleton et al., 2018). Mule deer (*Odocoileus hemionus*) migration is also proposed to have an energetic benefit if they follow the green wave (Aikens et al., 2017), but this species does not appear to be as plastic in its migration behavior (both routes and phenology) as elk (Sawyer et al., 2019), which might have future fitness consequences.

Migratory species interact with both predators and parasites along their routes, and if those species are not all responding identically to the changing environment, their interactions may change (as they will for stationary populations). Interestingly, brood parasitic cuckoos and their host bird species may exhibit more of a temporal mismatch in populations that migrate short distances, compared to those migrating long distances, making the point that it may be difficult to generalize across all of a species' range (Saino et al., 2009).

Migration is typically linked with reproduction for migratory birds. One study of long-term data for 73 boreal species looked at both beginning and end of the breeding period and found that 31% of species contracted their breeding period in at least one bioclimatic zone, as the end of the breeding period advanced more than the beginning (Hällfors et al., 2020). This contraction was found almost exclusively in resident and short-distance migrating species, which generally breed early in the season. This study is additional evidence for the value of collecting data beyond just the first observation of phenological events, in order to determine the whole distribution of phenological responses and the consequences for fitness.

3.3 | Hibernation

A variety of mammal species use hibernation as a strategy for surviving winter in ecosystems with significant cold and snow. As the climate warms, it is not surprising that these species might respond, given that hibernation poses some risks, such as running out of energy reserves and starving to death. One of the first publications about changes in hibernation was from a long-term study of phenology at the Rocky Mountain Biological Laboratory (at 2900 m in southwest Colorado), which showed that marmots (*Marmota flaviventris*) were emerging 38 days earlier than they used to (Inouye et al., 2000). Long-term studies of Columbian ground squirrels (*Urocitellus columbianus*) in Alberta, Canada showed contrasting results (Lane et al., 2012). Over a 20-year period emergence from hibernation showed a significant delay: 0.47 day per year in the hibernation emergence date of adult females. Females emerged later during years of lower spring temperature and the resulting delayed snowmelt (Lane et al., 2012). The later snowmelt is responsible for a consequent decline in individual fitness and population growth rate during the study period. Hibernation in another Sciurid, the Uinta ground squirrel (*Urocitellus armatus*), is showing a different pattern. A comparison of historical (1964–1968) and recent (2014–2017) data showed that the squirrels' phenology did not change over time, but that survival rates were influenced by season-specific climate variables; older age classes had lower survival when winters or the following springs were warm, while juveniles benefited from warmer winter temperatures (Falvo et al., 2019). Thus, it may be important to consider age classes independently in future studies of how hibernation is changing. A study of the effects of a March heatwave on reproduction of *Urocitellus richardsonii*), Richardson's ground squirrel, makes the point that differences in phenological responses of males and females to the same environmental event can have significant consequences for reproductive fitness (Kucheravy et al., 2021).

Warming temperatures have also been shown to affect the phenology of hibernation in animals as diverse as toads and bears. Shorter winters with warmer temperatures were found, in an experimental study, to increase the survival of hibernating toads, and there was a positive synergistic effect on body mass changes during hibernation (Üveges et al., 2016). Warmer temperatures also influenced hibernation of bears, which delayed entering hibernation (Johnson et al., 2018); the authors speculated that this increase in length of the activity period has the potential to increase human-bear conflicts, and human-caused mortalities, so the benefits of future warmer temperatures for bears are uncertain.

Hibernating animals underground could be responding to biological clocks or environmental cues to determine the appropriate time to exit hibernation, and potentially increase their fitness. Yellow-bellied marmots at the Rocky Mountain Biological Laboratory were found to be emerging 38 days earlier than 23 years ago, apparently in response to warmer spring air temperatures (Inouye et al., 2000). One consequence of their changing phenology, which now includes a later start to hibernation, is that winter mortality is not as common as it used to be, because marmots are able to put on more fat than previously due to the longer growing season (Ozgul et al., 2010). A more recent analysis of 40 years for the same population showed that summer and winter survival can be affected differently by climate change, with increased summer survival accompanying a longer growing season, and decreased winter survival in response to conditions the previous summer (Cordes et al., 2020). This result shows that researchers will have to consider seasonal differences in order to understand the future impacts of climate change on population dynamics.

Not much is known about how the phenology of other species that hibernate, or at least become inactive during the winter, such as some other mammals, snakes, lizards, turtles, amphibians, or insects, in response to the changing climate (Üveges et al., 2016). It seems likely that all those other categories of animals are likely to be affected, since temperature almost undoubtedly plays a role in the timing of their hibernation. Even within a group as restricted as just insects, there can be a wide variety of ways that phenology can be influenced by climate change (Forrest et al., 2010), so only broad generalizations may be possible.

3.4 | Growth and reproduction—Plants

The phenology of flowering can result from intrinsic physiology and genetics, or a dependence on an external environmental cue. External cues can be invariant, such as photoperiod, or vary from year to year, such as accumulation of growing degree days, date of snowmelt, or the timing of monsoon rains. Plants dependent on one or more of these latter clues are changing their flowering phenology as those environmental cues change. The most common pattern of response is to advance the timing of flowering, compared to historical flowering times, but that response is not universal. Changes are not distributed equally across the growing season, as some early-flowering species have been found to be changing their phenology more than later-flowering species (Kopp et al., 2020; Miller-Rushing & Inouye, 2009).

As winter temperatures warm, the accumulated time below freezing that is a requirement for normal flowering by some plants, including some fruit trees, may no longer be met. This loss of time of winter chilling can delay flowering, counteracting the effect of warming temperatures that can advance phenology (Martínez-Lüscher et al., 2017), and if chilling hours fall below a critical threshold some areas may no longer be able to support some kinds of fruit trees. Many deciduous tree species also require chilling hours to release dormancy for leafing out. A study of seven European tree species found that the response of leaf opening to climate warming decreased significantly from 1980 to 2013, a likely response to reduced chilling (Fu et al., 2015). The mechanism for this kind of change in temperature sensitivity has been modeled, including the increased temperature sensitivity with altitude and reduction in years with warmer springs (Güsewell et al., 2017).

A consequence of earlier snowmelt can be an earlier start to plant growth, and potentially a longer growing season. A study of experimental warming and consequent earlier snowmelt found earlier plant growth, but aboveground production varied among species (Livensperger et al., 2016), with early growing species benefiting the most.

The effect of changing phenology on plants can thus be significant, as when they grow will influence interactions with herbivores and their ability to sequester resources for growth and reproduction, and when they flower will influence their interactions with pollinators and seed predators, and their susceptibility to environmental events like late spring or early fall frosts (Iler et al., 2019; Inouye, 2000, 2008; Pardee et al., 2019).

4 | DIFFERENCES BETWEEN PLANTS AND ANIMALS

Many plants and animals use cues related to temperature and/or precipitation for phenological timing related to growth and reproduction, and to the degree that these environmental cues change, so will phenology. Another major cue used by some species of plants and animals is photoperiod, and for at least some animals, the timing of lunar cycles and tides can play a role. One difference between plants and animals, however, is related to their mobility. Many species of animals are mobile enough that they can move as the climate changes, in order to remain in their preferred climate and

maintain historic phenology. Few plants can respond as quickly to spatial gradients, even as seeds. Thus, it is possible that phenological responses to climate change, once the ability to respond with the plasticity inherent in their genomes is exhausted, may require more plants than animals to respond with evolutionary changes to avoid local or even global extinction.

