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Demographic Consequences of Phenological Shifts in Response to Climate Change

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Abstract

When a phenological shift affects a demographic vital rate such as survival or reproduction, the altered vital rate may or may not have population-level consequences. We review the evidence that climate change affects populations by shifting species' phenologies, emphasizing the importance of demographic life-history theory. We find many examples of phenological shifts having both positive and negative consequences for vital rates. Yet, few studies link phenological shifts to changes in vital rates known to drive population dynamics, especially in plants. When this link is made, results are largely consistent with life-history theory: Phenological shifts have population-level consequences when they affect survival in longer-lived organisms and reproduction in shorter-lived organisms. However, there are just as many cases in which demographic mechanisms buffer population growth from phenologically induced changes in vital rates. We provide recommendations for future research aiming to understand the complex relationships among climate, phenology, and demography, which will help to elucidate the extent to which phenological shifts actually alter population persistence.

INTRODUCTION

Phenological sensitivity: the degree to which a phenological event responds to climate—e.g., one day advance per degree Celsius

Demographic vital rate: life-cycle events that affect population growth rates or fitness: survival, growth, reproduction, and recruitment

Perturbation analysis: analysis applied to population models that slightly perturbs vital rates and measures how much population growth rate changes in response

Survival and reproduction often depend on the timing of life-cycle events (Forrest & Miller-Rushing 2010). Rates of survival and reproduction also directly affect population dynamics. Therefore, phenological shifts caused by climate change could affect population persistence. At least, that is the argument that has been made in numerous review papers and primary research articles over the past two decades (Both et al. 2006, Hegland et al. 2009, Memmott et al. 2007, Miller-Rushing et al. 2010). Given that phenological shifts have been documented in a wide variety of taxa across a range of habitats (Parmesan 2007), it is important to understand their demographic consequences, which could theoretically be widespread. In this review, we critically evaluate the evidence that climate change exerts demographic impacts on populations by shifting species' phenologies.

In the simplest sense, a phenological shift may allow an organism to maintain its historic climatic niche, through plasticity in the timing of life-cycle events. Although the life-cycle event will occur on a different calendar date, it will theoretically occur under the same or similar climatic conditions (e.g., Charmantier et al. 2008) (**Figure 1*a***). Conversely then, we might expect species that do not alter the timing of their life-history events to be exposed to novel climates, thereby creating the potential for a positive or negative demographic consequence (**Figure 1*b***). Indeed, species with unresponsive phenologies have been shown to experience reductions in performance or abundance (Cleland et al. 2012, Møller et al. 2008, Willis et al. 2008). However, a phenological shift may not occur at the appropriate magnitude to allow the organism to maintain its climatic niche or to perfectly track its niche, depending on how responsive or sensitive the event is to a change in climate (i.e., phenological sensitivity) (**Figure 1*c***). Furthermore, different components of the climate that cue phenological events, such as temperature and precipitation (Forrest & Miller-Rushing 2010), are changing at different rates as the climate changes (IPCC 2013). Therefore, even when perfectly tracking a single aspect of climate, organisms may still be exposed to different combinations of abiotic conditions (**Figure 1*d***). Consistent with this scenario, species with responsive phenologies sometimes experience reductions in performance (Inouye 2008, Ludwig et al. 2006). Given all of these possibilities (**Figure 1**), phenological shifts may be just as likely to expose organisms to novel climates as they are to allow organisms to track preferred climates.

Furthermore, phenological shifts are also likely to cause species to experience novel biotic interactions, regardless of the extent to which they shift their own phenologies (**Figure 1**). Species-specific phenological shifts within communities appear to be the norm (Edwards & Richardson 2004, Høye et al. 2007, Ovaskainen et al. 2013). These different rates of change across species result in novel patterns of temporal overlap among species and, therefore, the potential for altered biotic interactions (CaraDonna et al. 2014, Forrest et al. 2010). Species that already interact can experience altered degrees of temporal synchrony, and species can gain novel interaction partners, in addition to losing old interaction partners (Burkle et al. 2013, Kharouba et al. 2018, Robbirt et al. 2014).

When a phenological shift affects a demographic vital rate, it is commonly asserted that population persistence will be affected, but this is not necessarily the case (e.g., Wilson & Arcese 2003). Population growth rates are differentially affected by changes in vital rates, so that, for example, a change in reproduction is unlikely to have the same effect on population persistence as a change in survival (Franco & Silvertown 2004, Gaillard et al. 2000, Robinson et al. 2014) (**Figure 2**). Thus, an effect of a phenological shift on a vital rate is most likely to affect population persistence if population growth rate is sensitive to changes in that vital rate.

Perturbation analyses provide a framework for making informed hypotheses about which vital rates are likely to affect population growth (**Figure 2**). Specifically, sensitivity and elasticity analyses quantify additive and proportional perturbations, respectively (Caswell 2001). For example, across 20 plant and animal taxa, elasticities for reproduction are lower than those for survival and

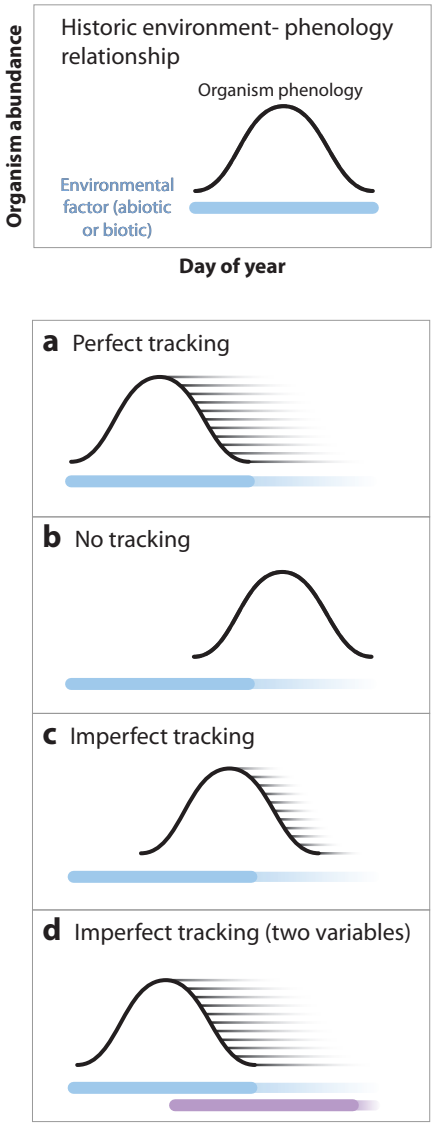

Figure 1

Phenological responses to climate change relative to a historic or pre-climate change baseline (*top* panel). Horizontal black lines indicate phenology shifting through time. Similarly, faded colors following solid colors indicate environmental factors shifting through time. (*a*) A shift in phenology represents perfect tracking of environmental conditions (both organism phenology and the environmental factor shift together). (*b*) Organism phenology remains unchanged while the environment shifts. (*c*) A shift in organism phenology represents partial or imperfect tracking of environmental conditions. (*d*) A shift in organism phenology allows an organism to track one aspect of the environment while failing to track other aspects.

growth (Pfister 1998). For these 20 taxa, we therefore might predict that effects of phenological shifts on reproduction will have smaller effects on population growth rates than survival and growth. However, the small changes in vital rates used in perturbation analyses may not reflect the magnitude of actual vital rate responses in nature. It is important to consider the magnitude of the

