

Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates

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Keywords

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Abstract

Phenological mismatch results when interacting species change the timing of regularly repeated phases in their life cycles at different rates. We review whether this continuously ongoing phenomenon, also known as trophic asynchrony, is becoming more common under ongoing rapid climate change. In antagonistic trophic interactions, any mismatch will have negative impacts for only one of the species, whereas in mutualistic interactions, both partners are expected to suffer. Trophic mismatch is therefore expected to last for evolutionarily short periods, perhaps only a few seasons, adding to the difficulty of attributing it to climate change, which requires long-term data. So far, the prediction that diverging phenologies linked to climate change will cause mismatch is most clearly met in antagonistic interactions at high latitudes in the Arctic. There is limited evidence of phenological mismatch in mutualistic interactions, possibly because of strong selection on mutualists to have co-adapted phenological strategies. The study of individual plasticity, population variation, and the genetic bases for phenological strategies is in its infancy. Recent work on woody plants revealed the large imprint of historic climate change on temperature, chilling, and day-length

thresholds used by different species to synchronize their phenophases, which in the Northern Hemisphere has led to biogeographic phenological regions in which long-lived plants have adapted to particular interannual and intermillennial amplitudes of climate change.

1. INTRODUCTION

The match/mismatch hypothesis was initially developed by the British fisheries biologist David Cushing (1920–2008) to explain the growth and survival of Atlantic cod larvae that depend on synchrony with their plankton food; it was later extended to upwelling areas farther south toward the equator (Cushing & Dickson 1977, Cushing 1990) and subsequently to trophic interactions on land (Visser et al. 1998, Stenseth & Mysterud 2002, Stenseth et al. 2002). In putting forward the idea that major climate cycles, for example, the North Atlantic Oscillation and the El Niño–Southern Oscillation, determine the synchrony of trophic interactions, Stenseth and colleagues (2002) stressed the need for long-term data, time-series modeling, and experiments.

Almost 20 years have passed, and some 300 studies (Section 1.2) have documented phenological shifts in plants, insects, and vertebrates that appear to match recent climate change. Reviews of this literature show that 42% of 4,000 species whose phenology has been studied are plants (Parmesan & Hanley 2015), and almost half (162) of the 352 analyses of population time series under climate change were on birds (Ockendon et al. 2014). Being botanists ourselves, in the present review we make the case for a better integration of data on how plants regulate their phenology with data on how animals do it, because this is one basis for understanding the origin of possible mismatches. Answering the “why?” question requires data on the evolutionary history of species, including the historic imprint of past climate cycles on the extent of phenological buffering via plasticity and interindividual variation found in local populations (Section 4).

1.1. Definition of Trophic Mismatch and Earlier Reviews of the Topic

When interacting species change the timing of regularly repeated phases in their life cycles at different rates, it will lead to phenological asynchrony among their populations. This continuously ongoing phenomenon is also known as phenological mismatch or trophic asynchrony (Visser et al. 1998, Harrington et al. 1999, Parmesan 2006). As pointed out in a benchmark article, “any differential impact of climatic variability on two species, such as predator and prey (or two areas, such as winter or summer ground), may affect the dynamics through a switch from matching to mismatching the environmental conditions” (Stenseth & Mysterud 2002, p. 13379). In antagonistic trophic interactions, mismatch will have positive fitness consequences for one of the species and negative impacts for the other. Trophic mismatch among herbivores and their food plants or among predators and prey is therefore expected to last for evolutionarily short periods. In mutualistic interactions, mismatch will have negative consequences for both partners and should also be evolutionarily unstable. This relatively short duration, depending on genetic variation in relevant traits, strength of selection, and generation lengths, probably adds to the difficulty of detecting and then attributing phenological mismatch to climate change, which requires long-term data. An added difficulty may be that mismatched interactions will benefit other mutualists or antagonists in an interaction network, depending on the degree of interdependence among partners, which is usually asymmetric (Renner 1998, Benadi et al. 2014).

Previous reviews of phenological mismatch (trophic asynchrony) have focused on migration dates of temperate zone birds, for which the best data have been gathered (Visser & Both 2005,

Ockendon et al. 2014; the latter used 46 search words but not “plants*” or “plant phenology”). Visser & Both (2005) concluded that trophic mismatch was common but acknowledged a possible publication bias against cases in which trophically linked species are adjusting to climate change in synchrony. Smooth synchronous adjustments of trophically linked populations could be due to individual plasticity, genetic variation among individuals, and fast microevolution. Plasticity, variation, and heritability of phenological traits have come into focus recently (Gienapp et al. 2007; Singer & Parmesan 2010; Phillimore et al. 2012, 2016; Franks et al. 2017), but much remains to be learned (Section 4).

1.2. Scope of the Present Review and Predictions

This review focuses on testing the hypothesis that the ongoing rapid change in the duration of winter, absolute air temperatures, and frequency of severe weather events (especially heavy rain-falls, unpredictable spring frost, and droughts) is causing detectable mismatches among trophically linked species due to uneven speeds of adaptation in plants, invertebrates, and vertebrates. The preponderance of data comes from plants and animals in the temperate zone and in the Arctic, and we treat antagonistic interactions and mutualistic interactions separately because, as explained above, selection on partner synchrony should differ in these two types of interactions.