5 | HOW CAN DIFFERENTIAL RESPONSES OF INTERACTING PARTNERS (MISMATCH) AFFECT FITNESS?

One of the potential consequences of phenological changes in response to climate change is that interacting species will not respond identically, disrupting interactions such as pollination, herbivory, competition, predation, and so forth. A migratory hummingbird may be timing its migration based in part on the climate in its overwintering ground, which may not match what is happening in the summer breeding grounds (McKinney et al., 2012). Bumble-bee queens overwintering underground may not respond to the same cues as the flowers they typically visit upon emergence (Thomson, 2010), although it may take decades of data to confirm whether this is or is not occurring (Thomson, 2019). Studies of phenologically mismatched pollinators and their plants have included both observational (Forrest & Thomson, 2011) and experimental (Morton & Rafferty, 2017; Rafferty & Ives, 2011) studies, sometimes taking advantage of elevational gradients (Benadi et al., 2014).

Even within a community of flowering plants, not all species respond identically to the changing climate, making it difficult to generalize about the consequences and forecast what the community will look like in the future. For example, species may or may not start earlier, change the shape of their flowering curves, extend or shorten their flowering period, and change the ending date of flowering (CaraDonna et al., 2014). Even within a category of pollinators, such as bumble bees, different species in the same area can respond differently to environmental cues and their impacts on floral resources, making it difficult to generalize (Ogilvie et al., 2017). At least in some systems, significant decreases in reproductive fitness have been observed or predicted for both pollinators and plants (Hutchings et al., 2018; Schenk et al., 2018).

Mismatches for herbivores can have significant consequences, for both plants and the animals, with examples coming from birds (Choi et al., 2019; Wann et al., 2020), roe deer (Rehnus et al., 2020), and insects (Huang & Hao, 2018; Kharouba et al., 2015; Schwartzberg et al., 2014), although warming may in some cases increase synchrony (Pureswaran et al., 2019; Ren et al., 2020). Tri-trophic interactions have the potential for even more complex interactions, such as those among oak trees, herbivorous caterpillars that eat their leaves, and insectivorous birds that eat the caterpillars (Burgess et al., 2018), and also increased opportunities for phenological mismatch.

6 | COMMUNITY-LEVEL EFFECTS OF CLIMATE ON PHENOLOGY

Species do not exist in isolation, but interact in communities. As each species in a community may respond in a unique way to the changing environment, its interactions with the other species may change, altering patterns of competition, predation, mutualism, or other connections. Studies of such community-level changes are becoming more common as we have learned more about how individual species are responding to climate change.

6.1 | Phylogenetic influence

In the search for generalities in ecological functions, which could help to make ecology a predictive science, investigations of phylogenetic influence have extended to phenological studies. For example, the mean and variance of flowering times of tropical species were found to be similar among congeners in an early study, while variance of flowering times was similar among confamilials (Wright & Calderon, 1995). A more recent study found that more closely related plant species tend to leaf out and to flower at similar times, due to their similar responses to abiotic cues, and bird communities also show a phylogenetic component to their phenological responses (Davies et al., 2013). Leaf-out times of woody plants were found to have a phylogenetic component, as well as relationships to deciduousness, growth habit, and wood anatomy (Panchen et al., 2014).

In contrast, a study of a sub-alpine flowering community found some support for a phylogenetic signal in flowering time in a 39-year record of flowering, when examining dates of first flowering (as most other studies have done), but the results for peak and last flowering dates, and duration of flowering, were inconsistent. Peak flowering date had the strongest phylogenetic signal, followed by the first flowering date, while the last flowering date and duration of flowering did not have a significant phylogenetic component. The sensitivities of all these measures to temperature and snowmelt date had no phylogenetic signal (CaraDonna & Inouye, 2015). Thus, when looking for evidence of a phylogenetic effect on phenology, it will be essential to specify which component of a phenological distribution is under consideration.

A regional (China) examination for phylogenetic effects of plant flowering phenology found that the signal became stronger toward temperate regions and that growth form plays a role (Du et al., 2015), while a global survey of shifts in flowering time found an effect for both whether species had shifted, and the magnitude of their response (Rafferty & Nabity, 2017). Finally, a global synthesis of animal phenological responses to climate change looking at hundreds of time series from around the planet, found that temperature primarily drives phenological responses at mid-latitudes, while precipitation became important at lower latitudes. There was an association between phylogeny and the strength of the phenological shifts (Cohen et al., 2018).

6.2 | Changes in competitors and mutualists

Species can only interact if they overlap spatially and temporally, so changes in temporal activity patterns have the potential to increase or decrease the opportunities for interactions such as competition and mutualism. Phenological separation should create temporal niche differences that reduce interactions, and potentially favor one species over another in terms of competition. This can hold true for both plants and animals. An example involving two annual grass species of *Vulpia* and the timing of their germination showed that increasing the separation of their germination resulted in parallel changes in their niches and fitness. Earlier germination provided a competitive advantage, to the degree that a 4-day head start allowed competitive exclusion of the generally superior competitor (Blackford et al., 2020). Thus, phenological differences can structure competitive interactions and influence species coexistence. A study of coexistence theory came to a similar conclusion, that differences in species' phenologies can have a strong influence on persistence and coexistence of competing species (Rudolf, 2019).

An additional example of how competitive interactions are influenced by phenology is a study of an introduced European annual plant. Prickly lettuce (*Lactuca serriola*) flowers earlier in arid climates such as those of southern California, and an experimental common-garden study showed that this earlier flowering resulted in stronger competition with native annuals than resulted from later-flowering plants (Alexander & Levine, 2019). Thus, this phenological interaction could facilitate a biological invasion. This example of how evolution resulting from new climate conditions can influence the success of invasive species in natural communities is a cautionary tale about what the future may bring if the climate continues to change.

Another recent study, but with a more global perspective, used a new database of long-term studies of phenological events and their influence on pairwise species interactions. The authors found evidence of substantial changes in the relative timing of these interactions, with the magnitude of shifts increasing as the climate has changed (Kharouba et al., 2018). Their meta-analysis approach provides support for the conclusion that additional research is needed to refine our ability to predict the direction of change, and to interpret results, so that we can make predictions about the consequences of these changes for ecological communities.

6.3 | Changes in predation

Climate change can affect multiple selective pressures, leading to a necessity to balance the need to stay in synchrony with the timing of maximum food, for example, and the benefits of minimizing predation, which may not result in a single optimum. Reduced fitness from a lack of plasticity to alter phenology in response to climate change can be detrimental, but a long-term study of an oak–caterpillar–songbird–sparrowhawk food web revealed that disruption of trophic interactions could also be important (Brook, 2009). The multiple selective pressures involved in trophic networks like this create "a tug-of-war between the need to stay in synchrony with the timing of maximum food, and the benefits of minimizing predation." (Brook, 2009).

