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REVIEW

Linking phenological shifts to demographic change

Satu Ramula[1,2,*], Jacob Johansson[3], Andreas Lindén[1], Niclas Jonzén[3]

[1]Åbo Akademi University and Novia University of Applied Sciences, Aronia Coastal Zone Research Team, Raseborgsvägen 9, 10600 Ekenäs, Finland
[2]Department of Biology, Biodiversity Unit, Lund University, 223 62 Lund, Sweden
[3]Department of Biology, Theoretical Population Ecology and Evolution Group, Lund University, 223 62 Lund, Sweden

ABSTRACT: Climate-induced phenological shifts may have serious consequences for organisms and populations, but it is challenging to link such shifts to demographic change. Here, we present an overview of current methodological approaches for studying the demographic consequences of phenological shifts, based on a literature survey of 62 studies on diverse taxa. The majority of these studies (66%) were conducted using an approach that linked phenological shifts to demography through the measurement of vital rates (survival, growth, and fecundity). About 18% of the studies used a population-based approach that linked the phenological shifts to changes in population size, and 16% took a combined approach by considering changes in both vital rates and population size. Birds and mammals were overrepresented in studies of the demographic consequences of phenological shifts, compared to their occurrence in nature, while insects were heavily underrepresented. The effects of phenological shifts often varied according to the particular vital rate under consideration, in many cases even within a single species. In the few studies that examined changes in phenology together with both vital rate and population data, the changes in vital rates did not always predict changes in population size. To better understand the ultimate causes of population-level effects we argue that further study is needed on density-dependent aspects of population dynamics and on the sensitivity of population dynamics to perturbations in vital rates. We encourage researchers to observe multiple vital rates throughout organisms' life-cycles in order to enable more meaningful examination of the consequences of phenological shifts for population dynamics.

KEY WORDS: Climate change · Demography · Fitness · Phenology · Population dynamics · Population size · Timing · Vital rates

1. INTRODUCTION

A large number of studies have documented shifts in the timing of seasonal events in the life-cycles of various organisms; these shifts have been linked to ongoing climate change and have been recorded in taxa as disparate as insects, mushrooms, plants, and vertebrates (reviewed by e.g. Dunn 2004, Parmesan 2006, Feehan et al. 2009, Kauserud et al. 2012). The majority of studies have reported ongoing advances in phenology, such as an earlier onset of flowering or breeding (e.g. Fitter & Fitter 2002, Menzel et al. 2006, Ziello et al. 2012), but delays have also been described (e.g. Fitter & Fitter 2002, Barbraud & Weimerskirch 2006, Lane et al. 2012). The consequences of such phenological shifts for individuals may be highly variable. For example, advanced flowering may be beneficial for individual plants if it lengthens the growing season and thus leads to an increase in annual reproductive output or growth (Price & Waser 1998, Arft et al. 1999, Cleland et al. 2012, Natali et al. 2012). On the other hand, ad-

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*Corresponding author: sramula@abo.fi

vanced flowering may be detrimental to individuals if it results in a decline in reproductive output because of a scarcity of pollinators early in spring (Schemske et al. 1978), or because of an increase in the costs of reproduction and growth during the growing season (Scheepens & Stöcklin 2013). Alternatively, advanced phenology may simply lead to a shift in the timing of different seasonal events during organisms' life-cycles without any apparent increases or decreases in vital rates, such as survival, growth or fecundity (e.g. Guo et al. 2009). What, then, are the consequences of these phenological shifts for population dynamics?

