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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Review

The effects of phenological mismatches on demography

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Climate change is altering the phenology of species across the world, but what are the consequences of these phenological changes for the demography and population dynamics of species? Time-sensitive relationships, such as migration, breeding and predation, may be disrupted or altered, which may in turn alter the rates of reproduction and survival, leading some populations to decline and others to increase in abundance. However, finding evidence for disrupted relationships, or lack thereof, and their demographic effects, is difficult because the necessary detailed observational data are rare. Moreover, we do not know how sensitive species will generally be to phenological mismatches when they occur. Existing long-term studies provide preliminary data for analysing the phenology and demography of species in several locations. In many instances, though, observational protocols may need to be optimized to characterize timing-based multi-trophic interactions. As a basis for future research, we outline some of the key questions and approaches to improving our understanding of the relationships among phenology, demography and climate in a multi-trophic context. There are many challenges associated with this line of research, not the least of which is the need for detailed, long-term data on many organisms in a single system. However, we identify key questions that can be addressed with data that already exist and propose approaches that could guide future research.

Keywords: climate change; demography; global warming; mismatch; phenology

1. INTRODUCTION

Climate-driven shifts in phenology are altering ecological relationships and processes around the world (Visser & Both 2005; Cleland *et al.* 2007; Forrest & Miller-Rushing 2010). However, the effects of these shifts on the vital rates of populations are not well understood. We do not adequately understand how such effects will come about, how often they might occur and how substantial their contributions to population dynamics will be. For example, phenological mismatches might occur when organisms that typically interact, such as predator and prey or plant and pollinator, are no longer active at the same time. Or, in contrast, shifts in phenology could alleviate existing mismatches and promote the exploitation of newly available resources. The creation and loss of phenological mismatches could be quite common given the substantial variation in phenological responses to climate change among taxa (Visser & Both 2005; Primack *et al.* 2009; Thackeray *et al.* 2010).

Although phenological mismatches are most frequently discussed in terms of intertrophic relationships (Stenseth & Mysterud 2002; Visser & Both 2005; Durant *et al.* 2007), demographic effects of changes in phenology are not restricted to trophic mismatches. Nearly every ecological process and phenomenon—e.g. competitive interactions, drought tolerance and nutrient cycling—has a temporal component that can affect its function. As the timing of various phenological events, such as reproduction, migration and diapause, change, so will related functional processes, such as pollination and primary productivity. Nevertheless, few empirical studies quantify the relationship between phenology and demography (but see Inouye 2008; Møller *et al.* 2008).

Here we identify some of the key gaps in our understanding of how climate-driven changes in phenology may alter demography, and we outline approaches to fill in those gaps. For example, how sensitive will species' demographies be to changes in phenology? Will species with specialist relationships be more sensitive to phenological shifts than generalists? Will species

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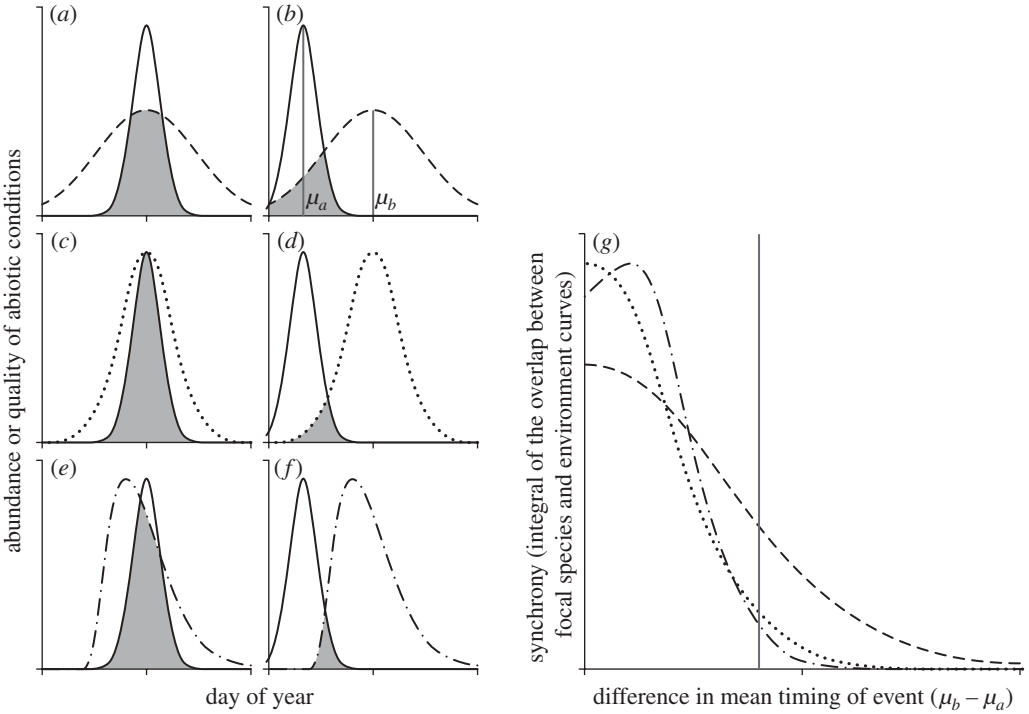