Although trophic mismatch situations are expected to persist over short temporal and spatial scales and thus will be difficult to detect (Section 1.1), the match/mismatch hypothesis makes two testable predictions. First, trophically mismatched species should show different multi-annual trajectories in traits linked to climate, such as leaf-out times, caterpillar emergence, or egg laying (Prediction 1). Second, mismatched species should react differently to environmental cues relevant to climate change, for example, air temperature, winter chilling, and day length (Prediction 2). Different cue reactions can lead to different multi-annual trajectories in species’ phenophases (*a*) because the relative importance of each environmental cue might differ among species (e.g., one species relying more on day length and thus responding less to temperature increases than the other) and (*b*) because, even if species are solely driven by temperature, species might rely on different temperature ranges and/or time intervals to time their phenophases. The latter point is especially important given that climate warming is not happening uniformly throughout the year (see **Figure 1**) and thus, in species for which the effective preseasons differ in length and/or average time, different phenological trajectories can be expected. Prediction 1 is the basis for detecting mismatch, whereas Prediction 2 gets at a possible underlying mechanism, although other mechanisms may also underlie trophic mismatch (e.g., a third antagonistic interaction). Because of a lack of integration of work on plant phenology and work on animal phenology, mismatch studies sometimes assume that the phenophases of plants and trophically linked animals are mostly regulated by temperature (e.g., Saino et al. 2011). Although this assumption may hold for flowering herbs and their pollinators, it does not hold for all insects (Section 2.4), birds (Dawson et al. 2001), other vertebrates, or long-lived plants of the temperate zone (Section 2.1), all of which rely on a combination of environmental signals to set their biological clocks and optimize phenophase to the environment. In most nontropical birds, photoperiod is the predominant proximate factor determining breeding. Increasing photoperiods, not temperatures, stimulate secretion of gonadotropin-releasing hormone and consequent gonadal maturation (Dawson et al. 2001).

The first to stress Prediction 1—that under mismatch, species’ phenological synchrony should decrease over time—were Visser & Both (2005), who referred to this as the “yardstick criterion.” Of the eight interactions that they found fulfilled this criterion, none involved mutualistic interactions, one was aquatic, five involved birds, and two involved egg laying and egg hatching in Lepidoptera. We take up the scarcity of phenological mismatches in mutualisms in Section 2.4.

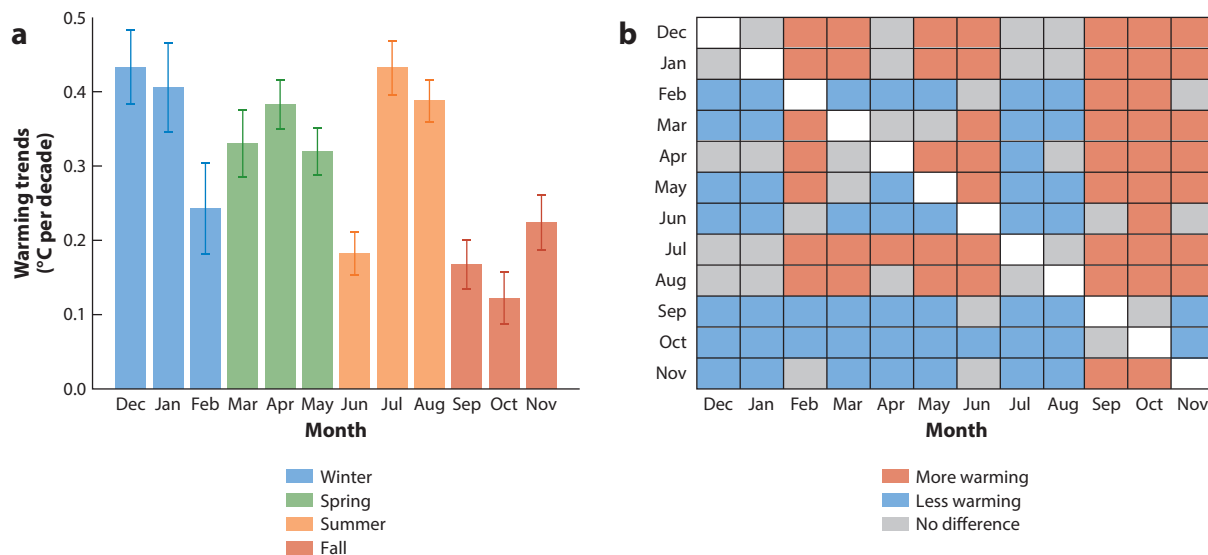


Figure 1

Seasonal differences in climate warming from 1960 to 2016 across 53 German weather stations. (a) Monthly warming trends (calculated as °C increase in air temperature per decade) inferred from linear mixed effects models including monthly mean air temperature as the dependent variable, year as the explanatory variable, and weather station as a random effect. Mean regression coefficients ± 2 standard errors are shown. (b) Differences in warming trends between two months. Colors indicate whether the respective month shown in the vertical axis experienced more (red) or less (blue) warming than the horizontal month. Gray boxes indicate that there was no significant difference in the warming trend between the respective two months. Statistical differences in warming trends between months were inferred from mixed effects models including an interaction term between month and year and the weather station as a random effect. Each weather station included in the analysis is located on a different pixel (1-degree resolution).

Our review is based on articles that appeared between 1974 and January 1, 2018, and that dealt with the topics “phenological mismatch” (270 articles), “phenological asynchrony” (145 articles), or “trophic mismatch” (320 articles) (Web of Science, accessed on March 14, 2017, and January 1, 2018). The most cited article on mismatch concerns the impact of climate change on marine pelagic phenology (Edwards & Richardson 2004), reflecting the origin of the match/mismatch hypothesis in marine fisheries science.

2. TEMPERATE ZONE PLANTS, INSECTS, AND BIRDS

The next three sections review data on plant phenology and antagonistic trophic interactions between leaf-out times, insect outbreak cycles, insect abundances, and egg-laying dates in insectivorous passerine birds. Section 2.4 reviews mismatches in mutualistic interactions, mostly from the timing of pollinator emergence and flowering in temperate zone herbs. In all cases, we focus on our two predictions, namely whether multi-annual trajectories show different speeds of phenological change in the trophically linked species as is required to match Prediction 1 and whether the mismatched species react differently to environmental cues (Prediction 2).