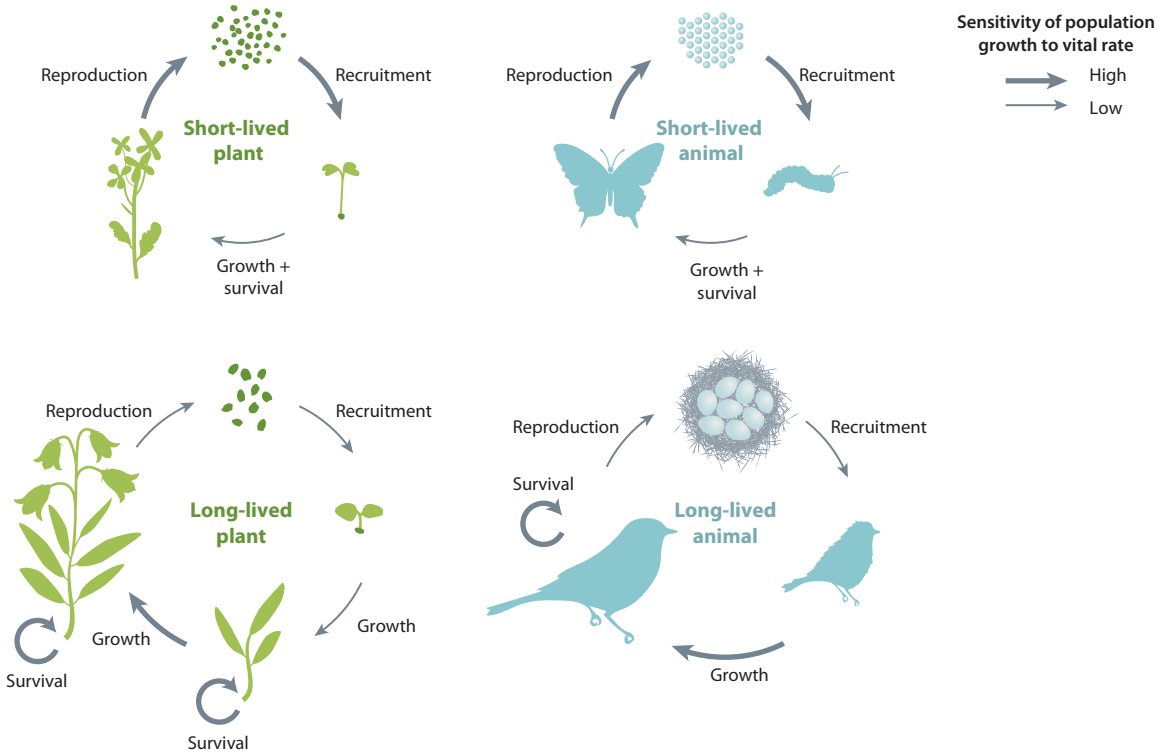

Figure 2

Life-cycle diagrams of short- and long-lived plants and animals. Arrows indicate transitions from one life stage to the next; circular arrows indicate survival of individuals to the next time step in long-lived species. The width of the arrows indicates the degree to which population growth rate is sensitive to perturbations in that vital rate, based on demographic life-history theory. Population growth rate in short-lived organisms is typically most sensitive to perturbations in reproduction (production of seed, eggs, or offspring in animals with live birth) or recruitment. Note that recruitment is shown here as a transition to the next life stage following a seed or an egg, but recruitment also inherently includes survival of that life stage to a certain time point; this survival of recruits is not explicitly shown. Population growth rate in long-lived organisms is typically most sensitive to perturbations in growth and survival. Although bird species can vary from short- to long-lived, here we use an example of a long-lived bird for illustrative purposes. Illustrations courtesy of P.J. CaraDonna.

change in a vital rate in combination with the sensitivity of a population to changes in that vital rate (e.g., Gaillard et al. 2013). In theory, a large change in a vital rate to which population growth is rather insensitive could still affect population growth rate (Boyce et al. 2006). (Note that sensitivity here refers to demographic sensitivity, as opposed to phenological sensitivity.) Additionally, perturbation analyses are based on population models that assume stable age or size distributions, and they do not account for trade-offs between vital rates or resource reallocation across years, which could allow organisms to compensate for losses in one vital rate by allocating resources to another (e.g., costs of reproduction in plants) (Obeso 2002). These potential discrepancies between modeling and empirical data highlight the crucial role of empirical, field-based studies in furthering our understanding of demographic consequences of phenological shifts.

Understanding the ability of populations to persist under climate change is critical because modifications to population growth rates have direct implications for species vulnerability to extinction, geographic ranges, and community composition (Doak & Morris 2010, Kimball et al. 2010, Macgregor et al. 2019). Here we review the evidence for demographic consequences

of phenological shifts in response to climate change from a life-cycle perspective and in the context of demographic life-history theory. We review the consequences of phenological shifts for plants and then animals, separated by life-cycle events: seedling emergence, leaf emergence, flowering, leaf senescence, animal emergence and reproduction, and animal migration and reproduction. Each life-cycle event is organized by demographic consequences via the abiotic and then the biotic environment. Our review showcases a variety of demographic consequences of phenological shifts across a diversity of organisms, in addition to highlighting why changes in vital rates may or may not translate to population-level consequences.

Demographic life-history theory: theory rooted in evolutionary biology that studies the demographic consequences of life-history strategies in the context of environmental variation

Leaf senescence: process of leaf death following a growth period, whereby resources from leaves are redistributed to other plant organs

Recruitment: survival of offspring to time step $t + 1$, often year two for organisms with one bout of annual reproduction

λ: proportional change in population size from one time step to the next; if $\lambda = 0.95$, population size at $t + 1 = 0.95(N)$

LITERATURE REVIEW

We used the following search criteria in Web of Science, applied to the Titles, Author Keywords, and Abstracts of Articles: (*synchron* OR phenolog* OR "temporal overlap" OR mismatch) AND "climate change" AND (demograph* OR reproducti* OR survival OR "vital rate*"). We included papers published either online via early access or with a hard publication date by August 2020. These parameters returned 1,273 papers. We then assessed whether each of these papers met two criteria: (1) Could the study quantify a phenological shift through time or phenological sensitivity to climate? (2) Did the study measure a demographic consequence? Demographic consequences included a change in a vital rate (survival, growth, reproduction, or recruitment), fitness, population abundance (number of individuals), or population growth rates (either the per capita or the finite rate of increase, λ). We considered a change in organism size to represent a demographic consequence because size has widespread effects on vital rates (Caswell 2001). The types of studies in our review included observational time series (time series of ≥5 years: 50% of studies; time series <5 years: 5%), field experiments (40% of studies), space-for-time substitutions (using variation in climate across elevation or latitude; 4% of studies), and observations across extreme climatic years (1% of studies). Of the field experiments, 61% were climate manipulations, 12% were phenology manipulations, 10% employed multiple approaches, 9% were common gardens, 5% were reciprocal transplants, and 3% used other techniques (e.g., translocation). We focused on studies with some field component and excluded purely theoretical studies and purely lab- or greenhouse-based studies in highly controlled environments.

A total of 238 publications met our criteria for inclusion. Not surprisingly, the number of papers that met our criteria increased through time, with 78% of papers having been published in the past decade (since 2010) (**Figure 3*a***). Throughout this review, percentages refer to the fraction of the 238 publications that met our review criteria; additional papers are highlighted in the main text. Of these 238 papers, 61% (146 papers) included animals as the focal study organism, and 39% (92 papers) included plants. Despite the fact that the timing of life-cycle events in fungi is sensitive to climate change (Diez et al. 2013), we found no studies of the demographic consequences of phenological shifts in fungi. There was a strong terrestrial bias, with 89% of studies occurring in a terrestrial habitat. Additionally, only 3% of papers focused on tropical study systems. Studies of both plants and animals tended to examine reproduction over other vital rates, with recruitment (see definition above) and population-level consequences (population abundance or population growth rate) being examined the least (**Figure 3*b***). Plant papers were strongly biased toward using experimental approaches, whereas animal papers mainly used observational time series (**Figure 3*c***). Because far more publications consider population-level consequences in animals compared to plants (**Figure 3*b***), most of the Plants section focuses on consequences of phenological shifts for vital rates, and much of the Animals section focuses on consequences for population abundance or growth rate.