Figure 1. Examples illustrating differing degrees and types of phenological mismatch. The left panel (*a–f*) illustrates how the synchrony (or degree of overlap) between a focal species (solid line) and its environment (broken line) diminishes as the species' phenology advances. The distribution of suitable environmental conditions can be wide (*a*,*b*) or narrow (*c*,*d*). The distribution could also be asymmetrical (*e*,*f*). The curves could represent relationships between phenological phases of individuals or populations of the same or different species—e.g. flowering and pollinator activity, or predator and prey activity. The curves could also represent the relationship between an individual or population and appropriate abiotic conditions—e.g. leaf development and frost-free conditions, or tadpole development and water level. The right panel (*g*) illustrates how the synchrony between a species and its environment varies in response to increasing differences in the timing of activity of a species and its environment for the three cases shown in the left panel (*a–f*). Here, we measure synchrony as the area of overlap between the focal species and environment curves. The vertical line indicates the degree of synchrony when the focal species' phenology is advanced relative to its environment (*b*,*d*,*f*). The dash and dot pattern in each curve in (*g*) matches the environmental curve (left panel) that it represents—dashed (*a*,*b*), dotted (*c*,*d*), and dot-dash (*e*,*f*).

with highly plastic phenologies increase in abundance relative to species with relatively fixed phenologies? Will changes in phenology affect rates of reproduction more than offspring survival? We emphasize the wide range of mechanisms by which phenology can affect demography (e.g. abiotic, intraspecific, intraguild and intertrophic interactions) and the various scales (e.g. local, landscape and even continental) at which these processes can operate, and discuss why linking phenology to demography is challenging and important.

2. DEFINITIONS, SCALES AND SELECTION

(a) *Demography and synchrony*

For the purpose of this paper, when we refer to the effects of phenology on demography, we generally refer to the effects of phenology on population vital rates—reproduction and survival. We also provide examples that highlight the relationship between phenology and population size, which is inextricably linked to population vital rates and is often the primary variable of interest to natural resource managers and policy-makers.

We use the term synchrony to refer to the degree of temporal match between two events that constitute a relationship—for example, the breeding season of a bird and the peak availability of its food source. Importantly, synchrony in this context is not a binary condition; rather, it is a measure of the overlap of two events, each of which has a temporal distribution (figure 1). The synchrony of events can be measured along a continuum from highly synchronous, in which case their temporal distributions overlap significantly, to total mismatch, in which case there is no overlap between their temporal distributions. In between, there are intermediate levels of synchrony and mismatch where the tails of the distributions overlap. The precision of synchrony required in most ecological relationships is unknown and is a key question for understanding the effects of phenology on demography (see §3).

(b) *Abiotic and species interactions*

The link between phenology and demography occurs at multiple spatial scales and through interactions at the intraspecific, intraguild or intertrophic level, or through interactions with abiotic factors (figure 2). The most basic interaction is between phenological events and abiotic conditions such as weather. The demographies of some arthropods, for example, depend on the timing and duration of temperatures that are warm enough to allow for foraging and growth (Merckx *et al.* 2006; Høye & Forchhammer 2008*b*).