2.1. Determinants of Woody Species Phenology

Studies have shown earlier bud burst in response to climate warming in dozens of woody species, with leaf out advancing by 3–8 days per 1°C increase in air temperature (Menzel et al. 2006,

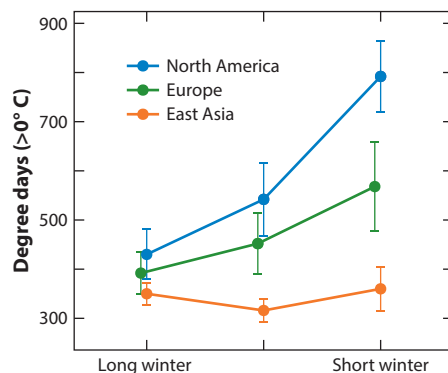


Figure 2

Contrasting responses of temperate zone North American, European, and East Asian species to experimentally reduced winter length. Median forcing requirements (accumulated degree days $>0^{\circ}\text{C}$ outdoors and in a climate chamber) $\pm 95\%$ confidence interval until leaf out under three chilling treatments for North American ($n = 72$ species), European ($n = 48$), and East Asian ($n = 88$) species are shown. Figure adapted from Zohner et al. (2017).

Amano et al. 2010). The duration of winter chilling (mostly considered as temperatures between 0°C and 8°C , although the exact temperature ranges are unknown) also influences leaf-out times by modulating the amount of spring warming required until leaf out, such that chilling-sensitive plants require much more warming if they had received only little chilling before. Chilling requirements are especially pronounced in eastern North American species, whereas in many East Asian species, the timing of spring development is independent from the duration of winter chilling (Zohner et al. 2017) (**Figure 2**). Few temperate zone woody plants use spring day-length increase as a leaf-out signal, although some dominant tree species, such as species in the genus *Fagus*, do (Zohner & Renner 2014, 2015). The relative importance of day length, winter duration, and air temperature as regulators of leaf out largely depends on the historical climate conditions under which a tree or shrub evolved. For example, species from regions with high interannual variation in the date of the last spring frosts have higher winter-chilling requirements and rely less on spring temperatures than species from regions with more predictable springs. This historic imprint on plant phenological strategies results in latitudinal- and continental-scale differences in the interannual predictability of leaf out. Thus, leaf out in East Asian species closely tracks spring temperature; leaf out in North American species does not (Zohner & Renner 2017, Zohner et al. 2017). These species- and region-specific differences in woody plant phenological behavior underscore that any mismatches between spring leaf out, herbivorous insects, and insectivorous birds—like all community interactions—need to be considered separately by region.

2.2. Outbreak Cycles of Insects Linked to Woody Plant Phenology

Climate change exerts direct effects, such as the rapid change in the leaf-out times of woody plants just described (Section 2.1), and indirect biotic effects, such as a higher frequency and intensity of insect outbreaks (Esper et al. 2007, Seidl et al. 2008, Iyengar et al. 2016). Long-term records of outbreaks in the European Alps of *Zeiraphera dimiana*, the larch bud moth, reconstructed from density variation in the tree rings of *Larix decidua*, the European larch, highlight the impact of contemporary climate change on ecological disturbance regimes (Esper et al. 2007, Iyengar et al. 2016). The $>1,000$ generations analyzed demonstrate that regular outbreak fluctuations

persisted over the past 1,173 years with population peaks averaging every 9.3 years. These regular oscillations recurred until 1981, followed by an absence of peak events since then. Comparison with past temperature records revealed that previous warming during medieval times and cooling during the Little Ice Age did not affect the regular insect population cycles. The absence of a major outbreak since 1981 corresponds to a period of regional warmth that is exceptional with respect to the past 1,000 years (Esper et al. 2007). The higher late winter and early spring temperatures in the Alps apparently increase egg mortality and reduce population growth rates so that *L. decidua* today might be leafing out too early for most larvae to have hatched, “creating a phenological mismatch between larval hatching and spring flush of larch leaves” (Johnson et al. 2010, p. 20579).

Leaf out in *L. decidua* is mainly regulated by spring temperatures and not by day-length increase or winter chilling (Zohner et al. 2016, 2017; Zohner & Renner 2017). Over the past 60 years, it has advanced by, on average, 2.5 days per decade (Figure 3). Confirming that the rapid advance in larch leaf out is indeed behind the longer outbreak cycles of larch bud moths will require large spatiotemporal data sets because of the inherent stochastic noise in the system (Johnson et al. 2010).

In micro-Lepidoptera feeding on young leaves, optimum timing of egg hatch must coincide with bud burst, but eggs cannot detect bud burst directly. A study of oak winter moth (*Operophtera brumata*) and bud burst in European *Quercus robur* under experimentally applied warming of 3°C in growth chambers found that eggs hatched about 11 days earlier and bud burst advanced similarly, so that synchrony was maintained (Buse & Good 1996). The applicability of these results to natural conditions has been criticized, however (Watt & McFarlane 2002, Singer & Parmesan 2010). Young moths can live without food for 4–10 days and can migrate short distances, and because individual oak trees vary by as many as 4 weeks in their timing of bud burst (Tikkanen & Julkunen-Tiitto 2003), some can leave trees where bud burst has not occurred and succeed in reaching other trees. Because the male and female moths do not move far, it is possible for the moths to evolve local adaptation (summarized in Singer & Parmesan 2010).