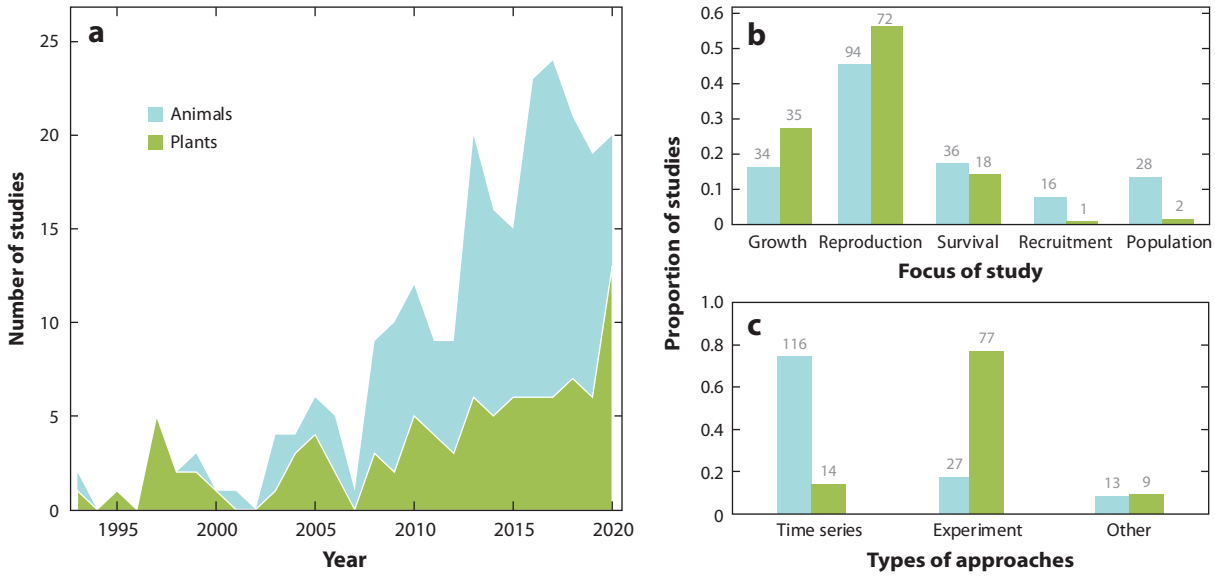

Figure 3

Summary results from a literature review of published papers of demographic responses to phenological shifts that met our search criteria outlined in the main text: (*a*) stacked area plot for the total number of papers published per year, broken down by studies that focus on plants vs. animals, (*b*) proportion of papers that focused on each type of demographic response, and (*c*) proportion of papers that used different approaches to study demographic responses to phenological shifts. The top line in panel *a* shows the total number of studies published per year, and colors indicate the proportion of those total studies that focus on plants vs. animals. Values in *b* and *c* are from all years pooled. See the main text for description of other approaches. Gray numbers above the bars represent the number of papers in each category.

PLANTS

Germination and Seedling Emergence

We begin with the first events in the life cycle of a plant: germination and seedling emergence. Germination is the emergence of a radicle from a seed, whereas seedling emergence occurs when a cotyledon protrudes above the soil, but here we treat germination and seedling emergence interchangeably. Phenological shifts in germination could affect multiple vital rates. Germination timing dictates the abiotic and biotic conditions (e.g., competition, herbivory, pathogen infection) to which a seedling is exposed, thereby affecting recruitment probability (Castro 2006, Donohue et al. 2010). Germination timing also affects conditions for postrecruitment growth, survival, and reproduction, especially in annual plants (Donohue et al. 2010). Climate change has great potential to alter the timing of seedling emergence because particular combinations of temperature and soil moisture trigger germination (Baskin & Baskin 2001). Despite this, only 3% of the papers that met our criteria examined germination (8/238 papers), and all but one of these were experiments.

Abiotic consequences. Most experimental studies find earlier germination or no change in germination date in response to warming (Flanigan et al. 2020, Richter et al. 2012, Wang et al. 2018), with only one study reporting a delay (Cochrane et al. 2014). Many studies of germination focused on the recruitment phase of the plant life cycle (i.e., survival of seedlings, or seedling establishment). For example, warming-induced shifts toward earlier germination in pine seedlings increased recruitment when seedlings had more time to grow and reached a larger size before summer drought set in, thereby increasing the probability of survival (Richter et al. 2012).

Similarly, warming-induced delays in germination have had negative effects. For example, in warming treatments where germination was delayed, the seedlings of four *Banksia* spp. were smaller by the time summer drought set in; however, this decrease in size was apparently not large enough to negatively affect seedling survival (Cochrane et al. 2014). Moving beyond recruitment, more variable precipitation, a general prediction under climate change, was associated with earlier germination, earlier flowering, and higher seed production in both an annual and a perennial herbaceous species (March-Salas et al. 2019). Presumably, earlier germination allowed for earlier flowering and more time to mature seeds. Yet, higher seed production in warmer or more variable climates will only benefit populations that are seed limited (for further discussion, see the section titled Flowering and Fruiting).

Seed limited: seed limitation occurs when recruitment is limited by seed inputs and population growth rate is sensitive to changes in recruitment

To our knowledge, only one study has linked shifts in the timing of germination in response to climate change to consequences for populations (Kimball et al. 2010). Germination, survival, and reproduction of winter annual plant species have been recorded annually in permanent plots in the Sonoran Desert, Arizona, USA, since 1982 (Venable 2007). Concurrently, rain events triggering germination have become later, with plants germinating later and being exposed to cooler fall and winter temperatures (**Figure 1*d***). Plant abundance (pooled across nine species) has declined across this same time period (Kimball et al. 2010). Importantly, germination rate—as opposed to survival or reproduction—was the main driver of changes in abundance in seven of the nine species. However, shifts in germination date were not explicitly tied to abundance or to climate in this study. Finally, species able to germinate under cool temperatures increased in abundance, which ultimately shifted community composition (Kimball et al. 2010). Although the hypothesis that demographic consequences of phenological shifts will alter population dynamics and community composition is often used to motivate studies of phenological shifts, this is the only study of which we are aware that, at least indirectly, links shifts in plant phenology to population-level consequences and altered community composition.

Biotic consequences. We found only one paper that considered the consequences of altered germination timing with regard to biotic interactions, in this case using a competition experiment during an extreme drought year and a non-drought year in a California grassland. Thomson et al. (2018) hypothesized that late germination of an annual forb (*Phacelia distans*) in the extreme drought year would increase competition with invasive grasses, but they did not find evidence to support this.

Leaf Emergence

Shifts in the timing of leaf emergence could affect somatic growth or survival. Leaf emergence establishes a start date for the growing season and can influence the length of time over which plants can photosynthesize and grow, a time frame that is also influenced by the timing of leaf senescence (Arft et al. 1999, Augspurger & Salk 2017) (see the section titled Leaf Senescence). Because population growth rates of perennial plants are sensitive to perturbations in growth and survival (Franco & Silvertown 2004), even minor effects of leaf emergence on plant growth or survival could have considerable demographic consequences in these species. Here we use leaf emergence as a broad term to represent several different phenological stages that denote the appearance or activation of photosynthetic leaf material following a dormant period: budburst, leaf-out, green-up, leaf flush, leaf expansion, or growth onset.