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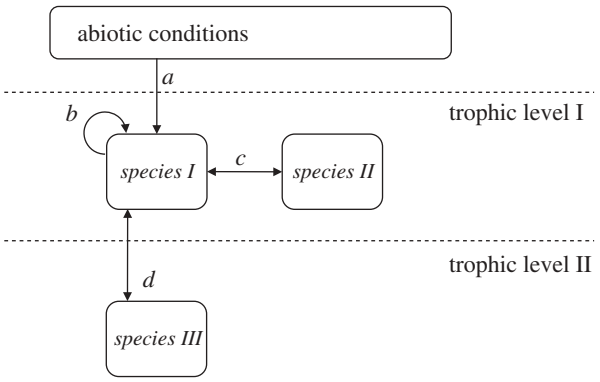


Figure 2. Conceptual model of various levels of interaction that might be affected by phenological mismatch: (*a*) organism–abiotic environment, (*b*) within organism and intraspecific, (*c*) intraguild and (*d*) intertrophic. Arrows represent relationships among abiotic conditions and species at various trophic levels, relationships that depend on the phenology of the species involved.

For instance, earlier spring snowmelt and longer growing seasons are associated with larger adult body size in arctic spider species, particularly in females (Høye *et al.* 2009; Høye & Hammel 2010). Large females have higher reproductive output, but increased sexual size dimorphism may also alter competition between males and females and thus affect survival. Longer growing seasons are also correlated with increased body mass, winter survival and reproduction of yellow-bellied marmots in the Colorado Rocky Mountains (Ozgul *et al.* in press). Changes in plant phenology, particularly at the beginning and end of the growing season, can also affect the risk of exposure to frost or other abiotic factors, altering rates of survival and reproduction (Inouye 2000, 2008).

Phenology may also play an important role in *intraspecific* interactions. For outcrossing plants, it is often important that many individuals of a particular species in an area flower synchronously to maximize the likelihood of cross-pollination, which can have important fitness benefits (Holtsford & Ellstrand 1990). Populations of dioecious species of plants for which males and females are spatially segregated along an environmental gradient (Bierzychudek & Eckhart 1988; Dawson & Ehleringer 1993) could be at risk if the spatial segregation starts to correspond to phenological segregation as well. In at least one study, sexual differences in reproductive phenology were shown to influence demography of a dioecious tropical shrub, *Baccharis dracunculifolia* (Espírito-Santo *et al.* 2003). Similarly, flowering synchrony within individual plants can play a key role in attracting pollinators and affect rates of self-fertilization (Barrett *et al.* 1994; Karron *et al.* 2004). Likewise, important *intraguild* interactions may be affected by phenological variation through facilitation or competition for resources such as water, nutrients, pollinators or food (Moeller 2004). Finally, in *intertrophic* interactions, such as those between plants and pollinators or predators and prey, timing is also critical. For example, the timing of food availability must match an organism's demand for food.

(c) *Scale of effects*

The critical spatial and temporal scales for a phenological match vary according to the species in question. For instance, we would expect that the appropriate spatial scale for studying the potential for resource mismatch in solitary bees, which have relatively small foraging ranges (Zurbuchen *et al.* 2010) differs substantially from that of hummingbirds, which can migrate long distances. Similarly, the demographic impacts of a change in phenology, such as the timing of leaf-out, will occur at multiple spatial scales. Changes in leaf-out at the scale of a single plant can affect the survival and reproduction of caterpillars (Visser & Holleman 2001), but changes at the scale of hundreds of square kilometres will be more relevant to large mammals that can forage over large areas (Post *et al.* 2008*b*).

(d) *Selection on phenology*

Although not particularly well studied in most species, evidence suggests that the timing of many life-history events is heritable, and hence able to respond to selection (Pulido *et al.* 2001; Burgess *et al.* 2007). The factors that influence selection on phenology are too numerous to cover in this paper, but we touch on some key points here. Phenology is often evaluated at the population level—i.e. first or mean arrival within a migratory bird population—yet the population-level patterns are essentially cumulative effects of generations of natural selection acting on individuals (Forchhammer & Post 2004). Individuals often must make decisions concerning time-sensitive phenological behaviours—e.g. leaf expansion, blooming or giving birth—prior to the time when those events occur and when selection acts on them (Visser *et al.* 2010). In a changing climate, the cues that species used historically to determine the timing of life-history events might become maladaptive, causing phenological events to occur at inopportune times (Iwasa & Levin 1995; figure 3). The optimal flowering time for a plant, for example, can be constrained by the importance of avoiding poor weather conditions at the beginning or end of the growing season, synchronizing reproduction with pollinators, minimizing overlap with florivores and competitors for floral resources, avoiding seed predators and maximizing time for fruit development, among other considerations. Mistiming in relation to any of these factors could, in theory, lead to severe consequences for the fitness of individuals and the demography of populations. Additionally, strong selection, as might occur in instances of mismatch, often entails demographic costs in the short term (Kinnison & Hairston 2007).