Another experimental warming experiment involved the tent caterpillar *Malacosoma californicum pluviale* and the North American tree *Alnus rubra*, of which branches were enclosed in clear plastic bags along with caterpillar egg masses that were placed on the twigs (Kharouba et al. 2015). The main experiment began in late January 2011, when single egg masses were deployed to warmed and control branches of each of 15 trees in each of the 2 sites (i.e., 30 pairs). Warming advanced egg maturation, but not leaf emergence, probably because North American tree species cannot react to warming until they have experienced long winter chilling (Zohner & Renner 2017, Zohner et al. 2017) (Figure 2). This led to varying degrees of phenological mismatch, with larvae emerging as many as 25 days before to 10 days after the emergence of leaves. Even the earliest-emerging larvae, however, had high survival in the absence of leaves for up to 3 weeks, and in the end, warming had no net effect on insect performance. It would be interesting to carry out the same experiment on a European or Asian species of *Alnus* and a European or Asian tent caterpillar.

Cynipid gall wasp (Hymenoptera; Cynipidae) abundance on 20 provenances of sessile oak (*Quercus petraea*) in a common garden trial in France also was unaffected by the degree of phenological mismatch between the wasps and the oak genotypes (Sinclair et al. 2015). Spring gall wasps were more abundant on early bud-bursting trees, whereas autumn generations of the same species were more abundant on late bud-bursting trees. The fluctuation presence of gall wasps should maintain diversifying selection on variation in *Q. petraea* bud burst.

Cyclic outbreaks of forest Lepidoptera species may not be regulated by climate but instead by parasitoids and pathogens (Berryman 1996). Determining how such other environmental parameters influence multiyear synchrony relationships between caterpillar egg hatch and bud burst will be critical to predicting forest pest cycles under climate change (Myers & Cory 2013).

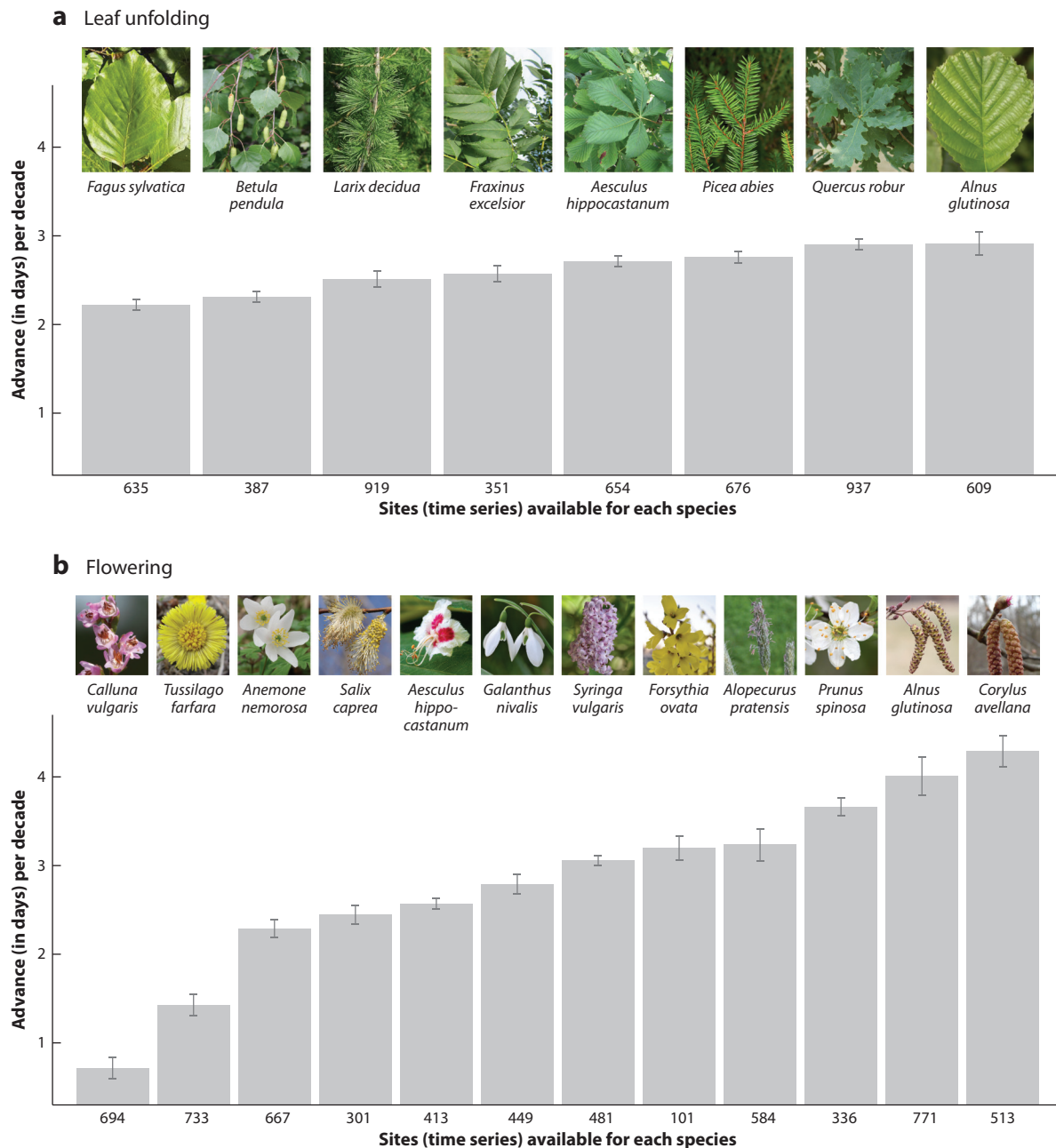


Figure 3

Species-specific phenological responses to climate change. Average advance per decade in the date of (a) leaf unfolding and (b) flowering from 1960 to 2016. Numbers below bars indicate the number of sites (time series) available for the respective species. Each time series ends in the year 2010 or later and goes back at least 40 years (maximally until 1960). To calculate phenological shifts over time, we applied linear mixed effects models including year as an explanatory variable and site as a random effect. Mean regression coefficients ± 2 standard errors are shown. Phenological data were taken from the Pan European Phenology Project PEP725 database (<http://www.pep725.eu>).