To answer this question, researchers often attempt to link observed changes in vital rates to population dynamics, a common challenge in ecological studies regardless of whether these changes are caused by e.g. abiotic factors, pesticides, or herbivores (Ehrlén 2003, Stark & Banks 2003, Ådahl et al. 2006). It is common to make inferences about population dynamics by extrapolating in a stepwise fashion: first linking phenological shifts induced by environmental changes to changes in vital rates, and then subsequently linking these vital rates to changes in population size (e.g. Ozgul et al. 2010). Although this seems straightforward, several factors may complicate outcomes (e.g. Tuljapurkar & Haridas 2006). Changes in vital rates do not necessarily map linearly onto population dynamics and changes in population size (Caswell 2001). For example, a change in fecundity is likely to have a different impact on population dynamics than a change in adult survival (e.g. Ramula et al. 2008). Generally, the populations of long-lived organisms with high adult survival, such as ungulates, large mammals, perennial plants, and long-lived birds, tend to be most sensitive to changes in adult survival, whereas sensitivity to fecundity increases for short-lived and more fecund organisms with a rapid life-cycle such as rodents, small carnivores, and short-lived herbs (Silvertown et al. 1993, Heppell et al. 2000, Sæther & Bakke 2000, Oli & Dobson 2003, Ramula et al. 2008). The sensitivity of population dynamics to changes in fecundity also increases with an increase in population growth rate, with rapidly growing populations being more sensitive than declining or stable populations (Heppell et al. 2000, Ramula et al. 2008). Due to these differences in sensitivity, climate-induced phenological shifts can be expected to have different consequences across populations and taxa. In addition, density dependence may also influence the relative contribution of different vital rates to population dynamics (Ådahl et al. 2006, Reed et al. 2013a), and thus invalidate the general expectations described above. To date, it is not known how such potential discrepancies between changes in vital rates and changes in population size manifest themselves in phenological research.

In addition, the ability to draw general conclusions regarding the demographic consequences of phenological shifts may be compromised by bias towards particular taxa or a particular type of data. For example, little is known about how invertebrates respond to changes in phenology induced by climate change, as they are underrepresented in conservation studies (Clark & May 2002). Moreover, warming experiments tend to underestimate phenological shifts in plants (Wolkovich et al. 2012), which could possibly affect further estimates of the demographic consequences of shifts. It is essential to identify and address knowledge gaps in phenological studies in order to more fully understand the consequences of phenological shifts for population dynamics.

Here, we focus on phenological shifts induced by climate change, and present an overview of the methodological approaches that are used for studying the demographic consequences of such shifts across various taxa. We also provide recommendations to improve predictions of the consequences of phenological shifts for population dynamics. Specifically, we consider (1) the methodological approaches used to link phenological shifts to demographic change, and how the popularity of these approaches has changed over time; and (2) the extent to which studies of the consequences of phenological shifts for demography are biased towards particular taxa or a particular type of data (i.e. observational or experimental).

2. MATERIALS AND METHODS

2.1. Literature review

To synthesise studies and approaches that have been used to link phenological shifts to demography, we reviewed articles that examine the demographic consequences of phenological shifts. We denoted phenological shifts as changes in the timing of seasonal events during individuals' life-cycles regardless of the mechanism involved (phenotypic or genetic). We searched for articles based on their topic on the Web of Knowledge site on 10 October 2013 without restrictions on year of publication using the search terms (phenol* OR timing) AND (change OR increase OR decrease OR decline OR shift) AND (climate change OR climate warming) AND (population OR fitness) AND (consequence OR effect OR impact OR assess*) AND (demograph*). This search identified 434 articles. We assessed the suitability of each article based on the title and abstract, and sometimes also the text. Additional relevant publications were found in the reference lists of the screened articles, and were added to the pool of studies. We are aware that our literature search parameters were strict, and that using a different combination of search words would have produced a different set of articles. However, our aim was not to review all published studies, but to focus on different approaches that have been used to link phenology and demography. We therefore considered our data set to be a representative sample of published phenological studies and appropriate for our overview.

We included only studies that linked phenological shifts (i.e. statistically significant advances or delays in the life-cycle) to changes in the vital rates of individuals (survival, fecundity, growth or recruitment) and/or population size, density or population growth rate. Studies that merely reported phenological shifts without any further links to vital rates or population dynamics were excluded. Similarly, we also discarded studies that reported no significant changes in phenology during the observation period, in order to explicitly focus on cases with phenological shifts. We believe that omitting such studies does not qualitatively affect our conclusions regarding the different methods used for linking phenology to demography.