Because life-history events are not isolated entities, observed phenological variation may not always result from direct climatic influence or selection on a particular event. For instance, reproduction in plants consists of several life-history events (e.g. flowering, seed set, dispersal and germination), and the timing of those events are often correlated such that the advancement or delay of one event, such as flowering, will often incur a change in the timing of later events, such as seed set (Primack 1987). Therefore, selection acting on germination often affects flowering time.

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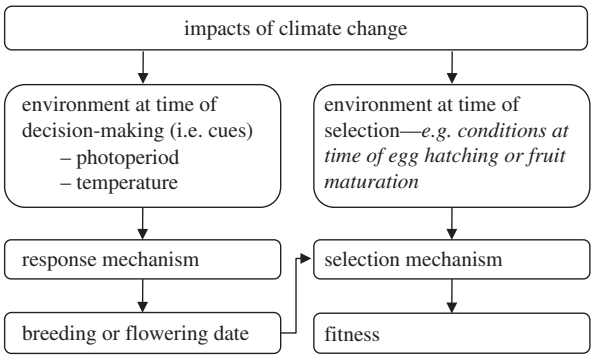


Figure 3. A schematic outline of how climate change may affect reproduction. Changes in the environment at the time of decision-making may affect the timing of reproduction via the response mechanism. For example, changes in temperature might affect the timing of breeding or flowering. However, changes in the environment at the time of selection (e.g. egg hatching or fruit maturation) will affect the fitness consequences of breeding at a particular date. Conditions at the time of decision-making may have historically provided reliable cues of conditions at the time of selection. Changes in climate may change the historical relationship and lead to maladaptive decisions. Adapted from Visser *et al.* (2004).

Unfortunately, we still know little about how fixed these links among life-history events are (Both & Visser 2001; Sola & Ehrlén 2007; Post *et al.* 2008*a*).

3. SENSITIVITY OF DEMOGRAPHY TO PHENOLOGICAL MISMATCH

Given the amount of variation among species' and populations' phenological responses to changes in climate—i.e. variation in the rates and directions of change (Fitter & Fitter 2002; Miller-Rushing & Primack 2008; Thackeray *et al.* 2010)—the likelihood of phenological mismatches occurring seems high. But how sensitive are species' demographies and population sizes to phenological mismatches? In any particular case, the answer depends on at least two factors—the importance of the interaction and the likelihood that a *significant* mismatch might occur. In this context, the importance of an interaction reflects the degree to which the demography or population size of one species relies on the interaction occurring. The likelihood of a significant mismatch reflects the probability that the interaction might fail (at least functionally) because of a shift in timing, often because of a complete loss of overlap between the timing of two events (figure 1). It is not clear how frequently demography-limiting ecological interactions are vulnerable to shifts in phenology—data on the temporal distributions of interactions are just too rare. Here, though, we describe several key factors involved in addressing the question.

(a) *Importance of interaction*

The sensitivity of a species' demography or population size to a phenological mismatch depends on the degree to which its survival or reproduction is limited by the other species or factors involved in the interaction. In some cases, reproduction or survival may rely entirely on another species being present and at a particular life-history stage at the right time. For example, yucca moths depend on yucca flowers and fruits for food and as habitat for eggs and larvae (Pellmyr & Thompson 1992). If, for some reason, the flowers are not open when the moths are active in their adult stage, an entire cohort of moth offspring could be lost. In other cases, the loss of an interaction may have little effect. For example, the loss of a predator–prey interaction may result in a substantial decline in predation on the prey species. However, if survival of the prey species is limited by food availability, not predation, the mismatch may have little impact on the demography of the prey species.