2.3. Insect Abundances and Bird Egg-Laying Dates

In this section, we review evidence for mismatches among spring insect abundances and passerine birds. Ideally, studies would link insect abundances to the emergence times of leaves, which are advancing under climate change, but we found no study that directly linked all three trophic levels. Instead, phenology change in one of the three trophic layers was always assessed from proxy data.

So far, limited evidence shows that asynchrony between peak insect abundances and egg-laying times in birds are influencing productivity (offspring per female) in Northern Hemisphere passerines (Knudsen et al. 2011; Reed et al. 2013a,b; Dunn & Møller 2014; Visser et al. 2015; Franks et al. 2017). Using survey data for spring emergence of 280 plant and insect species from 1983 to 2010 and the egg-laying phenology of 21 British songbird species, Franks et al. (2017) explored the effects of trophic asynchrony on avian population trends and potential underlying demographic mechanisms. Species that advanced their laying dates over the past three decades exhibited the most negative population trends. In warmer springs, birds were more asynchronous with insect abundances (and first leaf-out dates), but the number of offspring per parent was only marginally reduced; long-distance migrants, short-distance migrants, and resident bird species all exhibited effects of similar magnitude.

As expected, great variation exists in the speed of phenological adjustments. Thus, great tits (*Parus major*) in the Netherlands advanced their breeding time less than the advance in peak availability of their caterpillar prey (Visser et al. 1998), but great tits in Oxford have adjusted their breeding time to be completely in synchrony with the timing of peak caterpillar abundance (Cresswell & McCleery 2003). Pied flycatchers (*Ficedula hypoleuca*) in both regions have advanced laying dates in synchrony with local caterpillar advances (Visser et al. 2015).

Using caterpillar peak abundance dates as a yardstick for detecting mistiming, however, may not always be justified because flexibility in diet and foraging ranges probably buffers many species, such as the wood warbler (*Phylloscopus sibilatrix*), which between 1982/1984 and 2009/2011 has not kept up with the phenological advance of its preferred caterpillar food but is able to find alternative insect food (Mallord et al. 2016). Similarly, nest initiation in the black-throated blue warbler (*Setophaga caerulescens*) over the past 25 years appears not to be timed to coincide with a peak caterpillar availability for nestlings (Lany et al. 2016). Instead, warblers adjusted by shortening the interval between nest building and clutch initiation.

A combination of satellite data on plant green-up and citizen-science data on migratory bird arrival dates for 48 passerine species across North America (including all of Alaska and Canada, thus a major part of the Arctic; see also Section 3) showed increasing phenological mismatch, because nine of the species adjusted their arrival dates too slowly to keep up with rapidly changing green-up (which in turn advances peak insect abundances), and across all species the interval between arrival and green-up increased by more than half a day per year (Mayor et al. 2017). These results fulfill Prediction 1 of phenologies in trophically linked levels shifting at different rates, but there are no direct data on the insect trophic layer or on the causes of the different speeds in the nine species that did not match advanced leaf-out times.

2.4. Insects and Herbaceous Species: Mismatches in Mutualistic Interactions

Most pollinators are trophically linked to the flowers they pollinate, as in the case of bees via pollen and nectar and in the case of butterflies, moths, and flies via nectar or rarely floral egg-laying sites. One study focused on mismatch in a pollination interaction that involves sexual deceit (Hutchings et al. 2018). Throughout the Northern Hemisphere, increasing heat and drought adversely affect the growth and harvest times of herbaceous cultivated plants as well as the pressure of insect pests

on these crops. Two types of phenological mismatch situations in these interactions might occur: enhanced phenological asynchrony between crops and pests, for example, by crops being planted (and harvested) earlier, which might influence the population densities of leaf or fruit insect pests; or conversely, disassociation between crops and their pollinators, with negative effects on fruit set.

In spite of the potential economic importance of both these types of mismatches, one involving antagonistic, the other mutualistic interactions, little empirical evidence has been found for mismatches involving herbs and their trophically linked pests or pollinators. An earlier review of plant–pollinator phenological mismatch (Hegland et al. 2009) already pointed this out, concluding that timing of flowering in both herbs and pollinator activity appear regulated by temperature and therefore may show collinear responses to climate warming. The speed of phenological response to climate change, however, varies greatly among species (**Figure 3**), and much more work is needed to detect possible population-level mismatches.

Data accumulated since 2009 agree with Hegland et al.'s (2009) conclusion that plant–pollinator phenological synchrony so far is unaffected by climate change. Thus, an analysis of climate-associated flowering advance in bee-pollinated plants and the average dates at which 10 species of bees in northeastern North America were active (and caught and deposited in collections) over the past 130 years revealed that both advanced by a mean of 10.4 ± 1.3 days, most rapidly since 1970, paralleling air temperature increases (Bartomeus et al. 2011). Apple flowering times and the flight times of its bee community have also advanced at similar rates over the past 46 years (Bartomeus et al. 2013). Work in a Bavarian National Park that used plant–pollinator interactions along an altitudinal gradient as a proxy for plant–pollinator interactions differing in their synchrony found no relationship between the level of pollinator specialization and phenological synchrony with particular plants (Benadi et al. 2014). A caveat is that few of the bee species in these studies are pollen specialists (oligolectic). Generalist pollen collectors (polylectic species) are able to feed their brood on a mix of pollen species and are therefore less dependent on flowering times of particular plants. Although flowering times in temperate herbaceous species closely track temperature (e.g., Amano et al. 2010, Ovaskainen et al. 2013), the environmental triggers that regulate bee emergence and butterfly pupation are little known (Bosch & Kemp 2003, Sgolastra et al. 2012) and probably depend on the long-term winter and spring climates under which particular species evolved.