A total of 62 studies met our selection criteria (see Table S1 in the supplement at www.int-res.com/articles/suppl/c063p135_supp.pdf). For each study, we recorded the direction of the phenological shift (advanced or delayed) and the direction of the change in vital rates or population size (increased, decreased, unchanged) based on the statistics reported in the articles. For studies that reported changes in mortality, we included the result in the form of a survival rate. When a single study reported results for multiple species, we determined the direction of a change based on a single randomly chosen species that showed a statistically significant phenological shift. In the cases where contrasting effects were reported for different vital rates within the same species, we recorded the results for each vital rate separately (see Table S1). We also recorded the taxonomic group studied (e.g. bird, mammal, plant), study type (i.e. whether the study reported the vital rates of individuals and/or population dynamics), and whether the study was observational or experimental (i.e. involved experimentally manipulation of one or more climate variables). We chose to use a qualitative approach, because our aim was to reveal knowledge and methodological gaps in current phenological research rather than to quantify the effects of phenological shifts on vital rates and population sizes. Note that, for some taxa, such effects on vital rates have been partially investigated elsewhere (e.g. Arft et al. 1999, Cleland et al. 2012).

2.2. Analyses

Since we considered our data set to be a representative sample of studies that assess the demographic consequences of phenological shifts, we present the proportions of different types of studies (i.e. those that investigated vital rates, population data, or both) and the proportions of different types of data (observational vs. experimental) as point estimates, with 95% confidence intervals (CIs) estimated from the binomial distribution in R (function binom.test; R Development Core Team 2013).

To investigate whether the relative popularity of different types of studies has changed over time, we ran a generalised linear model (GLM with Wald's statistic) in R with log link and Poisson error, and accounted for overdispersion (quasi-Poisson family). The number of new studies for a given year was used as a response variable, study type (vital rate-based, population-based, or both) was used as a categorical explanatory variable, and the natural logarithm of the (cumulative) number of old studies was used as an offset variable in the model. Through testing the effect of study type versus an intercept-only model, we could explore the rate at which new articles using each study approach appeared.

To examine taxonomic bias in the studies, we compared the proportions of published studies across taxa with the expected proportions, based on the occurrence of the corresponding taxa in nature, using data for the numbers of described species from the IUCN (Hilton-Taylor et al. 2009). We plotted 95% CIs for the expected proportions under the assumption that the reviewed studies ($n = 62$) were a random binomially distributed variable with 62 trials.

3. RESULTS

3.1. Types of studies

Based on the 62 studies reviewed here, we identified 3 main approaches that were used to assess the demographic consequences of phenological shifts. (1) In a vital rate-based approach, phenological shifts

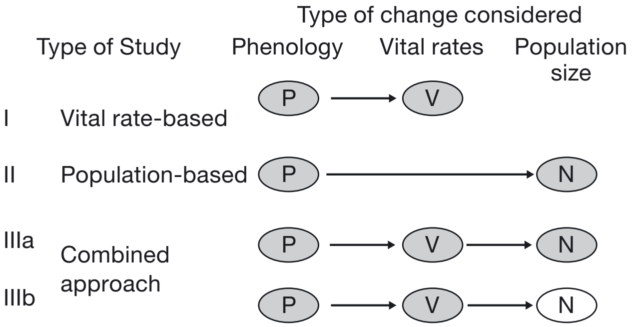

Fig. 1. The 3 types of studies identified that link phenology and demography: (I) A vital rate-based approach links phenological shifts (P) to demography through the measurement of vital rates (V). (II) A population-based approach links P to population size (N). A combined approach links P to V and N, using either (IIIa) counts of population densities or (IIIb) a demographic model to predict change in N. Filled ovals denote observed changes, while the open oval denotes a predicted change extrapolated from a demographic model