We found 30 papers (13%) that assessed the potential for a shift in leaf emergence and associated demographic consequences. The vast majority of these papers were experimental, and none examined population-level consequences. Therefore, this section focuses on the effects of shifts in leaf emergence on growth and survival.

Abiotic consequences. Warming spring temperatures and earlier spring snowmelt (in areas with seasonal snow cover) can promote earlier leaf emergence and allow more time for growth (Arft et al. 1999), provided leaf senescence does not advance as much as or more than leaf emergence (León-Sánchez et al. 2020, Starr et al. 2000). Many plants that leaf out earlier in response to altered climatic conditions exhibit increased growth, as expected (Choi et al. 2019, Jacques et al. 2015, Robson et al. 2013, Wipf 2010). However, other aspects of the environment can counteract the benefits of extended growing time: suboptimal temperatures, drought, reduced light availability, reduced mobilization of soil nutrients, and biotic interactions. For example, when earlier leaf emergence in response to changing climatic conditions exposes plants to temperatures suboptimal for growth or increases the likelihood of frost damage, plants have been shown to grow less, reach smaller size, and even experience lower survival rates than plants that leaf out later (Augspurger 2013, Augspurger & Salk 2017, Jacques et al. 2015, Wipf et al. 2006).

In contrast to spring warming, winter warming has been shown to delay leaf emergence. For example, leaves of subarctic shrubs that survived winter warm spells emerged later in the year and subsequently exhibited reduced growth (Bokhorst et al. 2011). Delayed leaf emergence presumably reflects prolonged accumulation of chilling requirements after warm spells (Laube et al. 2014).

Biotic consequences. In this section, we begin with biotic consequences within trophic levels and then move onto interactions across trophic levels. We found no studies that examined the effects of phenological shifts in leaf emergence on competition or facilitation directly (**Table 1**), highlighting an important research gap for future studies to address [but see Heberling et al. (2019), who show evidence that faster rates of advancement in tree leaf-out compared to wildflower leaf-out may lead to increased competition for light, with potential demographic consequences for herbs]. However, there is some support for indirect consequences for plant–plant interactions mediated by the abiotic environment. In particular, phenological shifts that expose plants to novel abiotic conditions may influence whether the demographic outcome of plant–plant interactions is positive or negative because the balance between competition and facilitation can depend on the level of abiotic stress (Callaway & Walker 1997, Wipf et al. 2006). If novel environments are more stressful, we might expect facilitation among plant species to replace competition (and vice versa). Wipf et al. (2006) find some experimental support for this hypothesis in subarctic tundra. Earlier snowmelt exposed plants to colder temperatures and more frost events, and when combined with neighbor removal resulted in advanced leaf-out, delayed shoot growth, and reduced vegetative growth and survival in one species (with no detectable effects of the climate or neighbor removal treatments on the other focal species) (Wipf et al. 2006). Importantly, earlier leaf-out was associated with reduced survival only when neighbors were removed, suggesting that neighbors may provide protection against colder winter temperatures when phenology is advanced (Wipf et al. 2006).

Phenological shifts in leaf emergence (or leaf senescence) that alter synchrony with herbivores are likely to affect plant populations because herbivory has been shown to affect population growth rates in several plant species (Maron & Crone 2006). In theory, phenological shifts in leaf emergence may allow plants to escape herbivores or may alter the time over which plants are exposed to herbivores, including exposure to herbivores with which the plant species has no prior experience (sensu Choi et al. 2019, Liu et al. 2011). However, research to date on phenological synchrony in plant–herbivore interactions has focused almost exclusively on demographic consequences for the herbivore (see the section titled Animal Emergence and Reproduction) or on changes in the quality of forage for herbivores (e.g., Doiron et al. 2014) and not on the vital rates of plants (**Table 1**). The only plant-centric study on this topic identified by our literature search used a field experiment to show that the timing of grazing by a goose had a greater effect on sedge

Table 1 Number of papers that examine demographic consequences of phenological shifts in response to climate change for various groups of organisms and species interactions

	Number of papers	
	Any demographic consequence	Population-level consequence
Organisms		
Amphibians	9	0
Aquatic invertebrates[a]	8	4
Birds	86	12
Fish	5	3
Fungi	0	0
Insects[b]	17	4
Mammals	19	7
Plants	92	2
Reptiles	7	3
Interaction type		
Competition/facilitation (plants)	6	0
Competition/facilitation (animals)	7	1
Consumer–resource (consumer)	64	9
Consumer–resource (resource)[c]	8	4
Host–parasite/pathogen (host)	4	0
Host–parasite (parasite/pathogen)	1	0
Plant–herbivore (plant)	1	0
Plant–herbivore (herbivore)	7	1
Plant–pollinator (plant)	8	0
Plant–pollinator (pollinator)	0	0
Plant–other mutualist (plant)	1	0
Plant–other mutualist (mutualist)	0	0

Any demographic consequence includes vital rates, fitness, population abundance, or population growth rate. Population-level consequence includes only population abundance or population growth rate. Papers are counted in each column if they measured both a vital rate and a population-level consequence. For interaction types, the organism for which the consequence is studied is listed in parentheses. Number of papers here pertains to all papers that we found using our search criteria, in addition to our own reading of the literature. For metadata of all studies meeting search criteria, see **Supplemental Table 1**.

[a]This includes copepods, coral, crustaceans, and zooplankton.

[b]One of these papers includes spiders.

[c]This includes a paper on florivory.

biomass than earlier leaf emergence (Choi et al. 2019). The sedge exhibited earlier growth and higher biomass in open-top warming chambers than controls. Delayed grazing—consistent with expectations for shifts in the timing of grazing at the site—also increased sedge biomass and had a three to five times larger effect than earlier sedge growth (Choi et al. 2019). Whether the sedge is leafing out earlier or the goose is arriving later at the site is unknown. Nonetheless, this study illustrates that the effects of herbivores on plant growth can exceed the effects of longer growing seasons, highlighting the importance of further research on how shifts in the timing of herbivory affect plant vital rates and ultimately population dynamics.

Finally, mutualistic interactions such as those between mycorrhizal fungi and plants have also been shown to influence demographic outcomes of phenological shifts in leaf emergence. For example, despite earlier growth under experimental warming, a semiarid shrub (*Helianthemum squamatum*) had lower biomass in warming treatments (León-Sánchez et al. 2018). Any phenological benefit of earlier growth seemed to be negated because of a reduction in the abundance of ectomycorrhizal fungi (EMF) in warming treatments. Reduced EMF abundance is likely due to direct effects of warming, as opposed to a shift in temporal overlap between plants and EMF. Thus, this scenario, like the facilitation between tundra plants mentioned above (Wipf et al. 2006), is one where a shift may expose plants to novel biotic conditions via the abiotic environment.

Flowering and Fruiting

Naturally, we expect phenological shifts in flowering and fruiting to affect reproduction (production of fruits or seeds) (**Figure 2**). Perturbations to reproduction are most likely to affect population growth rates in short-lived plants, such as annuals, whereas long-lived perennials are more sensitive to perturbations in survival and vegetative growth (Franco & Silvertown 2004). The production of offspring includes two life-cycle events for seed plants: seed production and subsequent seedling emergence (**Figure 2**). Therefore, the degree to which recruitment is limited by seed inputs is a critical consideration when examining the effects of shifts in flowering phenology on plant populations. Seed addition studies suggest that recruitment can be limited by both seed inputs and sites suitable for germination (Clark et al. 2007, Poulsen et al. 2007). This introduces the somewhat counterintuitive notion that changes to seed production can have minimal consequences for plant populations if recruitment is not seed limited (e.g., Lundgren et al. 2015).