Effects of climate change on phenology and consequent impacts on predator–prey interactions have been documented in aquatic systems such as fish and zooplankton (Ohlberger et al., 2014), seed predation (Straka & Starzomski, 2015), and nest predation by polar bears (Dey et al., 2017). A model of synchrony of zooplankton prey and their Arcto-boreal fish predators indicates that frequent desynchronization of the predators and prey may lead to a pronounced population decline of the fish, but also suggests that temperate fish may be better able to track prey phenology (Durant et al., 2019). Such responses in predator–prey interactions are not surprising given that climate change is generating new spatial distributions as species change or expand their historical ranges, encountering new communities of interacting species.

The behavioral plasticity inherent in individuals can provide significant latitude to respond to environmental changes, as was found in a long-term study of great tits (*Parus major*; Charmantier et al., 2008). In this population individual adjustment of behavior in response to the environment has enabled the birds to track a rapidly changing environment very closely. At some point, however, the ability of predators and prey to respond based on the plasticity in their current genomes will be exceeded, requiring responses such as changes in range, or evolution, to avoid extinction. Charmantier et al. point out that understanding the limits of plasticity is an important goal for future research.

7 | A CASE HISTORY: CLIMATE EFFECTS ON ROCKY MOUNTAIN WILDFLOWERS AND POLLINATORS

7.1 | Changes in local climate

Most aspects of phenology in the montane habitats at 2900 m near the Rocky Mountain Biological Laboratory, in southwestern Colorado, are controlled by one environmental variable, snowmelt date, which in turn, is a consequence of how much snow falls during the winter, spring temperatures, and more recently, the effects of dust-on-snow events (Maurer & Bowling, 2014). In recent years, the ratio of annual precipitation that falls as rain versus snow has been changing, with rain earlier in the spring and later in the fall, spring temperatures are increasing, and dust-on-snow events are becoming more common (Maurer & Bowling, 2014; Painter et al., 2018). The net effect of these changes is earlier snowmelt (Figure 1), and hence an earlier start to the growing and flowering seasons (Figure 2), and longer growing seasons (Figure 3).

The environmental changes we are seeing are in part the effects of global warming, in part probably the effects of regional changes including the Pacific Decadal Oscillation, El Niño Southern Oscillation, Quasi-Biennial Oscillation, and probably more-local effects too. These regional effects occur on different time scales, ranging from 2 years for the QBO, a few years (ENSO), and as long as 40–60 years (PDO). Acting in concert, the net effect appears to be responsible

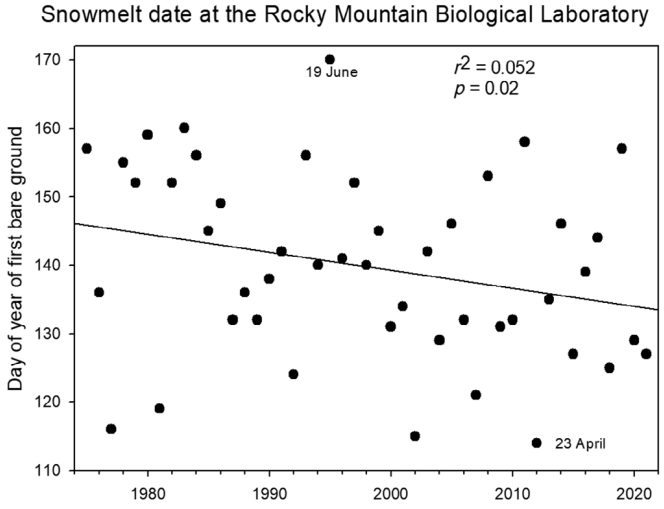


FIGURE 1 The day of year when the last snow melts in a permanent site at the Rocky Mountain Biological Laboratory at 2,921m in southwest Colorado. Dates have ranged from 23 April to 19 June and are getting earlier. Data courtesy of billy barr

for a 12–14 year cycle in the central Rocky Mountains (Ault & St. George, 2010) that is reflected in snowmelt dates and flowering by at least some species.

7.2 | Effects on flowering phenology and abundance

Flowering phenology at this high-altitude montane site is driven largely by the date of snowmelt, which signals the beginning of the growing season (although a few early species can grow up through the last few cm of snow). The earlier dates of snowmelt are resulting in flowering beginning as early as mid-April, in contrast to dates as late as early June only a few decades ago (Figure 2). Although it might seem that a longer growing season would be beneficial, the earlier start has led to an increase in damage from frost (Inouye, 2008), as the date of the last spring frost has not been advancing (although it has in some parts of the world; Zohner et al., 2020). When the growing season did not start until late May or early June, a frost around 10 June had little effect on the wildflowers. But when it starts in mid-April, many frost-sensitive plant species can lose their buds with a June frost. This can have a major effect on flower abundance, affecting pollinators, and seed production, affecting seed predators (Inouye, 2000).

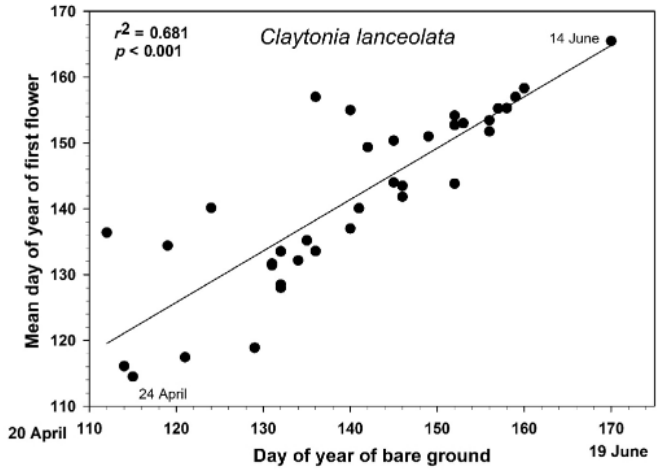


FIGURE 2 The mean day of year when the first flower of *Claytonia lanceolata* (Portulacaceae) has opened in permanent plots at the Rocky Mountain Biological Laboratory, 1975 – 2014. Data from the RMBL phenology project

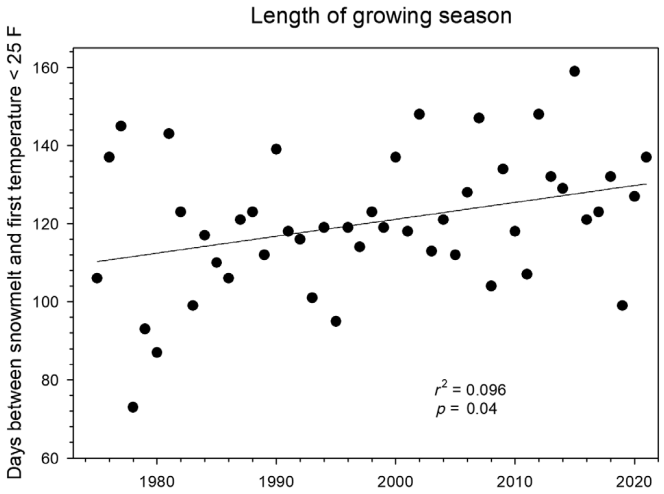


FIGURE 3 The length of the growing season, defined here as the interval between snowmelt at the RMBL measuring station in the spring until the first recorded temperature < 25° F (3.9° C) in Crested Butte, Colorado (2,703m, 9.4 km from RMBL)

This loss of flowers due to frost damage can have subsequent effects on plant demography—if there are no seeds produced, there will be no seedlings the next spring (Campbell, 2019). Drought risk associated with earlier snowmelt may also contribute to the potential for negative demographic effects on wildflower populations (Iler et al., 2019). The increasingly common occurrence of "false springs", with an unusual early spring warm spell triggering flowering, followed by a frost event, is also having consequences for agriculture around the world (Andrew et al., 2015; Ault et al., 2013; Chamberlain et al., 2019; Chmielewski et al., 2018; Gu et al., 2008; Ladwig et al., 2019; Marino et al., 2011; Peterson & Abatzoglou, 2014).