were linked to organisms' biology by examining the relationship between phenology and different vital rates (Fig. 1). However, only one-fifth of the studies (20 %, CI = 9–35 %) that used this approach observed multiple vital rates over an organism's entire lifecycle (Table S1). Most focused on a single or a few vital rate(s) at a particular life stage, such as fecundity (e.g. Alatalo & Totland 1997, Winkler et al. 2002, Zhang et al. 2009) or juvenile survival (e.g. Burthe et al. 2011, Moyes et al. 2011). The vital rate-based approach was the most popular of the 3 methodologies in the current data set (66 % of the studies, CI = 53–78 %; Fig. 2). (2) The second approach for linking phenological shifts to demography was a population-based approach (18 % of the 62 studies, CI = 9–30 %), in which the effects of phenological shifts on population demographics were assessed by examining the relationship between phenology and population size (Fig. 1). (3)The third approach (16 % of the 62 studies, CI = 8–28 %) combined the 2 previous approaches and examined the demographic consequences of phenological shifts both for vital rates and populations, hereafter referred to as the combined approach (Fig. 1). This approach included studies that investigated the effect of phenological shifts either directly on population size, using estimates of population density, or on population growth rate, using a demographic model (Fig. 1). Despite the fact that these different approaches were first applied at different times, we found that studies using each of the 3 approaches are accumulating at the same annual rate, about 17 % per year (Fig. 2; Wald's statistic = 3.26, df = 2, p = 0.196, GLM), which suggests that the relative popularity of study types is not changing.

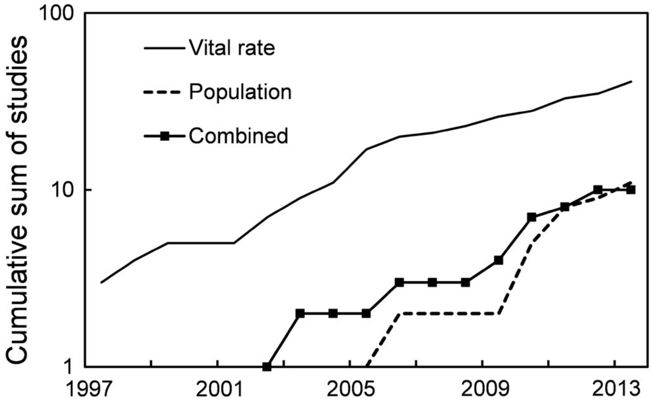

Fig. 2. The cumulative sum of reviewed studies (n = 62) that examined the demographic consequences of phenological shifts using different study approaches (vital rate-based, population-based, and combined). Note that the *y*-axis is on the log-scale

3.2. Consequences of phenological shifts for demography

When data from all 3 of the above-described study approaches were pooled, there was no apparent relationship between the direction of phenological shifts and effects on either vital rates or population size (Table S1). As an example, in studies that reported the consequences of phenological advances for vital rates (n = 45), 36 % (CI = 22–51 %) reported an increase (beneficial change) in all vital rates under consideration, while 64 % (CI = 47–88 %) reported a decrease or no change for at least one vital rate (Table S1). For example, a study of the grasshopper *Oedaleus asiaticus* found that advanced phenology was associated with an increase in survival, but had no effect on fecundity (Wu et al. 2012). Similarly, studies that considered population size showed mixed relationships between phenological shifts and population-level effects (Table S1). Phenological advances were associated with population growth in 33 % (CI = 13–59 %) andpopulation decline in 28 % (CI = 10–53 %) of the studies (n = 18), while there was no change in population size in 39 % (CI = 17–62 %) of these studies (Table S1). The consequences of phenological advances for population size sometimes varied in direction even within the same taxonomic group (Table S1).