Similarly, a change in a relationship with an abiotic factor could have a very large or very small effect on the demography or population size of a species. For example, in Colorado, some plant species are initiating growth earlier in the spring, exposing flower buds to frosts; consequently, seed production has declined dramatically for some species (Inouye 2008). In theory, the effect on the population size of the species could be large if recruitment is limited by seed production, but small if it is not. The actual effects on recruitment have, in fact, been large. There has been little change in population sizes to date because these species are all long-lived perennials, but there is an ongoing shift in the size- and age-distribution (Inouye 2008).

Additionally, many relationships lost through phenological mismatches may be replaced by new interactions. For example, recent evidence has shown that plant–pollinator interactions shift substantially each year based on changes in the phenology and abundance of both plants and pollinators (Alarcón *et al.* 2008). The strength and frequency of relationships between particular plant and pollinator species may decline from one year to the next, but they are generally replaced by new relationships. Similarly, many herbivores and predators are generalists and eat a variety of foods, depending on what is available at a particular time. This generalist tendency would probably decrease the species' sensitivity to a phenological mismatch with any particular species, assuming that there is adequate variation in the phenology of the species that constitute the food resource.

(b) *Likelihood of significant phenological mismatch*

A species will probably be more sensitive to mismatches, and mismatches will more probably occur, if the resource it interacts with has a narrow, bell-shaped temporal distribution (Durant *et al.* 2007). A narrow temporal distribution increases the probability that an interaction will be completely lost in any given year (figure 1). For example, all else being equal, a bird species is more likely to suffer food shortages during the breeding season (and possibly reduced reproduction and offspring survival) in any given year if it is dependent on a food source that is abundant for only two weeks. In another example, the timing of caribou calving in Greenland is tightly linked to leaf-out phenology every year, but minor deviations from near-perfect synchrony translate to very large (four-fold) reductions in calf production (E. Post 2008, unpublished data).

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Similarly, a species is likely to be more sensitive to an abiotic factor if there is a threshold beyond which the effect of the abiotic factor becomes substantial. For example, some insects might suffer complete mortality if they have not yet entered diapause when freezing temperatures arrive in the autumn or winter. Thus, if they enter diapause too late in the season, the effects on survival could be substantial.

Abundance of the species involved in an interaction can also compensate for a phenological mismatch (Durant *et al.* 2005). Typically, mismatches are more likely to occur when abundance of a species is low, which can narrow the temporal duration of particular phenophases (i.e. particular life-history stages or behaviours) at the population level and reduce the likelihood of encounters with individuals at the 'tails' of the distribution. In contrast, increases in abundance can broaden the temporal duration of the availability of a phenophase (Durant *et al.* 2005), potentially reducing the impact of a slight loss in synchrony between species.

4. PHENOLOGICAL EFFECTS ON SURVIVAL AND REPRODUCTIVE SUCCESS

Under what circumstances will phenological changes alter rates of survival (offspring and adult) versus reproduction? Three general patterns come to bear on this question. First, reproduction tends to require more resources than survival, so that in the absence of adequate resources, rates of reproduction will tend to decline before rates of survival (Barboza *et al.* 2009). Second, general life-history theory postulates that, all things being equal, individuals will tend to abandon their offspring before they risk their own lives. Third, relative to adults, young offspring tend to have lower reserves and tolerances for unfavourable conditions, and have a diminished capacity to seek out new resources (Barboza *et al.* 2009). Together, these generalities suggest that there will be a succession of effects on demography, starting with effects on reproduction, then offspring survival and finally adult survival.

However, there are certainly exceptions to this conclusion. For some species, phenology is less critical for reproduction than for survival, particularly for the survival of offspring (Williams 1966). For these species, the succession of effects and their order may vary. In systems where mates and food are plentiful, timing may not be important for a species to mate and raise young—but timing may be important for its offspring to avoid predation, pests and harmful abiotic conditions like freezing and drought.

In addition, the relative role of phenology in affecting reproduction and survival will differ between species with income or capital breeding systems—that is, those that provision offspring with resources available during the reproductive period versus those that provision with resources gained prior to reproduction (Houston *et al.* 2007). The reproductive success and offspring survival of income breeders are likely to depend much more on the availability of food resources at the proper time and place. Capital breeders, on the other hand, rely primarily on stored energy reserves that can buffer them against the effects of changing food availability.