7.3 | Effects on bumble bees

Queen bumble bees (*Bombus* spp.) overwinter underground and emerge in the spring to establish colonies. Temperature plays a role in their emergence times (Goodwin, 1995), as it does for flowering times, and in an alpine community in Japan flowering was found to advance more than bee emergence times in early springs, so that early-flowering p had lower seed production (Kudo, 2014; Kudo & Ida, 2013). Other studies at our Colorado field site have also found that changes in resource phenology are likely to impact bumble bee populations and communities (Ogilvie & Forrest, 2017), and that bumble bee altitudinal distributions are changing, likely in response to warming temperatures and the consequent changes in floral resources (Pyke et al., 2011, 2012, 2016). A long-term study of bumble bee abundances found that they were driven primarily by the indirect effects of climate on the temporal distribution of floral resources (Ogilvie et al., 2017). This study also found that even within bumble bees there are species-specific differences in response to the changes in precipitation, temperature, and flower availability, making it difficult to generalize from a single species. Temporal gaps in availability of floral resources can have a negative impact on populations of bumble bees and other pollinators (Timberlake et al., 2019), and may be becoming more pronounced (Aldridge et al., 2011).

7.4 | Effects on a butterfly species

Speyeria mormonia is a butterfly with unusual dependence as an adult on a single nectar food source, *Erigeron speciosus* (aspen fleabane; Asteraceae; Figure 4). The number of eggs a female can lay depends in large part on how much nectar she collects. Its populations can vary by an order of magnitude or more from year to year, but most of this variation can be explained by the ratio of butterflies to flowers; if there are a lot of flowers the population grows, and if not, it shrinks. The abundance of *Erigeron speciosus* flowers is in turn strongly affected by the interaction of snowmelt date and frost, as the flower buds are frost sensitive (Figure 5). In years in which snow melts early, there



FIGURE 4 A *Speyeria mormonia* the butterfly on a flower its preferred nectar plant, *Erigeron speciosus* (Boggs & Inouye, 2012)

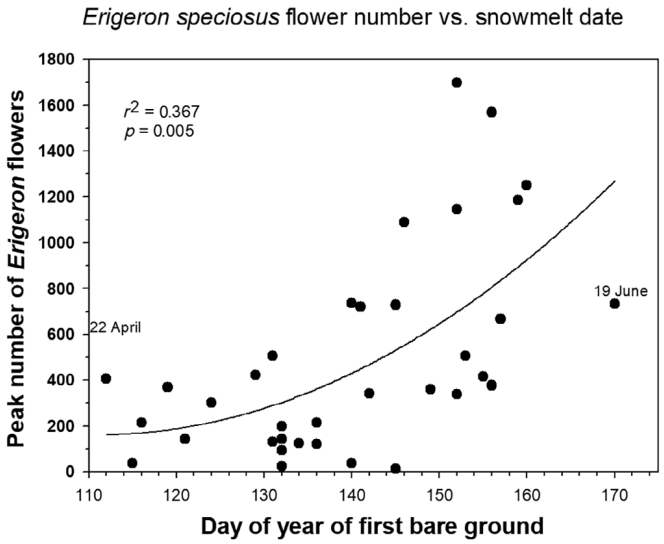


FIGURE 5 The number of *Erigeron speciosus* flower at peak flowering is strongly influenced by when the snow melts. In years with early snowmelt there is likely to be frost damage to flower buds, which sometimes results in the loss of almost all flowers in this long-lived perennial daisy. Data from the RMBL Phenology Project, 1974 – 2011

is a greater probability of frost damage, fewer flowers, and consequently, of the butterfly population declining the next year (Boggs & Inouye, 2012).

7.5 | Effects on hummingbirds

Most of the breeding bird species at the Rocky Mountain Biological Laboratory are migratory, and as has been documented elsewhere, migration times are trending earlier, most likely in response to warming temperatures at lower altitudes and latitudes where the birds are overwintering. For example, the arrival dates of male Broad-tailed Hummingbirds (*Selasphorus platycercus*) between 1975 and 2011 advanced by 1.5 ± 0.93 days per decade (McKinney et al., 2012). However, the change in phenology of the first wildflower to bloom that the hummingbirds visit, *Erythronium grandiflorum*, was not matched by the hummingbirds. First and peak flowering advanced by 4.6 ± 1.6 and 2.7 ± 1.4 days per decade during this same time period, and flowering by the second species of flower visited by the hummingbirds, *Delphinium nuttallianum*, advanced by 4.3 ± 1.5 and 2.8 ± 1.4 days. If these trends continue, at some point the birds will miss the flowering by these early floral resources.

Nonmigratory species may be able to respond more quickly to the changing environment, as they are more closely tied to local conditions, rather than changes occurring over widely-spaced winter and summer habitats. For example, a long-term study of *Parus major* in the UK found that "individual adjustment of behavior in response to the environment has enabled the population to track a rapidly changing environment very closely." (Charmantier et al., 2008).

8 | NEEDS FOR RESEARCH TO IMPROVE OUR UNDERSTANDING

Many phenological events occur annually, which means that you can only collect one data point per year. One consequence is that it can take many years of observation before a significant trend can be discerned; loss of a year's datum, due to events such as the COVID-19 pandemic, or a gap in research grant funding, is a significant risk of such studies. One impediment to such long-term studies is that most research grants are for 2–3 years, so multiple grants may be required in order to fund a project for long enough to obtain significant data. Even in environments with significant environmental variation, it will likely take multiple years to span a sufficient range of temperature, precipitation, snowmelt date, or a combination of them, to identify the dependence of phenology on these variables (Kudo & Ida, 2013). Experimental manipulations, such as changing snowpack in order to influence snowmelt date, could shorten the time required to gain such insights (Kudo & Cooper, 2019).

Most phenological studies have emphasized observations of the first occurrence of an event each year, such as the arrival date of the first migratory bird, or first flower. Yet reliance on these first dates has multiple problems, ranging from needing to be present when they occur, to statistical issues (Inouye et al., 2019; Miller-Rushing et al., 2008). In addition, a more complete investigation of the full suite of phenological markers, for example for the beginning, peak, and end of flowering, has shown that not all of the phenological measures are changing uniformly within or among species (CaraDonna et al., 2014). This lack of congruence makes it essential for researchers to begin collecting more complete phenological datasets.