In Great Britain, the mean date of first flowering of garlic mustard (*Alliaria petiolata*) and the mean first appearance of the orange tip butterfly (*Anthocharis cardamines*) from 1883 to 1947 have tracked each other closely, with the butterfly always emerging after its plant host (Sparks & Yates 1997; Phillimore et al. 2012). Comparison of the slopes of phenology on temperature over space versus over time can identify the relative roles of plasticity and local adaptation in generating spatial phenological variation in these two interacting species as well as the cuckoo flower, *Cardamine pratensis* (Phillimore et al. 2012). Pronounced phenological variation was found in all three species, and the butterfly's phenology was better predicted by temperature than by the flowering times of either host plant. Even more impressive long-term data are available for British *Ophrys sphegodes* orchids, which are pollinated by sexually deceiving male *Andrena nigroaenea* bees (Hutchings et al. 2018). Using climate records, museum collections, and observations made between 1659 and 2014, together with well-established correlations between air temperature, flowering, and bee emergence, Hutchings and colleagues were able to show that as spring temperatures have risen, male and female bees fly at the same time more often, and more often both fly earlier than the orchid's peak flowering time. This is not a problem for the bees but likely has negative consequences for the orchid's pollination, which depends on males attempting to copulate with the flowers before females have emerged.

Trapping of solitary bees and wasps at sites along an elevational gradient at the Rocky Mountain Biological Laboratory, reciprocal transplanting of nesting bees, and monitoring of flowering times at each site revealed that local conditions are the primary determinants of bee emergence phenology (Forrest & Thomson 2011). The phenology of the six focal species of plants and eight species of bees and wasps was well described by thermal (degree-day) models, with degree-day requirements for the bees and wasps lowest in locations with the longest winters. This finding suggests that chilling requirements were more completely fulfilled at colder sites or that there is a critical day length before which degree-day accumulation does not contribute to development (Forrest & Thomson 2011).

Manipulation of the flowering phenology of the spring herb *Claytonia lanceolata* (Portulacaceae), again at the Rocky Mountain Biological Laboratory, by altering snow pack (snow removal versus control treatments) or by inducing flowering in a greenhouse before placing plants in experimental outdoor arrays (early, control, and late treatments) showed that flowering occurred approximately 10 days earlier in snow-removal plots than in control plots during all years of snow manipulation (Gezon et al. 2016). However, plants in the snow-removal treatment often experienced frost damage, and frost-damaged plants suffered low reproduction despite lack of pollen limitation. Plants that escaped frost damage had higher pollinator visitation rates and reproduction than controls. *Bombus* queens that collect pollen and nectar from the spring ephemeral *Corydalis am-bigua* in Hokkaido, Japan, emerged as the temperatures rose after snowmelt (1999 to 2008), with flowering ahead of bees when spring came early (Kudo & Ida 2013), but bees appeared 10 days ahead of flowers in an unusually warm spring (Kudo 2014). Such interannual variation does not constitute phenological mismatch because Prediction 1, that species synchrony should decrease in correlation with climate change, is not fulfilled. Also in Russian Karelia, dates of first appearance of bumblebees, goat willow (*Salix caprea*), and coltsfoot (*Tussilago farfara*) are highly synchronous with each other, and all were positively correlated with mean temperatures during a preceding 30-day period (Ovaskainen et al. 2013). No mismatch was detectable.

In an understory plant-bee community in Illinois, United States, peak forb bloom in 2009/2010 was 9.5 days earlier, and peak bee activity 11 days earlier, than 120 years ago (from the late 1800s to 2009/2010) (Burdle et al. 2013), but because of the data structure, it remains unclear if a possible mismatch increased over time. Similarly, the modeled overlap until 2050 in flowering peaks of apples, pears, and plums with peak abundances of bees and syrphid flies in Great Britain (Polce et al. 2014) does not address phenological mismatch, because these abundances disregard the unequal roles of these insects as pollinators and the human-managed densities of domesticated honeybees in the relevant orchards.

Analyses of syrphid fly abundances and flowering times in Colorado, United States, between 1992 and 2011, showed that syrphids, like bees, generally emerged after the onset of flowering and ended their activity before the end of flowering (Iler et al. 2013). Neither flowering nor syrphid phenology changed significantly over the 20-year record, consistent with a lack of directional change in climate variables over the same time frame. Timing of snow melt was the best predictor of flowering onset and syrphid emergence, whereas degree days best predicted the end of flowering and degree days and precipitation predicted the end of syrphid activity. Again, no mismatch was apparent.

In conclusion, neither experimental results nor long-term data for herbs and their pollinators suggest that phenological mismatch may be increasing. Instead, all data indicate that, at least in the temperate zone, selection over thousands of years has led to strongly buffered synchronization mechanisms in bees, flies, moths, and butterflies and their flower hosts. We found no long-term empirical data on the synchrony of trophic interactions in the tropics.

3. ARCTIC AND HIGH-ALTITUDE ECOSYSTEMS

3.1. Tundra Greening, Birds, and Polar Bears

In arctic and alpine environments, plant phenology is highly sensitive to the timing of snowmelt, which in turn is dependent on snow depth and spring temperature. Snowmelt and spring temperature are therefore only partially correlated (Cooper 2014). Phenological mismatch in the Arctic arises from shorter winters, possibly from less snowfall, and from warmer springs, all of which affect the phenology of the long-lived plants that dominate in Arctic steppes and tundra, as recently reviewed by Cooper (2014). In the following section, we therefore focus on work not covered in her review.