Clearly, much more work is required to distinguish between cases in which changes in phenology might affect survival and when they might affect reproduction, and when these will in turn affect population sizes. To illustrate the complexity of this question, we present examples of how phenology can alter demography in temperate and arctic plants. To emphasize the diversity of mechanisms by which phenology affects survival and reproduction, we present the examples according to the levels of interaction involved.

(a) *Reproduction*

(i) *Interactions between plants and abiotic factors*

Flowering too early can expose plants to cold weather conditions and damaging frosts (Inouye 2000, 2008; Høye *et al.* 2007). Flowering too late can leave too little time for fruits to develop or for germination to occur before the end of the growing season.

(ii) *Interactions within an individual and a population*

Producing a large number of flowers synchronously within an individual may increase the chances of self-pollination and decrease the chances of outcrossing (Williams 2007). Extended floral longevity or duration of flowering can increase the chances of receiving pollen from another plant and enhance fitness through outcrossing (Ashman & Schoen 1994). However, extended flowering within an individual may also increase the chances of being infected or being eaten by flower herbivores (Shykoff *et al.* 1996; McCall & Irwin 2006). Flowering synchronously with conspecific individuals can improve the chances of outcrossing and may reduce the incidence of seed predation.

(iii) *Intraguild interactions*

In the case of animal-pollinated species, flowering synchronously can create competition for pollinators, although a long flowering period may help to minimize the effects (Campbell & Motten 1985; Mitchell *et al.* 2009). In some cases, co-flowering with other species may facilitate the attraction of pollinators (Moeller 2004).

(iv) *Intertrophic interactions*

Species that rely on animals for pollination have an additional hurdle: to flower synchronously with effective pollinators. For plants with specialist pollinators—such as *Ipomopsis aggregata*, which relies primarily on hummingbirds for pollination (Caruso 1999)—or for plants that flower particularly early, before many pollinators are active, synchronizing flowering with pollinator activity can be especially important (Thomson 2010). For other species that host a variety of pollinators, it is of less importance. In some cases, mistiming may, in theory, lead to a year in which an individual or an entire population fails to reproduce. Coincidence with herbivores or seed predators, however, can negate the benefits of synchrony with pollinators (Brody 1997).

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(b) *Survival*

(i) *Interactions between plants and abiotic factors*

In addition to affecting reproduction, abiotic factors such as frost and drought can alter rates of mortality. Young plants are often more susceptible to unfavourable abiotic conditions than are older, more vigorous plants (Graae *et al.* 2009). In cases where a species' phenology is shifting at a different rate than these abiotic conditions, mismatches can develop (Inouye 2008). Young and older parts of a plant can also exhibit differential susceptibility to abiotic factors like frost, with new growth or reproductive parts often being more susceptible.

(ii) *Intertrophic interactions*

Plant–herbivore relationships are often time-sensitive, and depend on the timing of many factors, including leaf emergence, the emergence of herbivores and the development of defence compounds in leaves. For example, climate-driven changes in the phenologies of spruce trees and spruce budworm have led to increased synchrony between the life cycle of the budworm and the spruce growing season in the Pacific Northwest of North America (Chen *et al.* 2001, 2003). As a result, the level of spruce mortality in the region has dramatically increased. Many other plant–herbivore relationships are similarly dependent on the match between plant and herbivore phenology (Visser & Holleman 2001; Post & Forchhammer 2008; Jepsen *et al.* 2009; Singer & Parmesan 2010).

5. KEY CHALLENGES

(a) *Data limitations*

The demographic consequences of phenological changes are still largely unknown (Visser & Both 2005). The most significant reason for this gap in our understanding is that demonstrating demographic consequences of phenological variation typically requires an intensive monitoring effort, which is costly and time-consuming. It involves long-term monitoring of the phenology and demography of populations, generally for 5 years (preferably 10 years) or more, depending on the variability of the system in question (J. Che-Castaldo & D. Inouye 2010, unpublished data). Researchers attempting to generate time series long enough to make inferences about climate-driven changes often accumulate just one data point per year. However, latitudinal or elevational gradients can sometimes substitute for time series (see §6*b*). Most of the long-term studies with data relevant to the links between climate-driven changes in phenology and demography were started prior to the widespread recognition of recent phenological changes; they were typically begun for other reasons. Therefore, much of our current understanding of phenological impacts on demography is based on serendipitous results. As more investigations of phenology and demography begin and as researchers identify new historical datasets, like those held in museums and botanical gardens (Miller-Rushing *et al.* 2006), more data are slowly becoming available.