Species do not exist in isolation in ecological communities, but interact with competitors, mutualists, parasites, and predators. To date, there are enough studies of individual species for us to know that there can be significant variation within and among individuals (Forrest & Thomson, 2010), so that sample sizes need to be large enough to encompass such variation. But there are still relatively few studies of enough species to constitute community-level studies, and very few consider how changes in phenology are impacting community-level interactions of multiple species.

There is an opportunity for an increased use of two resources available for phenological studies. One is the use of herbaria and other museum collections, which serve as archives of the phenological history of specimens. Although the value of herbaria for this purpose was recognized at least 25 years ago (Borchert, 1996), there is still a lot of untapped potential. As an increasing amount of museum collection data becomes available digitally, the analysis of their phenological data is becoming more feasible (Brooks et al., 2014; Denney & Anderson, 2020). Finally, citizen scientists are now collecting a lot of phenological data that are available to scientists. For example, a variety of phenological data are now being archived through the USA National Phenology Network, and bird data through the Cornell Lab of Ornithology and Audubon Society.

9 | CONCLUSION

The ongoing changes in the planet's climate are altering historical patterns of variation in temperature and precipitation, the two major environmental cues that influence the phenological components of most species' life histories. Not surprisingly, this sets the stage for alterations in the variety of ecological interactions among members of communities. We now know enough about how some species have responded that it is clear that not all species in existing interactions are responding the same way. This means that some interactions are likely falling apart, while new ones are being created, both spatially and temporally. Interactions like competition, predation, and mutualisms are changing in ways that we are just beginning to understand. Terrestrial, freshwater, and marine ecosystems are dynamic entities even when the environment is relatively stable, and with the ongoing changes, they are all evolving rapidly as species adapt, move, or go extinct. This is undoubtedly an interesting (if depressing) time to be studying ecology.

CONFLICT OF INTEREST

The author has declared no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

No new data were created for this study. Data referred to from the RMBL phenology project are available; see https://www.bio.fsu.edu/~nunderwood/homepage/RMBLphenologyproject.html.

ORCID

David W. Inouye https://orcid.org/0000-0003-2076-7834

RELATED WIREs ARTICLES

Detection and attribution of anthropogenic climate change impacts
Climate change vulnerability assessment of species

FURTHER READING

Haggerty, B. P., & Mazer, S. J. (2008). *The phenology handbook: A guide to phenological monitoring for students, teachers, families, and nature enthusiasts*. University of California, Santa Barbara.

Noormets, A. (Ed.). (2009). *Phenology of ecosystem processes*. Springer.

Schwartz, M. D. (Ed.). (2003). *Phenology: An integrative environmental science, Tasks for Vegetation Science*. Kluwer Academic Publishers. See resources and data available through the USA National Phenology Network. Retrieved from. http://usanpn.org/

REFERENCES

Aikens, E. O., Kauffman, M. J., Merkle, J. A., Dwinnell, S. P. H., Fralick, G. L., & Monteith, K. L. (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters*, *20*, 741–750.

Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A., & Miller-Rushing, A. J. (2011). Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *Journal of Ecology*, *99*, 905–913.

Alexander, J. M., & Levine, J. M. (2019). Earlier phenology of a nonnative plant increases impacts on native competitors. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 6199–6204.

Andrew, J. A., Stephen, J. V., Patricia, J. H., Anna, M. P., Wayne, E. T., & Volker, C. R. (2015). Spring plant phenology and false springs in the conterminous US during the 21st century. *Environmental Research Letters*, *10*, 104008.

Ault, T. R., Henebry, G. M., de Beurs, K. M., Schwartz, M. D., Betancourt, J. L., & Moore, D. (2013). The false spring of 2012, earliest in north American record. *Eos, Transactions American Geophysical Union*, *94*, 181–182.

Ault, T. R., & St. George, S. (2010). The magnitude of decadal and multidecadal variability in North American precipitation. *Journal of Climate*, *23*, 842–850.

Benadi, G., Hovestadt, T., Poethke, H.-J., & Blüthgen, N. (2014). Specialization and phenological synchrony of plant–pollinator interactions along an altitudinal gradient. *Journal of Animal Ecology*, *83*, 639–650.

Bischof, R., Loe, L. E., Meisingset, E. L., Zimmermann, B., Moorter, B. V., & Mysterud, A. (2012). A migratory northern ungulate in the pursuit of spring: Jumping or surfing the green wave? *The American Naturalist*, *180*, 407–424.

Blackford, C., Germain, R. M., & Gilbert, B. (2020). Species differences in phenology shape coexistence. *The American Naturalist*, *195*, E168–E180.

Boers, N. (2021). Observation-based early-warning signals for a collapse of the Atlantic Meridional overturning circulation. *Nature Climate Change*, *11*, 680–688.

Boggs, C. L., & Inouye, D. W. (2012). A single climate driver has direct and indirect effects on insect population dynamics. *Ecology Letters*, *15*, 502–508.

Borchert, R. (1996). Phenology and flowering periodicity of Neotropical dry forest species: Evidence from herbarium collections. *Journal of Tropical Ecology*, *12*(Part 1), 65–80.

Brook, B. W. (2009). Global warming tugs at trophic interactions. *Journal of Animal Ecology*, *78*, 1–3.

Brooks, S. J., Self, A., Toloni, F., & Sparks, T. (2014). Natural history museum collections provide information on phenological change in British butterflies since the late-nineteenth century. *International Journal of Biometeorology*, *58*, 1749–1758.

Burgess, M. D., Smith, K. W., Evans, K. L., Leech, D., Pearce-Higgins, J. W., Branston, C. J., Briggs, K., Clark, J. R., du Feu, C. R., Lewthwaite, K., Nager, R. G., Sheldon, B. C., Smith, J. A., Whytock, R. C., Willis, S. G., & Phillimore, A. B. (2018). Tritrophic phenological match–mismatch in space and time. *Nature Ecology & Evolution*, *2*, 970–975.

Cadahia, L., Labra, A., Knudsen, E., Nilsson, A., Lampe, H. M., Slagsvold, T., & Stenseth, N. C. (2017). Advancement of spring arrival in a long-term study of a passerine bird: Sex, age and environmental effects. *Oecologia*, *184*, 917–929.

Cai, W., Santoso, A., Wang, G., Yeh, S.-W., An, S.-I., Cobb, K. M., Collins, M., Guilyardi, E., Jin, F.-F., Kug, J.-S., Lengaigne, M., McPhaden, M. J., Takahashi, K., Timmermann, A., Vecchi, G., Watanabe, M., & Wu, L. (2015). ENSO and greenhouse warming. *Nature Climate Change*, *5*, 849–859.

Campbell, D. R. (2019). Early snowmelt projected to cause population decline in a subalpine plant. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 12901–12906.

Cappello, C. D., & Boersma, P. D. (2021). Consequences of phenological shifts and a compressed breeding period in Magellanic penguins. *Ecology*, *102*, e03443.

CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 4916–4921.

CaraDonna, P. J., & Inouye, D. W. (2015). Phenological responses to climate change do not exhibit phylogenetic signal in a subalpine plant community. *Ecology*, *96*, 355–361.