A textbook case of phenological mismatch comes from Sanderling (*Calidris alba*) populations in northeastern Greenland (Reneerkens et al. 2016) (**Figure 4**). Over the past 17 years (1996–2013), the difference between average hatch dates of Sanderling chicks and the median peak in arthropod abundance has increased dramatically, because peak insect abundance advanced by 1.3 days/year while Sanderling hatching dates did not change, fulfilling Prediction 1 that the phenological mismatch should increase as the climate warms. The mechanism for this mismatch is that insects, but not Sanderlings, are free to track the advances in plant phenology, whereas the predation pressure on the earliest Sanderling nestlings prevents the bird from tracking peak insect abundance.

Another clear example of phenological mismatch concerns Canadian Arctic snow geese and their graminoid food plants. Using the 50% annual maximum Normalized Difference Vegetation Index (NDVI50) as a proxy for the timing of peak nitrogen availability in the plants, Ross et al. (2017) used a time series of 23 breeding seasons (1992–2014) to estimate the median date of NDVI50 in several Canadian Arctic goose brood-rearing regions. The median day of year when NDVI50 was attained for all vegetation was used as a proxy for the phenology of the plants most eaten by the geese, and phenological mismatch between the geese and their food plants was quantified as the mean annual hatch date (of each snow goose species) minus the date of NDVI50. The phenological mismatch between peak gosling hatch and peak forage quality is increasing, because goose nesting time has not advanced as fast as peak forage quality, fulfilling Prediction 1 for a phenological mismatch. Gosling hatch preceded or coincided with the date of NDVI50 in only 2 of 24 years (namely, 1992 and 1997). What keeps geese from matching plant phenology—as for the Sanderlings—has to do with changes in other trophic interactions, including those with polar bears. The eggs of snow geese are a nutrient resource for polar bears, used to offset energy shortfalls related to earlier sea ice breakup and onshore arrival (Rockwell et al. 2011). Currently, a two-day overlap exists between arriving polar bears and incubating snow geese, with early breeding geese suffering the worst predation.

3.2. Shorter Winters and Population Cycles in Terrestrial Vertebrates

Color-molting animals in the Arctic are famous for their annual cycles, and decreasing snow cover duration due to climate warming is expected to change the duration of coat color phases. So far, however, whether the annual periods of mismatch between coat color and background color (either snow or vegetation) are increasing is unclear, as plasticity and interindividual variation are extremely high (Zimova et al. 2016). Surprisingly, how much of the observed variation in molt phenology reflects heritable genetic variation is unknown, as is whether phenotypic plasticity itself is evolving.

Shorter winters might dampen population cycling in Arctic lemmings, voles, and foxes (Cooper 2014), but natural high-amplitude fluctuations in density make it difficult to test whether mismatch

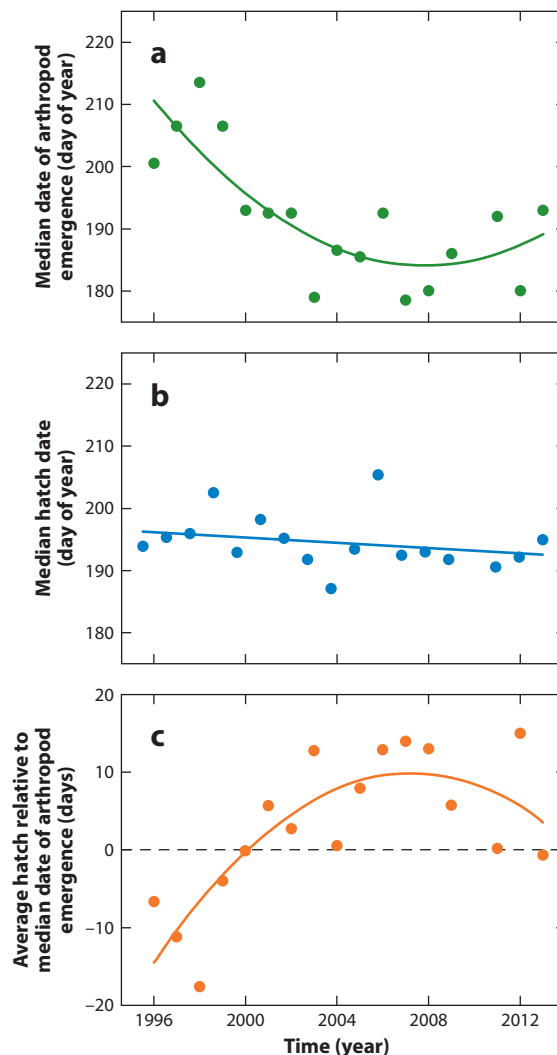


Figure 4

(a) The dates of peak insect abundance, and (b) the dates of hatching of Sanderling chicks at Zackenberg, Greenland, 1996–2013. (c) The phenological mismatch between Sanderlings and their prey has increased over time. The dashed horizontal line in panel c indicates when Sanderling hatching and median arthropod peak abundance happened on the same date. Adapted with permission from Reneerkens et al. (2016).

cycles are changing in frequency. An illustration of this difficulty comes from an analysis of vole population sizes and climate data from Finland between 1970 and 2011, which showed that climate had a profound influence on the interactions between small mustelids and voles but was unable to detect phenological mismatch (Korpela et al. 2014).

3.3. Warmer Temperatures, Crossbills, and Pine Seeds in the Rocky Mountains

A new form of trophic mismatch due to rapid climate warming was recently documented from high elevations in the Rocky Mountains in Idaho, United States (Benkman 2016). The South

Hills crossbill (*Loxia curvirostra* complex) relies on seeds in the closed cones of the fire-adapted Rocky Mountain lodgepole pine (*Pinus contorta latifolia*). Historically, most of the seeds remained within the cones for decades until the heat of a stand-replacing fire causes the cone scales to separate. Hot days, which are increasing in frequency, however, mimic the effect of fire and cause the immediate release of a fraction of the seeds so they are no longer available to the birds. Such events have caused an 80% decline in the crossbill population between 2003 and 2011. Climate warming in this case is reducing food abundance, rather than the time (phenology) of its availability. Strictly speaking, therefore, the South Hill crossbill and lodgepole pine are not exhibiting different speeds of phenological change (as is required to match Prediction 1). However, the birds are mismatched (spatially) to the extremely hot hilltops where they occur and no longer find sufficient seeds because pines and crossbills react differently to environmental cues (matching Prediction 2).