(b) *Imperfect knowledge of species ecology*

Despite the rapid progression of studies of phenological and demographic responses to climate change, much of the basic ecology of species remains largely unknown (Høye & Forchhammer 2008*a*). This is particularly true of alpine, polar and tropical species, some of which might be most vulnerable to recent changes in climate (Rodenhouse *et al.* 2008; Post *et al.* 2009). However, even the demography of most common species (e.g. plants, birds, amphibians and mammals) in the best-studied locations (e.g. eastern North America and western Europe) is poorly understood. The areas in which we lack adequate information range from a basic understanding of interannual variation in ecological interactions and climate-driven changes taking place to more complex topics, such as identifying the consequences, conservation implications and management decisions dictated by those changes.

(c) *Estimating the strength of ecological relationships*

Species with specialist relationships are among those most likely to show significant demographic effects of phenological shifts. Species that depend on particular resources that are available for limited times are more vulnerable than are generalists, which may be able to switch to sources to meet their needs as phenologies change. Any difference in nutritional value (or other aspects) of that new resource may cause increases or declines in survival and reproduction, but subsequent changes in abundance will likely be slower than in specialists.

Yet, specialist interactions are rare in most biomes and establishing the existence of a specialist or very strong interaction can be difficult, especially if the species in question are rare. In most cases, species interactions occur as a network of interactions rather than as a one-to-one relation (Ings *et al.* 2009). Even in the case of apparent specialist interactions, a species' behaviour may be plastic enough to interact with another species or resource when one becomes rare or disappears. This potential presence of latent plasticity poses a particular challenge for forecasting the vulnerability of species to phenological mismatches.

6. RECOMMENDATIONS FOR FUTURE RESEARCH

(a) *Optimize monitoring protocols*

The impact of climate-driven phenological changes on species abundance and persistence will be important as natural-resource managers and policy-makers try to anticipate, mitigate or adapt to the challenges presented by climate change. Thus, enhanced efforts to gather data on both phenology and demography of interacting species are needed. In many cases, the easiest approach may be to add phenological and demographic observations at sites where investigations of ecological interactions are already taking place (e.g. Forchhammer *et al.* 2008).

In many instances, though, observational protocols can be optimized to characterize timing-based multitrophic interactions. These optimizations include

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actions such as monitoring the temporal distribution of phenological events like flowering, rather than simply the onset of them, as is often done (Miller-Rushing *et al.* 2008*a*,*b*; van Strien *et al.* 2008). Temporal distributions reflect the behaviour of the entire population and allow for comparisons of the degree of overlap between one species and another (e.g. Forrest *et al.* 2010; figure 1), whereas first observations do not necessarily reflect population-level phenology (Miller-Rushing *et al.* 2008*b*; Moussus *et al.* 2010). Additionally, in many cases, following a sample of randomly chosen individual plants and animals will yield higher-quality data than will population-level observations, although observations of individuals will also require much more effort.

The timing of observations of demographic parameters is also important. For example, there may be a relatively short period during the growing season when the effects of seasonal frost on inflorescence production or seedling survival can be made. A single population census in midsummer could miss mortality that results from a late-summer drought or heat wave. Because phenology is time-sensitive by its nature, repeated observations of demographic parameters are necessary to understand the linkages between many aspects of phenology and demography. Moreover, the timing of these observations may need to change over time as conditions change. For example, the Zackenberg Research Station has expanded its field season of comprehensive ecosystem monitoring in response to earlier springs and longer growing seasons (M. Rasch 2010, personal communication).

For measuring changes in interactions within and among species, we need observations of interaction networks, their variability and reliable measures of the strength of interactions (Basilio *et al.* 2006). Often, frequency of interaction is substituted for strength of interaction because the former is easier to measure. Vázquez *et al.* (2005) show that the relationship between interaction frequency and total effect are generally strongly correlated, despite the fact that interaction frequency is not correlated with per-interaction effect. Thus, although it is not ideal, observations of the frequencies of interactions could yield key insights into the strengths of interactions in communities.