For plants, flowering has by far been the most-studied life-cycle event, with 64 papers (27% of all papers) exploring some consequence of a shift in flowering time (10 papers also considered fruiting time). Most of these were experimental (45 papers; 73% of all flowering papers). Only one study has examined consequences of shifts in flowering for plant population growth rate in relation to the abiotic environment (Iler et al. 2019), and no studies have linked altered temporal synchrony between flowering and interaction partners to altered plant population growth rate. Thus, we focus mainly on consequences for reproduction in this section.

Abiotic consequences. Most experiments report earlier flowering under warmer temperatures, often associated with increased reproduction (Alatalo & Totland 1997, Cleland et al. 2012, Price & Waser 1998, Stenström & Jonsdottir 1997, Wookey et al. 1993). However, it is unclear whether changes in reproduction reflect shifts in flowering phenology per se or a direct effect of altered climate. For example, tundra and arctic plant seed production appears to be temperature limited (Henry & Molau 1997), so increased seed production under warming would likely occur irrespective of earlier flowering. This is important because over half (54%) of experiments on flowering phenology occur in high-latitude and high-elevation sites (**Supplemental Table 1**).

To date, evidence of negative abiotic consequences of shifted flowering dates is limited mainly to increased risk of frost damage in years when flowering is early, and subsequent reductions in seed production (Augspurger 2013, Gezon et al. 2016, Inouye 2008, Thomson 2010; but see Thomson 2019), but exposure to drought and heat stress are also plausible consequences of shifted flowering dates (Franks et al. 2007). For example, frost damage due to climate change–induced earlier flowering in a perennial sunflower increases when snowmelt occurs early, and this can dramatically reduce seed production (Iler et al. 2019, Inouye 2008). However, early snowmelt reduces projected population growth rates mainly through reductions in survival, not seed production, showing that earlier flowering in this case has little population-level consequence (Iler et al. 2019).

Biotic consequences. Changes in flowering time can also affect temporal overlap between flowers and their pollinators, florivores, and seed predators. In fact, altered temporal synchrony between flowers and pollinators is one of the most-discussed consequences of phenological changes, with most authors highlighting likely adverse effects for plants and/or flower visitors (Hegland et al. 2009, Memmott et al. 2007). Species flowering at the beginning of seasonal transitions (e.g., Gezon et al. 2016, Kudo & Cooper 2019), or specialists that are reliant on a single visitor taxon for pollination (e.g., Robbirt et al. 2014), are probably most susceptible to negative reproductive consequences of altered synchrony with pollinators, if flowering precedes pollinator activity. For example, the early-flowering *Corydalis ambigua* suffers depressed seed set in early-snowmelt years (or when snowmelt is experimentally advanced), corresponding to a larger gap between flowering onset and emergence of bumble bee queens (*Bombus hypocrita*) (Kudo & Cooper 2019). Despite a few cases of reduced reproduction related to changes in plant–pollinator synchrony, we stress that negative population consequences of decreased synchrony between flowering and pollinator activity are likely only if reproduction is altered substantially and the plant is short-lived, or, for long-lived plants, if population growth rate is seed limited and sensitive to changes in reproduction.

As others have observed (Forrest 2015, Miller-Rushing et al. 2010), plants may be buffered from changes in plant–pollinator synchrony because lost interactions can be replaced by new ones (Burkle et al. 2013, CaraDonna et al. 2017). However, experiments indicate that plants with shifted flowering dates can be exposed to less effective pollinators (Rafferty & Ives 2012), suggesting that early flowering may reduce reproduction even if pollinator visitation rates increase with earlier flowering (as in Rafferty & Ives 2011). Alternatively, phenological shifts that decouple flowers from their interaction partners may enable plants to escape ineffective pollinators (sensu Wilson & Thomson 1991) or antagonists or expose them to antagonists with which they had no previous interaction. The latter has received less study, even though antagonists can severely depress seed production. Indeed, earlier flowering by a gentian inside passive, open-top warming chambers exposed flowers to a noctuid moth that caused substantial damage, resulting in a 50% drop in flowers that developed into fruits compared to controls (Liu et al. 2011).

Species-specific shifts in flowering dates have reshuffled patterns of temporal overlap among flowering plant species (CaraDonna et al. 2014, Forrest et al. 2010), with potential reproductive consequences if the degree of coflowering with heterospecifics affects interactions for pollinators or floral antagonists (e.g., competition or facilitation of pollination). Experimental evidence suggests this is a possibility (Giejsztowt et al. 2020; M.N. Faust & A.M. Iler, unpublished data). Although it seems logical that plant species should experience reduced reproduction as overlap with competitors increases or as overlap with facilitators decreases, this is not necessarily the case (Waters et al. 2020). For example, the original interaction (facilitation, competition, or neutral) did not predict the direction of change in seed set for focal plant species exposed to altered flowering synchrony with two invasive plant species (Waters et al. 2020). Nonetheless, the evidence so far suggests that asynchronous rates of change among coflowering plant species can affect seed production in both positive and negative directions via indirect interactions for pollinators.

Of course, the effects of altered pollination are of little consequence if the abiotic environment is not conducive to reproduction. For example, *Claytonia lanceolata* plants induced to flower earlier than normal exhibited the lowest reproduction despite receiving the most pollinator visits because early flowers were more likely to be frost damaged (Gezon et al. 2016). This result held whether plants were induced to flower via a snow removal treatment or in a greenhouse (Gezon et al. 2016). Similarly, an experimental decrease in the degree of coflowering with a competitor improved seed production only in plants that were not drought stressed (M.N. Faust & A.M. Iler, unpublished data). Neither of these studies found evidence of pollen limitation, suggesting that seed production in these plants is limited by the abiotic environment or some other biotic factor.

Leaf Senescence

Shifts in the timing of leaf senescence can affect somatic growth, reproduction, and survival. Leaf senescence is often measured as a loss in chlorophyll or change in leaf coloring. However, these visible color changes do not always reflect the end of photosynthetic activity, at least in trees where leaves can stop photosynthesizing before color changes occur (Bauerle et al. 2012). Thus, although leaf senescence and leaf emergence can together determine the length of time over which plants may photosynthesize and grow (Augspurger & Salk 2017), leaf coloration as an indicator of growth cessation should be treated with caution. Alternative measures to leaf coloration include fall bud set for woody species and leaf spectral indices (Cooper et al. 2019, Zohner & Renner 2019).

We found only 15 papers (~6%) that assessed the potential for a shift in leaf senescence along with consequences for plant vital rates, but no population-level consequences. Thus, leaf senescence is understudied, despite its potential to affect multiple vital rates. All studies of leaf senescence focused on consequences relative to the abiotic environment and used some kind of experimental manipulation.

Delayed leaf senescence in response to climatic changes has been associated with positive demographic consequences in multiple studies (Cooper et al. 2019, Cui et al. 2017, Etterson et al. 2020). For example, later leaf coloring in the Tibetan Plateau was the primary driver of a longer active period under warmer conditions for an annual forb, resulting in larger plants with higher seed production, presumably because seeds had more time to ripen when senescence was delayed (Cui et al. 2017). Similarly, oak seedlings from southern ecotypes exhibited later leaf senescence than northern ecotypes, and later senescence was directly related to greater survival and higher growth rates (Etterson et al. 2020). However, no demographic consequences of earlier leaf senescence under experimental climate change conditions have been detected (Bjorkman et al. 2017, Legault & Cusa 2015), potentially because leaf emergence was also earlier in many cases, thereby resulting in a similar duration of above-ground activity.