Chamberlain, C. J., Cook, B. I., García de Cortázar-Atauri, I., & Wolkovich, E. M. (2019). Rethinking false spring risk. *Global Change Biology*, *25*, 2209–2220.

Chan, D., Cobb, A., Zeppetello, L. R. V., Battisti, D. S., & Huybers, P. (2020). Summertime temperature variability increases with local warming in midlatitude regions. *Geophysical Research Letters*, *47*, e2020GL087624.

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., & Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*, 800–803.

Chmielewski, F.-M., Götz, K.-P., Weber, K. C., & Moryson, S. (2018). Climate change and spring frost damages for sweet cherries in Germany. *International Journal of Biometeorology*, *62*, 217–228.

Choi, R. T., Beard, K. H., Leffler, A. J., Kelsey, K. C., Schmutz, J. A., & Welker, J. M. (2019). Phenological mismatch between season advancement and migration timing alters Arctic plant traits. *Journal of Ecology*, *107*, 2503–2518.

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, *8*, 224–228.

Cordes, L. S., Blumstein, D. T., Armitage, K. B., CaraDonna, P. J., Childs, D. Z., Gerber, B. D., Martin, J. G. A., Oli, M. K., & Ozgul, A. (2020). Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 18119–18126.

Davies, T. J., Wolkovich, E. M., Kraft, N. J. B., Salamin, N., Allen, J. M., Ault, T. R., Betancourt, J. L., Bolmgren, K., Cleland, E. E., Cook, B. I., Crimmins, T. M., Mazer, S. J., McCabe, G. J., Pau, S., Regetz, J., Schwartz, M. D., & Travers, S. E. (2013). Phylogenetic conservatism in plant phenology. *Journal of Ecology*, *101*, 1520–1530.

Denney, D. A., & Anderson, J. T. (2020). Natural history collections document biological responses to climate change. *Global Change Biology*, *26*, 340–342.

Dey, C. J., Richardson, E., McGeachy, D., Iverson, S. A., Gilchrist, H. G., & Semeniuk, C. A. D. (2017). Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. *Global Change Biology*, *23*, 1821–1831.

Du, Y., Mao, L., Queenborough, S. A., Freckleton, R. P., Chen, B., & Ma, K. (2015). Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. *Global Ecology and Biogeography*, *24*, 928–938.

Durant, J. M., Molinero, J.-C., Ottersen, G., Reygondeau, G., Stige, L. C., & Langangen, Ø. (2019). Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. *Scientific Reports*, *9*, 15213.

Eilperin, J. (2020). 2°C: Beyond the limit. This giant climate hot spot is robbing the west of its water. *The Washington Post*, 7 August 2020.

Falvo, C. A., Koons, D. N., & Aubry, L. M. (2019). Seasonal climate effects on the survival of a hibernating mammal. *Ecology and Evolution*, *9*, 3756–3769.

Fisher, J., Mustard, J., & Vadeboncoeur, M. (2006). Green leaf phenology at Landsat resolution: Scaling from the field to the satellite. *Remote Sensing of Environment*, *100*, 265–279.

Forrest, J., Inouye, D. W., & Thomson, J. D. (2010). Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? *Ecology*, *91*, 431–440.

Forrest, J., & Thomson, J. D. (2010). Consequences of variation in flowering time within and among individuals of *Mertensia fusiformis* (Boraginaceae), an early spring wildflower. *American Journal of Botany*, *97*, 38–48.

Forrest, J. R. K., & Thomson, J. D. (2011). An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecological Monographs*, *81*, 469–491.

Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Penuelas, J., Song, Y., Vitasse, Y., Zeng, Z., & Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, *526*, 104–107.

Gill, J. A., Alves, J. A., & Gunnarsson, T. G. (2019). Mechanisms driving phenological and range change in migratory species. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *374*, 20180047.

Goodwin, S. G. (1995). Seasonal phenology and abundance of early-, mid- and long-season bumble bees in southern England, 1985-1989. *Journal of Apicultural Research*, *34*, 79–87.

Gu, L., Hanson, P. J., Post, W. M., Kaiser, D. P., Yang, B., Nemani, R., Pallardy, S. G., & Meyers, T. (2008). The 2007 eastern US spring freeze: Increased cold damage in a warming world? *Bioscience*, *58*, 253–262.

Güsewell, S., Furrer, R., Gehrig, R., & Pietragalla, B. (2017). Changes in temperature sensitivity of spring phenology with recent climate warming in Switzerland are related to shifts of the preseason. *Global Change Biology*, *23*, 5189–5202.

Hällfors, M. H., Antão, L. H., Itter, M., Lehikoinen, A., Lindholm, T., Roslin, T., & Saastamoinen, M. (2020). Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 18557–18565.

Horton, K. G., La Sorte, F. A., Sheldon, D., Lin, T.-Y., Winner, K., Bernstein, G., Maji, S., Hochachka, W. M., & Farnsworth, A. (2020). Phenology of nocturnal avian migration has shifted at the continental scale. *Nature Climate Change*, *10*, 63–68.

Huang, J., & Hao, H. (2018). Detecting mismatches in the phenology of cotton bollworm larvae and cotton flowering in response to climate change. *International Journal of Biometeorology*, *62*, 1507–1520.

Hutchings, M. J., Robbirt, K. M., Roberts, D. L., & Davy, A. J. (2018). Vulnerability of a specialized pollination mechanism to climate change revealed by a 356-year analysis. *Botanical Journal of the Linnean Society*, *186*, 498–509.

Iler, A. M., Compagnoni, A., Inouye, D. W., Williams, J. L., CaraDonna, P. J., Anderson, A., & Miller, T. E. X. (2019). Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology*, *107*, 1931–1943.

Inouye, B. D., Ehrlén, J., & Underwood, N. (2019). Phenology as a process rather than an event: From individual reaction norms to community metrics. *Ecological Monographs*, *89*, e01352.

Inouye, D. W. (2000). The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, *3*, 457–463.

Inouye, D. W. (2008). Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, *89*, 353–362.

Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 1630–1633.

IPCC. (2021). Climate Change 2021: The Physical Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.

Jin, H., Jönsson, A. M., Olsson, C., Lindström, J., Jönsson, P., & Eklundh, L. (2019). New satellite-based estimates show significant trends in spring phenology and complex sensitivities to temperature and precipitation at northern European latitudes. *International Journal of Biometeorology*, *63*, 763–775.

Johnson, H. E., Lewis, D. L., Verzuh, T. L., Wallace, C. F., Much, R. M., Willmarth, L. K., & Breck, S. W. (2018). Human development and climate affect hibernation in a large carnivore with implications for human–carnivore conflicts. *Journal of Applied Ecology*, *55*, 663–672.

Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., & 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*, 5211–5216.

Kharouba, H. M., Vellend, M., Sarfraz, R. M., & Myers, J. H. (2015). The effects of experimental warming on the timing of a plant–insect herbivore interaction. *Journal of Animal Ecology*, *84*, 785–796.

Kluen, E., Nousiainen, R., & Lehikoinen, A. (2017). Breeding phenological response to spring weather conditions in common Finnish birds: Resident species respond stronger than migratory species. *Journal of Avian Biology*, *48*, 611–619.