(b) *Identify hidden data sources*

Despite the need for enhanced monitoring efforts, there are still many questions that can be answered with data that have already been collected. Long-term ecological research sites, bird observatories, botanical gardens, farms, field stations and university extension facilities, for example, may host relevant data sources and provide ideal locations for further work on the impacts of phenological responses to climate change on demography. Data from museum and herbarium collections have been useful in reconstructing historical phenological patterns (Miller-Rushing *et al.* 2006; MacGillivray *et al.* 2010). Data currently being collected by national and international phenology networks and through remote sensing via satellites and cameras (Zhang *et al.* 2004; Betancourt *et al.* 2005; Menzel *et al.* 2006; Primack *et al.* 2009; Richardson *et al.* 2009) could provide additional phenological data that could be combined with demographic data collected by individual sites or from large networks, like the Monitoring Avian Productivity and Survivorship (MAPS) program (Saracco *et al.* 2008). Together, these sources of data could be used to identify species and locations for which temporal relationships are likely to change.

Substituting space for time along latitudinal or elevational gradients can also provide data to explore the relationships among climate variables, phenology and demography. Although it can be difficult to isolate the effects of particular factors along these gradients—including genetic factors (i.e. local adaptation)—they provide among the most powerful 'natural experiments' available to ecologists and are currently underused (Körner 2007).

(c) *Integrate observations, experiments and predictive models*

Observational data can be very good at reflecting long-term changes taking place, but experiments are generally necessary to identify conclusively the mechanisms driving the changes. Much experimental work has explored abiotic controls of phenology (Augspurger 1981; Berthold & Terrill 1991; Farnsworth *et al.* 1995), but relatively few studies have explored the subsequent effects of phenology on demography, in part because it is difficult to separate the effects of abiotic conditions from those of phenology on demography (Galloway & Burgess 2009). Additionally, the demographic effects of experimental manipulations of phenology are often not realistic because they occur in laboratory conditions or manipulate the phenology of individuals on a scale much smaller than the scale of their relevant ecological interactions. To understand better the effects of changing phenology on demography, we propose better integration of observational, experimental and modelling approaches. An understanding of long-term population dynamics from observational data and mechanistic insights gained from experiments can be combined in models to allow testing of hypotheses that would be impractical to address with experiments.

In particular, we believe that it is important to generate models that couple phenological changes to changes in abundance. One approach that may prove useful is integration of data on phenological responses to environmental change with models used for population viability analysis (Marrero-Gómez *et al.* 2007; Mondragòn 2009) or agent-based models, in which individual variation and spatio-temporal dynamics can be explicitly taken into account (Grimm *et al.* 2005). Additionally, the development of population models that incorporate the timing of life-history events (Post *et al.* 2001) will help provide a theoretical framework for quantifying the role of phenology in shaping demographic consequences of climate change. These models can generate hypotheses that can be tested with empirical observations and experiments.

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(d) *Life-history theory in a climate change context*

No clear theoretical framework exists for addressing questions regarding the demographic effects of phenological variation. For instance, longevity can play a role in how quickly growth rate in a population responds to climate change (Morris *et al.* 2008). In their meta-analysis of demographic data for 36 plant and animal species, Morris *et al.* (2008) found that the population growth rates of long-lived species were buffered from changes in rates of reproduction and survival relative to short-lived species. Thus, long-lived species may be better equipped to persist in an environment in which phenological mismatches become increasingly common. On the other hand, examples of declines in abundance of long-lived species in relation to climatic events are well known (Vibe 1967; Klein 1968; Vors & Boyce 2009). Meanwhile, the abundance of short-lived species may respond relatively quickly to changes in climate conditions—a relatively short series of years with favourable conditions (low mortality and high reproduction) could lead to rapid increases in population sizes, whereas unfavourable conditions could lead to sharp declines. For some populations, just one or two unfavourable years could lead to extinction.

It is important that we further develop life-history theory in the context of rapidly shifting phenology to provide investigators with a framework for understanding the interactions and changes taking place, and to provide hypotheses that can be tested empirically. Many aspects of current theory assume that phenology is relatively stationary, varying from year to year around a mean, whereas now the phenologies of many species are changing directionally because of changing climatic conditions (Forrest & Miller-Rushing 2010). Together, new observational studies, experiments, models and theory will help us to clarify the answers and improve predictions of future ecological responses to climate change.

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