ANIMALS

The most-studied phenological shifts in animal life cycles are emergence from dormant periods, reproduction, and migration. According to demographic life-history theory, population growth rates will be most sensitive to changes in survival in medium- to long-lived animals that produce relatively few offspring or have long generation times (Gaillard et al. 2013, McLean et al. 2016). In contrast, population growth rates are likely to be sensitive to changes in reproduction in shorter-lived animals that produce many offspring or have short generation times (McLean et al. 2016). Although many species fall somewhere between these life-history extremes, classifying organisms as representative of longer- versus shorter-lived strategies permits inferences about which vital rates are most likely to influence population growth rates, in the absence of species-specific empirical data.

Animal Emergence and Reproduction

We combine our review of shifts in animal emergence and reproduction into one section and migration and reproduction into another because reproduction in many animals occurs nearly simultaneously with either emergence or arrival at summer breeding grounds, and these events can be difficult to separate in practice (e.g., the emergence of the adult phase of many insects and hibernating mammals, and the arrival of migratory birds to breeding grounds).

Abiotic consequences. Shifts toward earlier reproduction can have negative demographic consequences for animals due to exposure to suboptimal abiotic conditions, similar to plants that

experience frost damage. Negative effects of exposure to suboptimal abiotic conditions do not appear to be as common in animals as in plants, probably because animals can thermoregulate and move, although it may also reflect the fact that the topic has received less research attention in animals. Negative demographic effects of cold exposure should be most likely for precocial animals that can become isolated from necessary parental thermoregulation shortly after hatching or birth, such as grouse, ducks, geese, and other bird species that leave the nest shortly after hatching. For example, black grouse egg hatching dates have advanced in response to warmer springs in Finland, but early summer temperatures have not warmed, resulting in exposure of chicks to colder temperatures, increased chick mortality rates, and decreased reproductive output (number of offspring) (Ludwig et al. 2006). Such declines in the number of offspring could affect black grouse populations because reproductive output is associated with population size (Lindström et al. 1997, Ludwig et al. 2006). Furthermore, black grouse exhibit cyclical population dynamics, and simulation modeling shows that these cycles can be disrupted by density-independent processes such as the observed match between timing of reproduction and hatching temperatures, providing further evidence that declining reproductive output may be driving an observed population decline in Finland (Ludwig et al. 2006).

Precocial animals: animals that are born or that hatch with fairly advanced development, are mobile, and require little parental care

One of the best-documented consequences of earlier emergence and reproduction with regard to changes in the abiotic environment is the production of an extra generation (increased voltinism) or brood within a single breeding season, for those species that are developmentally capable. This has been reported in numerous terrestrial and aquatic arthropods (Altermatt 2010, Kristiansen et al. 2016, Pöyry et al. 2011), birds (Bulluck et al. 2013), fish (Hovel et al. 2017), and lizards in an experimental study (Bestion et al. 2015). In many cases, increased voltinism appears to be due to longer growing seasons rather than only a consequence of faster growth rates under warmer temperatures. For example, aphids emerge earlier and reproduce earlier in response to experimental warming, promoting development of an extra generation and an 11-fold increase in the number of overwintering eggs compared to controls (Strathdee et al. 1993). Even in the short growing seasons of the Arctic, earlier snowmelt can lead to an earlier first clutch of eggs and a higher probability of a second clutch in wolf spiders (Høye et al. 2020). Similarly, earlier spawning in response to earlier lake ice breakup allows three-spined sticklebacks to produce an additional cohort in late summer (Hovel et al. 2017). Multivoltine or multi-brooded species may also benefit from longer growing seasons by having more time in between reproductive events. For example, multi-brooded bird species show larger advances in egg-laying dates than species that lay only one clutch of eggs (Dunn & Møller 2014, Halupka & Halupka 2017), and earlier egg-laying has been shown to increase the time between clutches in barn swallows, thereby increasing the number of offspring (Møller 2007).

Yet, the effects of increased voltinism on population growth remain unclear. Given that most of the examples in the previous paragraph are relatively short-lived species with high reproductive output, it is tempting to hypothesize that increases in annual reproductive output due to earlier emergence should lead to population increase. Consistent with this hypothesis, a long-term record of lepidopteran phenology from Great Britain finds that earlier emergence of multivoltine species is associated with greater population growth between the first and second generation, increased abundance in years t and $t + 1$, and poleward range expansions (Macgregor et al. 2019). However, increasing the number of generations per year may not be reliably beneficial. Increased voltinism will not benefit dietary specialists who rely on food that is present during a limited time window. In the absence of perfect climate tracking (**Figure 1*a***), an earlier start to development could theoretically be accompanied by more rapid development under warmer temperatures, which often leads to smaller adult size and subsequent negative effects on other vital rates (Kingsolver & Huey 2008). Additionally, if the seasonal window conducive to development ends before development is

Density dependence: when a process, here a vital rate, varies with population abundance

complete, the additional generation may fail, which is known as a developmental trap (Van Dyck et al. 2015). There is evidence for this in the wall brown butterfly (*Lasiommata megera*), which is declining in some parts of its range: In areas with population declines, the butterfly is emerging earlier, and the appearance of a third generation that is destined to fail is becoming more frequent (Van Dyck et al. 2015).

Biotic consequences. Much of the research on the consequences of phenological shifts in animal emergence and reproduction has focused on consumer–resource interactions: 89% (71/80 papers) of the animal papers that considered a biotic consequence. Over half of these papers are based on long-term data sets of bird breeding (59%; 42/71 papers).

Timing of reproduction is important for insectivorous birds in which offspring success depends on timing the energetic demand of developing chicks to a brief period of high insect abundance (Both et al. 2006, Visser et al. 1998). For example, two populations of great tits (*Parus major*) have been studied extensively, in England and in the Netherlands. In the English population, egg-laying occurs earlier than in the past, and the timing of peak abundance of the main food source, winter moth caterpillars (*Operophtera brumata*), has advanced to a similar degree, thereby maintaining synchrony (Charmantier et al. 2008). Recruitment and population size are both increasing (Charmantier et al. 2008), although the reason for these increases is unclear. In contrast, in the Dutch population, caterpillars have advanced their phenology, whereas egg-laying dates have not shifted, resulting in decreased synchrony between chick demands and food availability (Visser et al. 1998, 2006). Offspring production declines with decreasing synchrony between demand and food availability, partly because fewer second broods are observed in less-synchronized years (Reed et al. 2013b). However, among-year variation in synchrony between the great tit and caterpillars does not affect projected population growth rate (Reed et al. 2013a). Here, losses in the number of offspring appear to be counteracted by reduced intraspecific competition among chicks for food, which increases survival of recruits, thereby decoupling the number of offspring in year t from recruits in year $t + 1$ (Reed et al. 2013a; see also Wilson & Arcese 2003). This is an example of negative density dependence in one vital rate (recruitment) compensating for reductions in a different vital rate (reproduction) because recruitment is higher at lower offspring densities. The great tit–winter moth study system exemplifies how consideration of the whole life cycle can provide key insights into unexpected demographic consequences of phenological shifts—or lack thereof.