Kolarova, E., Matiu, M., Menzel, A., Nekovar, J., Lumpe, P., & Adamik, P. (2017). Changes in spring arrival dates and temperature sensitivity of migratory birds over two centuries. *International Journal of Biometeorology*, *61*, 1279–1289.

Kopp, C. W., Neto-Bradley, B. M., Lipsen, L. P. J., Sandhar, J., & Smith, S. (2020). Herbarium records indicate variation in bloom-time sensitivity to temperature across a geographically diverse region. *International Journal of Biometeorology*, *64*, 873–880.

Kovach, R. P., Gharrett, A. J., & Tallmon, D. A. (2012). Genetic change for earlier migration timing in a pink salmon population. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3870–3878.

Kucheravy, C. E., Waterman, J. M., dos Anjos, E. A. C., Hare, J. F., Enright, C., & Berkvens, C. N. (2021). Extreme climate event promotes phenological mismatch between sexes in hibernating ground squirrels. *Scientific Reports*, *11*, 21684.

Kuczynski, L., Chevalier, M., Laffaille, P., Legrand, M., & Grenouillet, G. (2017). Indirect effect of temperature on fish population abundances through phenological changes. *PLoS One*, *12*, 13.

Kudo, G. (2014). Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecological Research*, *29*, 571–581.

Kudo, G., & 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*, 20190573.

Kudo, G., & Ida, T. Y. (2013). Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, *94*, 2311–2320.

Kullberg, C., Fransson, T., Hedlund, J., Jonzén, N., Langvall, O., Nilsson, J., & Bolmgren, K. (2015). Change in spring arrival of migratory birds under an era of climate change, Swedish data from the last 140 years. *Ambio*, *44*, 69–77.

Ladwig, L. M., Chandler, J. L., Guiden, P. W., & Henn, J. J. (2019). Extreme winter warm event causes exceptionally early bud break for many woody species. *Ecosphere*, *10*, e02542.

Laforge, M. P., Bonar, M., & Vander Wal, E. (2021). Tracking snowmelt to jump the green wave: Phenological drivers of migration in a northern ungulate. *Ecology*, *102*, e03268.

Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., & Dobson, F. S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature*, *489*, 554–557.

Livensperger, C., Steltzer, H., Darrouzet-Nardi, A., Sullivan, P. F., Wallenstein, M., & Weintraub, M. N. (2016). Earlier snowmelt and warming lead to earlier but not necessarily more plant growth. *AoB Plants*, *8*, plw021.

Marino, G. P., Kaiser, D. P., Gu, L., & Ricciuto, D. M. (2011). Reconstruction of false spring occurrences over the southeastern United States, 1901-2007: An increasing risk of spring freeze damage? *Environmental Research Letters*, *6*, 024015.

Martínez-Lüscher, J., Hadley, P., Ordidge, M., Xu, X., & Luedeling, E. (2017). Delayed chilling appears to counteract flowering advances of apricot in southern UK. *Agricultural and Forest Meteorology*, *237–238*, 209–218.

Matthysen, E., Adriaensen, F., & Dhondt, A. A. (2011). Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). *Global Change Biology*, *17*, 1–16.

Maurer, G. E., & Bowling, D. R. (2014). Dust effects on snowpack melt and related ecosystem processes are secondary to those of forest canopy structure and interannual snowpack variability. *Ecohydrology*, *8*, 1005–1023.

McDevitt-Galles, T., Moss, W., Calhoun, D., & Johnson, P. (2020). Phenological synchrony shapes pathology in host–parasite systems. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20192597.

McKinney, A. M., CaraDonna, P. J., Inouye, D. W., Barr, B., Bertelsen, C. D., & Waser, N. M. (2012). Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. *Ecology*, *93*, 1987–1993.

McLean, B. S., & Guralnick, R. P. (2021). Digital biodiversity data sets reveal breeding phenology and its drivers in a widespread north American mammal. *Ecology*, *102*, e03258.

Merkle, J. A., Monteith, K. L., Aikens, E. O., Hayes, M. M., Hersey, K. R., Middleton, A. D., Oates, B. A., Sawyer, H., Scurlock, B. M., & Kauffman, M. J. (2016). Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society of London B: Biological Sciences*, *283*, 20160456.

Middleton, A. D., Merkle, J. A., McWhirter, D. E., Cook, J. G., Cook, R. C., White, P. J., & Kauffman, M. J. (2018). Green-wave surfing increases fat gain in a migratory ungulate. *Oikos*, *127*, 1060–1068.

Millán, M. F., Carranza, J., Pérez-González, J., Valencia, J., Torres-Porras, J., Seoane, J. M., de la Peña, E., Alarcos, S., Sánchez-Prieto, C. B., Castillo, L., Flores, A., & Membrillo, A. (2021). Rainfall decrease and red deer rutting behaviour: Weaker and delayed rutting activity though higher opportunity for sexual selection. *PLoS One*, *16*, e0244802.

Miller-Rushing, A. J., & Inouye, D. W. (2009). Variation in the impact of climate change on flowering phenology and abundance: An examination of two pairs of closely related wildflower species. *American Journal of Botany*, *96*, 1821–1829.

Miller-Rushing, A. J., Inouye, D. W., & Primack, R. B. (2008). How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *Journal of Ecology*, *96*, 1289–1296.

Morton, E. M., & Rafferty, N. E. (2017). Plant–pollinator interactions under climate change: The use of spatial and temporal transplants. *Applications in Plant Sciences*, *5*, 1600133.

Moyes, K., Nussey, D. H., Clements, M. N., Guinness, F. E., Morris, A., Morris, S., Pemberton, J. M., Kruuk, L. E. B., & Clutton-Brock, T. H. (2011). Advancing breeding phenology in response to environmental change in a wild red deer population. *Global Change Biology*, *17*, 2455–2469.

Ogilvie, J. E., & Forrest, J. R. K. (2017). Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science*, *21*, 75–82.

Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W., & Irwin, R. E. (2017). Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecology Letters*, *20*, 1507–1515.

Ohlberger, J., Thackeray, S. J., Winfield, I. J., Maberly, S. C., & 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*, 20140938.

O'Leary, D., Inouye, D., Dubayah, R., Huang, C., & Hurtt, G. (2020). Snowmelt velocity predicts vegetation green-wave velocity in mountainous ecological systems of North America. *International Journal of Applied Earth Observation and Geoinformation*, *89*, 102110.

Ozgul, A., Childs, D. Z., Oli, M. K., Armitage, K. B., Blumstein, D. T., Olson, L. E., Tuljapurkar, S., & Coulson, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, *466*, 482–485.

Painter, T. H., Skiles, S. M., Deems, J. S., Brandt, W. T., & Dozier, J. (2018). Variation in rising limb of Colorado River snowmelt runoff hydrograph controlled by dust radiative forcing in snow. *Geophysical Research Letters*, *45*, 797–808.

Panchen, Z. A., Primack, R. B., Nordt, B., Ellwood, E. R., Stevens, A.-D., Renner, S. S., Willis, C. G., Fahey, R., Whittemore, A., Du, Y., & Davis, C. C. (2014). Leaf out times of temperate woody plants are related to phylogeny, deciduousness, growth habit and wood anatomy. *New Phytologist*, *203*, 1208–1219.