4. INDIVIDUAL PLASTICITY, GENETIC VARIATION, AND REDUCED WITHIN-POPULATION PHENOLOGICAL SYNCHRONY AS BUFFERS AGAINST PHENOLOGICAL MISMATCH

Phenological mismatch implies microevolutionary responses to selection, but few data on the heritability of phenological strategies (presumably involving thresholds to environmental signals) are available. Therefore, currently it is rarely possible to predict the speed with which populations will come back into synchrony. Although researchers focusing on climate change-induced phenological mismatch have always stressed a need to quantify microevolution (Stenseth et al. 2002, Parmesan 2006, Visser 2008, Buckley & Kingsolver 2012), the study of individual plasticity, population variation, and the genetic bases for phenological strategies is in its infancy.

Our own work on 20 temperate herb, shrub, and tree species, including beech (*Fagus sylvatica*), has revealed the extent of within-population variation in how conspecific individuals respond to winter chilling, photoperiod, and temperature (CM Zohner & SS Renner, Loss of Within-Population Phenological Synchrony Under Global Warming, unpublished manuscript). One counterintuitive finding is that rising pre-season temperatures, meaning temperatures during the 60 days before the average leaf unfolding or flowering date, reduced among-individual synchrony in both leaf-out and flowering times. Warming increased leaf-out and flowering variation among individuals by up to 51% and 55%, respectively, that is, an 11-day or 23-day lengthening of the period during which 95% of individuals in a population leaf out or start flowering. The mechanism underlying this result is that some individuals of the same species are more day length-sensitive than others, causing them to track temperature less consistently than day length-insensitive individuals. The individual differences then result in an overall reduction in population leaf-out and flowering synchrony. Such reduced within-population synchrony should act as a buffer against climate change-induced phenological mismatches between plants and leaf-feeding or pollen-collecting insects.

A modeling framework applied to >100,000 first egg dates from 4 single-brooded British passerine species showed that the average temperature during a specific (sliding with latitude) time window predicts spatial variation in the egg-lay date (Phillimore et al. 2016). The species advanced egg laying by 2–5 days per 1°C temperature increase, and Phillimore and colleagues argue that a model combining photoperiod and mean temperature is consistent with the current understanding of phenological cues in passerines. They further conclude that each bird species could respond to projected increases in spring temperatures through plasticity alone. With longer time series and more sophisticated statistical models (Gienapp et al. 2013, Iyengar et al. 2016, Phillimore et al. 2016) combined with experimental data (Forrest & Thomson 2011, Kharouba

et al. 2015; CM Zohner & SS Renner, Ongoing Seasonally Uneven Climate Warming Leads to Earlier Autumn Growth Cessation in Deciduous Trees, unpublished manuscript), the roles of interindividual variation and plasticity in buffering populations against mismatch in antagonistic interactions should become clearer.

5. CONCLUSIONS

In light of the rapid shifts in the phenology of plants and animals in the temperate zone and in the Arctic (Menzel et al. 2006, Amano et al. 2010, Cooper 2014, Ockendon et al. 2014, Parmesan & Hanley 2015, Thackeray et al. 2016), the scarcity of cases of phenological mismatch that fulfill Prediction 1 (uneven rates of change in the phenology of interacting species) or Prediction 2 (differential use of environmental cues in mismatched species) at first may seem surprising. The scarcity becomes less surprising when considering that mutualistic interactions can only be evolutionarily stable if partners have strongly co-adapted phenological strategies and that all mismatches (also those in antagonistic interactions) are expected to persist for only a short time and at small spatial scales (Section 1.1.). Nevertheless, this review identified a few clear cases of mismatch due to the ongoing rapid climate change (Reneerkens et al. 2016, Mayor et al. 2017, Ross et al. 2017), all of them involving antagonistic interactions at high latitudes (Greenland; central Canadian Arctic; and North America, including Alaska and Canada).

Twenty years ago, the first major studies to focus on phenological asynchrony under climate change (Visser et al. 1998, Harrington et al. 1999) discussed the key importance of understanding how environmental signals (including day length) are perceived and used to synchronize transitions between annually repeated stages in the life cycles of long-lived plants, herbivorous insects, and passerine birds. Answering this question will require experiments, not only monitoring data, although statistical analyses of data from latitudinal or altitudinal transects can help tease apart day length–sensitive phenologies from purely temperature–driven phenologies (Phillimore et al. 2016).

Comparison of the environmental cues used by species from different regions has revealed the imprint of historic climate change on temperature, winter-chilling, and day-length thresholds that species rely on to synchronize their phenophases. Common garden experiments on hundreds of woody species show that American, European, and East Asian woody species in the same genus differ greatly in their chilling and spring temperature requirements, probably because of the distinct interannual and intermillennial amplitudes of climate predictability in these regions (Zohner & Renner 2017, Zohner et al. 2017). It is likely that insect and bird phenological strategies also are optimized to the long-term climate regime under which they evolved. The possibility of functional, albeit not biogeographic, communities was one of four research priorities listed by Harrington et al. (1999, p. 149), who asked, “Can functional groups of organisms be defined on the basis of their responses to environmental variables and can these groups be used to predict the likely degree of dissociation of current community structure under predicted environmental conditions?” As far as we are aware, the possibility of phenological functional groups in Northern Hemisphere invertebrate or vertebrate communities has never been considered. This is surprising, given that such groups are now known to exist in woody species.

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