Trade-offs among different components of fitness or vital rates should be common, according to life-history theory (Roff 2000). Therefore, measuring a single vital rate can paint a picture of demographic consequences of phenological shifts that is incomplete or even backward. For example, in the tropical bird *Forpus passerinus*, there is a trade-off between reproduction and adult survival: In years with high rainfall, birds lay eggs earlier, producing more fledglings but exhibiting decreased adult survival (Tarwater & Beissinger 2013). A projected decrease in rainfall in the study area should therefore delay egg-laying and decrease offspring production but could also indirectly increase survival. Similarly, in a North American bee (*Osmia lignaria*), Farzan & Yang (2018) observed a survival–reproduction trade-off among experimental cohorts released at different times relative to the phenology of the natural population. Offspring production was highest in the cohort synchronous with the natural population because of high nest provisioning rates and low parasitism rates. However, the earliest cohort exhibited the highest survival (perhaps related to food quality) and overall the highest fitness. Thus, measuring only reproduction would suggest that earlier timing is worse, and we would miss the critical response of survival, which in this case ultimately influenced fitness.

Herbivores often time their life-cycle events to coincide with a relatively short time period when new plant leaves are most nutritious and least defended. Mistiming with these ephemeral,

high-quality resources has been shown to have negative consequences for insect and mammal herbivores. For example, the early-instar caterpillars of many lepidopteran species consume young plant material, and if they emerge from diapause outside the time window when leaves have initiated expansion, developing caterpillars may die (van Asch & Visser 2007). Not all caterpillars are so susceptible to asynchrony with young leaves, and some may have longer time windows over which to complete development, as shown in at least one warming experiment on tent caterpillars (Kharouba et al. 2015). Additionally, host switching is likely to be an option for many species (Liu et al. 2011, Renner & Zohner 2018), which could buffer insect herbivores from demographic consequences of changes in synchrony with their current primary host plants. Along similar lines, mammalian herbivores may be buffered from changes in synchrony with high-quality plant forage if they are closer to the capital breeder end of the life-history spectrum and rely on stored resources for reproduction (e.g., muskox), as opposed to species closer to the income breeder end of the spectrum that rely on resource availability for reproduction, such as roe deer and caribou (Eikelenboom et al. 2021, Kerby & Post 2013). For example, birth dates of roe deer in France are not advancing, while the vegetation on which they forage is becoming available earlier in response to warmer springs (Plard et al. 2014). This lack of a shift in birth dates has resulted in deer being born after the peak availability of high-quality forage, which in turn is associated with decreased survival of fawns, decreased recruitment, and decreased population growth rate (Gaillard et al. 2013, Plard et al. 2014). For a similar scenario with migratory caribou, see the section titled Migration and Reproduction (Post & Forchhammer 2008).

In general, interactions that occur over longer time windows with no clear peak in food availability seem to be less susceptible to demographic consequences of altered synchrony (Both et al. 2010, Dunn et al. 2011). At the same time, however, there is also evidence of demographic consequences of phenological shifts in interactions that occur over longer time windows. For example, earlier emergence from hibernation in marmots (*Marmota flaviventris*) results in more time for plant consumption, increased weight gain over the growing season, higher survival, and increased population growth rate (Ozgul et al. 2010; for a similar response in the opposite direction in ground squirrels—later emergence and decreased population growth rate—see Lane et al. 2012). However, a more recent study reveals variation in season-specific vital rate responses and brings into question whether this population will continue to increase (Cordes et al. 2020), especially if marmots have to wait for forage plants to appear after emerging, because their emergence is advancing more quickly than spring snowmelt dates, or if there are low periods of plant abundance during extended growing seasons (Cordes et al. 2020, Inouye et al. 2000). In another example, the timing of snowshoe hare molt has not kept pace with delays in fall snow cover or advances in spring snowmelt dates, resulting in a mismatch of fur color with the environment, increased predation, decreased survival, and a projected population decline if the current degree of mismatch continues (Mills et al. 2013, Zimova et al. 2016). Although the effects of this camouflage mismatch on other vital rates (body size or reproduction) have not been measured, population growth rate in snowshoe hare is sensitive to changes in survival (Griffin & Mills 2009), suggesting that the population could indeed decline in response to the mismatch.

Migration and Reproduction

Migratory animals may be especially prone to demographic consequences of phenological shifts because environmental conditions at overwintering grounds or along the migration route differ from those at the summer range, thereby decoupling the timing of arrival to the summer range from phenological events (Lehikoinen et al. 2004). Additionally, many migratory species depend on photoperiod cues to depart overwintering grounds, which can also decouple arrival

Mismatch hypothesis: consumer resource demand should temporally align with peak resource availability, and a change in timing will result in mismatch

from phenology in the summer range (Bradshaw & Holzapfel 2007). For example, long-distance migratory species have advanced their arrival and timing of reproduction to a lesser extent than short-distance migrant and resident species, and therefore are often unable to keep pace with earlier springs at breeding sites (the vast majority of the evidence comes from studies of birds; Eikelenboom et al. 2021, Lehikoinen et al. 2004, Saino et al. 2011). Insufficient advances in arrival and timing of reproduction have been associated with population declines or reduced population growth rates in numerous migratory bird species (Franks et al. 2018, Møller et al. 2008, Saino et al. 2011; but see Dunn & Møller 2014) in addition to migratory caribou (Eikelenboom et al. 2021).

It has been repeatedly hypothesized that population declines in species that fail to sufficiently advance their arrival or breeding dates at higher latitudes may relate to altered synchrony with food resources (i.e., the trophic asynchrony or mismatch hypothesis). There is some observational evidence to support this hypothesis. For example, when spring arrives early in Greenland, calving dates of migratory caribou lag behind the time of year when young leaves are most nutritious and least defended, and calf production and population growth rate are reduced (Eikelenboom et al. 2021, Post & Forchhammer 2008). Pied flycatcher populations across the Netherlands with the highest estimated degree of mistiming with caterpillar prey exhibit the largest population declines (although mistiming was not directly measured) (Both et al. 2006). There is additional, indirect evidence in support of the trophic asynchrony hypothesis for long-distance migratory birds (57 species in the Netherlands) (Both et al. 2010). In particular, long-distance migrants that rely on food that is available over a short time window (here, in forests compared to open meadows) are the most likely to experience population declines (Both et al. 2010). We have mainly highlighted studies with data on population abundance or population growth rate, but many more studies have investigated the effects of climate change–induced shifts in trophic synchrony on individual vital rates in migratory animals (**Supplemental Table 1**). Most studies focus on offspring production or recruitment (**Supplemental Table 1**), but adult survival can also be compromised if more effort is required for feeding offspring when synchrony between offspring demand and food is decreased (Thomas et al. 2001).

Whether climate change–induced phenological mismatch between consumers and resources is a widespread driver of population growth rate is still largely unknown, for both migratory and nonmigratory animals (Franks et al. 2018), in addition to plants. There are several reasons why changes in temporal synchrony between consumers and resources may not affect population growth, especially for migratory species. First, conditions at overwintering grounds or during migration could have a larger effect on vital rates and population growth than conditions at breeding grounds (Vickery et al. 2014). Second, as previously mentioned for nonmigratory animals and plants, vital rates other than those affected by altered synchrony could be more important for population growth. Third, negative effects of decreased synchrony with food resources can be compensated by increases in other vital rates, such as increased chick growth under warmer temperatures, as shown for the migratory dunlin (*Calidris alpina*) (McKinnon et al. 2012). Fourth, the abiotic environment may have larger effects on vital rates than synchrony with food (Visser et al. 2015). Finally, different rates of phenological change between migratory species and species with which they interact could also alter competition, mutualism, or parasitism (Ahola et al. 2007, McKinney et al. 2012, Saino et al. 2009); these interactions have not received nearly as much attention as consumer–resource interactions (**Table 1**), presumably because the phenological mismatch hypothesis was developed for consumer–resource interactions (reviewed in Kharouba & Wolkovich 2020). For example, long-distance migrants whose breeding dates are not keeping pace with advancing springs could experience altered competition with resident species for food or nest sites. Indeed, less synchronous breeding dates between the migratory pied flycatcher and resident great

tits in warmer years are associated with a decrease in fatal competition for nest sites, with increased survival of flycatchers (Ahola et al. 2007).