Pardee, G. L., Jensen, I. O., Inouye, D. W., & Irwin, R. E. (2019). The individual and combined effects of snowmelt timing and frost exposure on the reproductive success of montane forbs. *Journal of Ecology*, *107*, 1970–1981.

Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports*, *7*, 17966.

Peterson, A., & Abatzoglou, J. T. (2014). Observed changes in false springs over the contiguous United States. *Geophysical Research Letters*, *41*, 2156–2162.

Power, S., Delage, F., Chung, C., Kociuba, G., & Keay, K. (2013). Robust twenty-first-century projections of El Niño and related precipitation variability. *Nature*, *502*, 541–545.

Pureswaran, D. S., Neau, M., Marchand, M., De Grandpré, L., & Kneeshaw, D. (2019). Phenological synchrony between eastern spruce budworm and its host trees increases with warmer temperatures in the boreal forest. *Ecology and Evolution*, *9*, 576–586.

Pyke, G. H., Inouye, D. W., & Thomson, J. D. (2011). Activity and abundance of bumble bees near crested Butte, Colorado: Diel, seasonal, and elevation effects. *Ecological Entomology*, *36*, 511–521.

Pyke, G. H., Inouye, D. W., & Thomson, J. D. (2012). Local geographic distributions of bumble bees near crested Butte, Colorado: Competition and community structure revisited. *Environmental Entomology*, *41*, 1332–1349.

Pyke, G. H., Thomson, J. D., Inouye, D. W., & Miller, T. J. (2016). Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere*, *7*, e01267.

Rafferty, N. E., & Ives, A. R. (2011). Effects of experimental shifts in flowering phenology on plant–pollinator interactions. *Ecology Letters*, *14*, 69–74.

Rafferty, N. E., & Nabity, P. D. (2017). A global test for phylogenetic signal in shifts in flowering time under climate change. *Journal of Ecology*, *105*, 627–633.

Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, *82*, 131–144.

Reed, T. E., Warzybok, P., Wilson, A. J., Bradley, R. W., Wanless, S., & Sydeman, W. J. (2009). Timing is everything: Flexible phenology and shifting selection in a colonial seabird. *Journal of Animal Ecology*, *78*, 376–387.

Rehnus, M., Peláez, M., & Bollmann, K. (2020). Advancing plant phenology causes an increasing trophic mismatch in an income breeder across a wide elevational range. *Ecosphere*, *11*, e03144.

Ren, P., Néron, V., Rossi, S., Liang, E., Bouchard, M., & Deslauriers, A. (2020). Warming counteracts defoliation-induced mismatch by increasing herbivore-plant phenological synchrony. *Global Change Biology*, *26*, 2072–2080.

Rivrud, I. M., Sivertsen, T. R., Mysterud, A., Åhman, B., Støen, O.-G., & Skarin, A. (2018). Reindeer green-wave surfing constrained by predators. *Ecosphere*, *9*, e02210.

Rudolf, V. H. W. (2019). The role of seasonal timing and phenological shifts for species coexistence. *Ecology Letters*, *22*, 1324–1338.

Saino, N., Rubolini, D., Lehikoinen, E., Sokolov, L. V., Bonisoli-Alquati, A., Ambrosini, R., Boncoraglio, G., & Møller, A. P. (2009). Climate change effects on migration phenology may mismatch brood parasitic cuckoos and their hosts. *Biology Letters*, *5*, 539–541.

Sawyer, H., Merkle, J. A., Middleton, A. D., Dwinnell, S. P. H., & Monteith, K. L. (2019). Migratory plasticity is not ubiquitous among large herbivores. *Journal of Animal Ecology*, *88*, 450–460.

Schenk, M., Krauss, J., & Holzschuh, A. (2018). Desynchronizations in bee–plant interactions cause severe fitness losses in solitary bees. *Journal of Animal Ecology*, *87*, 139–149.

Schwartzberg, E. G., Jamieson, M. A., Raffa, K. F., Reich, P. B., Montgomery, R. A., & Lindroth, R. L. (2014). Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. *Oecologia*, *175*, 1041–1049.

Sims, D. W., Wearmouth, V. J., Genner, M. J., Southward, A. J., & Hawkins, S. J. (2004). Low-temperature-driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology*, *73*, 333–341.

Straka, J. R., & Starzomski, B. M. (2015). Fruitful factors: What limits seed production of flowering plants in the alpine? *Oecologia*, *178*, 249–260.

Taylor, S. G. (2008). Climate warming causes phenological shift in pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology*, *14*, 229–235.

Therrien, J.-F., Lecomte, N., Zgirski, T., Jaffré, M., Beardsell, A., Goodrich, L. J., Bêty, J., Franke, A., Zlonis, E., & Bildstein, K. L. (2017). Long-term phenological shifts in migration and breeding-area residency in eastern North American raptors. *The Auk*, *134*, 871–881.

Thomson, J. D. (2010). Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *365*, 3187–3199.

Thomson, J. D. (2019). Progressive deterioration of pollination service detected in a 17-year study vanishes in a 26-year study. *New Phytologist*, *224*, 1151–1159.

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*, 1585–1596.

Üveges, B., Mahr, K., Szederkényi, M., Bókony, V., Hoi, H., & Hettyey, A. (2016). Experimental evidence for beneficial effects of projected climate change on hibernating amphibians. *Scientific Reports*, *6*, 26754.

van der Wiel, K., & Bintanja, R. (2021). Contribution of climatic changes in mean and variability to monthly temperature and precipitation extremes. *Communications Earth & Environment*, *2*, 1.

van Leeuwen, C. H. A., Museth, J., Sandlund, O. T., Qvenild, T., & Vøllestad, L. A. (2016). Mismatch between fishway operation and timing of fish movements: A risk for cascading effects in partial migration systems. *Ecology and Evolution*, *6*, 2414–2425.

Vázquez, D. P., Gianoli, E., Morris, W. F., & Bozinovic, F. (2017). Ecological and evolutionary impacts of changing climatic variability. *Biological Reviews*, *92*, 22–42.

Wann, G. T., Aldridge, C. L., Seglund, A. E., Oyler-McCance, S. J., Kondratieff, B. C., & Braun, C. E. (2020). Mismatches between breeding phenology and resource abundance of resident alpine ptarmigan negatively affect chick survival. *Ecology and Evolution*, *9*, 7200–7212.

Wright, S. J., & Calderon, O. (1995). Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology*, *83*, 937–948.

Zohner, C. M., Mo, L., Renner, S. S., Svenning, J.-C., Vitasse, Y., Benito, B. M., Ordonez, A., Baumgarten, F., Bastin, J.-F., Sebald, V., Reich, P. B., Liang, J., Nabuurs, G.-J., De-Miguel, S., Alberti, G., Antón-Fernández, C., Balazy, R., Brändli, U.-B., Chen, H. Y. H., … Crowther, T. W. (2020). Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 12192–12200.

How to cite this article: Inouye, D. W. (2022). Climate change and phenology. *Wiley Interdisciplinary Reviews: Climate Change*, e764. https://doi.org/10.1002/wcc.764