SYNTHESIS OF FINDINGS

Our review reveals that phenological shifts in response to climate change can affect demographic vital rates both positively and negatively across a diversity of plant and animal taxa. Improved performance can occur when organisms gain more time to grow or reproduce as life-cycle events shift earlier, or when organisms are released from antagonistic interactions (although there is much less evidence for the latter). Although it is often argued that phenological sensitivity to changing climatic conditions (i.e., tracking) will improve or maintain organism performance, phenological sensitivity in response to climate change can also expose organisms to novel environments (**Figure 1*c*,*d***), resulting in negative demographic consequences. Thus, it should not be assumed that a phenological shift is beneficial and the lack of a shift is adverse. Negative demographic consequences of phenological shifts appear to be most likely (*a*) when there is a short time window over which a consumer–resource interaction occurs (including plant–pollinator interactions), (*b*) near a seasonal transition when a shift puts consumers at risk of having no or reduced resources or plants at risk of having no or fewer (or less effective) pollinators, or (*c*) in animals that are income breeders (relying on the environment for resources for reproduction, rather than stored resources). All three of these scenarios are exacerbated for migratory animals in which migration timing is decoupled from the proximal abiotic cues of resource phenology.

Our review also reveals that phenological shifts can affect population growth rates both positively and negatively, although there is much less evidence for this. In many cases, a phenological shift affects a vital rate to which population growth rate is sensitive, as has been shown for plants, birds, and mammals (Gaillard et al. 2013, Kimball et al. 2010, Martin et al. 2014, Ozgul et al. 2010, Plard et al. 2014, Zimova et al. 2016). All but one of these cases are consistent with demographic life-history theory and results of perturbation analyses: Shifts that affect survival in medium- to long-lived organisms, or that affect reproduction or recruitment in shorter-lived organisms, have population-level consequences (**Figure 2**). The exception is for roe deer, in which recruitment is reduced when birth dates fall behind spring plant phenology, which in turn reduces population growth, even though population growth rate is most sensitive to changes in survival (Gaillard et al. 2013, Plard et al. 2014).

In contrast, we find a similar number of cases in which demographic mechanisms buffer population growth rate from changes in vital rates. First, vital rates can be affected by a phenological shift but then have little influence on population growth rate (Bestion et al. 2015, Iler et al. 2019, McLean et al. 2016). Second, negative density dependence can compensate for losses in one vital rate by increasing another vital rate (Reed et al. 2013a, Wilson & Arcese 2003). Conversely, positive density dependence could amplify the effects of altered density on another vital rate, thereby having larger effects on population growth rate than expected; we did not find evidence of this in our review, but it is theoretically plausible. Third, although to our knowledge it has not been explicitly shown, density-independent trade-offs between vital rates (e.g., Tarwater & Beissinger 2013) or resource reallocation across years (e.g., Iler et al. 2019) could also buffer population growth rate from changes in vital rates.

CONCLUDING THOUGHTS AND FUTURE DIRECTIONS

That relatively few studies can convincingly link demographic consequences of phenological shifts to consequences for population growth rate is striking, especially in light of the frequency with which population-level consequences are cited as a motivation to understand phenological shifts.

Integral projection model (IPM): model that integrates vital rates across continuous ranges of size or age to predict population growth in discrete time steps

Structural equation modeling: a statistical analysis that allows one to disentangle direct and indirect effects of a single predictor on multiple responses

Life table response experiment (LTRE): an analytical approach for determining the vital rates responsible for treatment or other driver effects on population growth rate

Community science: the systematic collection of data by people who are not professional scientists; replaced citizen science as a more inclusive term

At the same time, it is also perhaps unsurprising given the difficulty of gathering data on the complex ways in which climate, phenology, vital rates, and populations are inter-related, as Miller-Rushing et al. (2010) emphasized over a decade ago. It is particularly challenging to disentangle direct effects of climate on demography from effects of climate that operate via phenological shifts. Studies that correlate phenological shifts with changes in population size generate useful hypotheses, but the demographic mechanisms underlying the changes in population size are unknown, which means forecasts about the consequences of future phenological shifts may be inaccurate.

Three approaches that can overcome some of these challenges are integral projection models (IPMs), structural equation modeling, and analysis of residuals. Recent progress in understanding the effects of climate and species interactions on population growth rates has largely been made possible by IPMs (reviewed for plants in Ehrlén et al. 2016), which require less data than traditional matrix population models (Ellner & Rees 2006). Because IPMs make use of continuous size variation, it is easier to incorporate environmental drivers compared to a traditional matrix modeling approach. Studies to date that have employed IPMs or that rely on preexisting IPMs provide some of the most convincing evidence of population-level consequences of phenological shifts, or lack thereof (Gaillard et al. 2013, Iler et al. 2019, Martin et al. 2014, Ozgul et al. 2010, Plard et al. 2014, Reed et al. 2013a), and therefore are a promising approach for further advancing our understanding of the effects of phenological shifts on populations. Most importantly, perturbation analyses (see the Introduction) and life table response experiments (LTREs) can be applied to IPMs (and matrix models) to determine through which vital rate an environmental driver exerts the strongest influence on population growth rate (given model assumptions). Another promising approach is outlined by McLean et al. (2016), who use structural equation modeling to investigate the direct and indirect effects of climate, via phenological shifts, on vital rates and population growth. Additionally, identification of latent pathways of interaction could dissect direct climatic effects from those operating through phenology in cases where phenology is less well quantified. An alternative approach, and one that requires less data, is to extract the residuals from the responses of phenology and demography to climate (or year) and then examine evidence for a relationship between the residuals (sensu Iler et al. 2017). In this way, one can account for direct effects of climate on both phenology and demography and then examine remaining covariation between the two.

Finally, we offer some strategies for the design of future studies of demographic consequences of phenological shifts, informed by our review.

1. Measure multiple vital rates across more than one year. This allows one to account for trade-offs that could decouple changes in vital rates from population growth.
2. If it is only feasible to measure one or a subset of vital rates, then demographic life-history theory should be used to select the vital rates to which population growth is likely to be most sensitive (e.g., survival or growth in long-lived organisms) (Franco & Silvertown 2004, Gaillard et al. 2000). Additionally, the COMPADRE and COMADRE databases are a useful source of demographic data that could be used to inform vital rate selection (**http://demography-portal.ex.ac.uk/**) (Salguero-Gómez et al. 2014, 2016).
3. When possible, design experiments informed by observational data on the phenology of the study organism or on phenological shifts (e.g., Farzan & Yang 2018, Gezon et al. 2016, Rafferty & Ives 2011). In particular, community science data and museum and herbarium specimens are important but underutilized sources for documenting phenological shifts and pre-climate change, baseline phenology (for a discussion of the importance of baselines, see Kharouba & Wolkovich 2020).

We encourage researchers to statistically relate vital rates to phenology, as opposed to limiting analyses to changes in phenology through time and vital rates through time (or in response to climatic variation) separately. Only 57% of publications meeting our review criteria examined direct phenology–demography relationships (**Supplemental Table 1**). This issue is not simply restricted to studies that manipulate climate because the publications that did not examine a direct relationship comprised almost equal numbers of time series analyses and climate manipulations. Structural equation modeling or analysis of residuals are especially relevant here for separating direct effects of climate on vital rates from indirect effects on vital rates mediated by phenology.

Although there is no substitute for a long-term demographic study, especially when combined with experiments and population modeling, we can substantially advance our understanding of the demographic consequences of phenological shifts using the approaches outlined above.

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