Among the 62 studies reviewed here, 10 adopted the combined approach and assessed the consequences of phenological shifts for both vital rates and population sizes (Table 1). In 6 of these 10 studies,

Table 1. Summary results of studies of climate-induced phenological shifts that used the combined approach, which links phenological shifts (advances or delays) to changes in both vital rates (survival, fecundity, growth, recruitment) and population size. The direction of change, where measured, is shown as increased/advanced (+), decreased/delayed (−), or no change (0). Survival indicates either juvenile or adult survival per study (not both); fecundity represents either annual reproductive output or reproductive probability; population denotes observed or predicted change in population size. All studies that are included here were observational, with the exception of that by Griffith & Loik (2012), which used experimental data

Taxonomic group	Phenological shift	Vital rates				Population	Reference
		Survival	Fecundity	Growth	Recruitment		
Bird	+	+				+	Doxa et al. (2012)
Bird	+	−	−			−	Ludwig et al. (2006)
Bird	+		0			+	Wesolowski (2011)
Bird	+		+		0	0	Wilson & Arcese (2003)
Plant	+		+			+	Ehrlén & Münzbergová (2009)
Plant	−	−	0	−	−	−	Griffith & Loik (2010)
Plant	+	−	−		+	+	Hutchings (2010)
Plant[a]	+	0	0	0		0	Picó et al. (2002)
Mammal	−	−	−			−	Lane et al. (2012)
Mammal	+	+		+		+	Ozgul et al. (2010)

[a] The study considered multiple model scenarios, but the results here show only one scenario with advanced phenology

changes in all the vital rates under consideration were consistent with changes in population size (Table 1). However, in the remaining 4 studies, there were discrepancies between the effects on population size and at least one vital rate (Table 1). Two of these studies demonstrated positive effects of phenological shifts on population size, while reporting either no effect on fecundity (Wesolowski 2011), or negative effects on survival and fecundity (Hutchings 2010). The other 2 studies detected effects on either fecundity (Wilson & Arcese 2003) or population size (Griffith & Loik 2010), but not on both. In the cases in which effects on survival had been explored together with effects on population size, changes occurred in the same direction (i.e. both positive or both negative) in the majority of the studies (6 out of 7; Table 1). However, when effects on fecundity had been explored together with effects on population size, changes occurred in the same direction in only half of the studies (4 out of 8; Table 1).

3.3. Taxonomic and methodological bias in phenological studies

The phenological studies reviewed here were biased towards certain taxonomic groups (Fig. 3). Specifically, studies of birds and mammals were clearly overrepresented in relation to their species' proportions in nature, while studies of insects were heavily underrepresented (Fig. 3). Studies of plants were very slightly overrepresented in comparison with the 95% CI (Fig. 3). In contrast, the numbers of studies of fish and reptiles were proportionate with the relative abundance of these taxa in nature

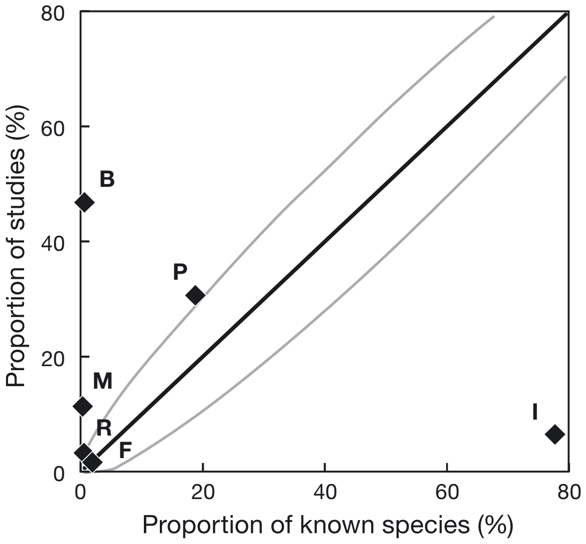

Fig. 3. The observed proportions of reviewed studies (n = 62) that examined the demographic consequences of phenological shifts across taxa (diamonds), plotted in relation to their expected proportions, i.e. the proportion of all known species in nature belonging to the corresponding taxa (black diagonal line). Grey lines indicate 95% CIs for the expected proportion. Taxonomic groups outside CIs and above the diagonal are overrepresented, while groups outside CIs and below the diagonal are underrepresented. B: birds; P: plants; M: mammals; R: reptiles; F: fish; I: insects

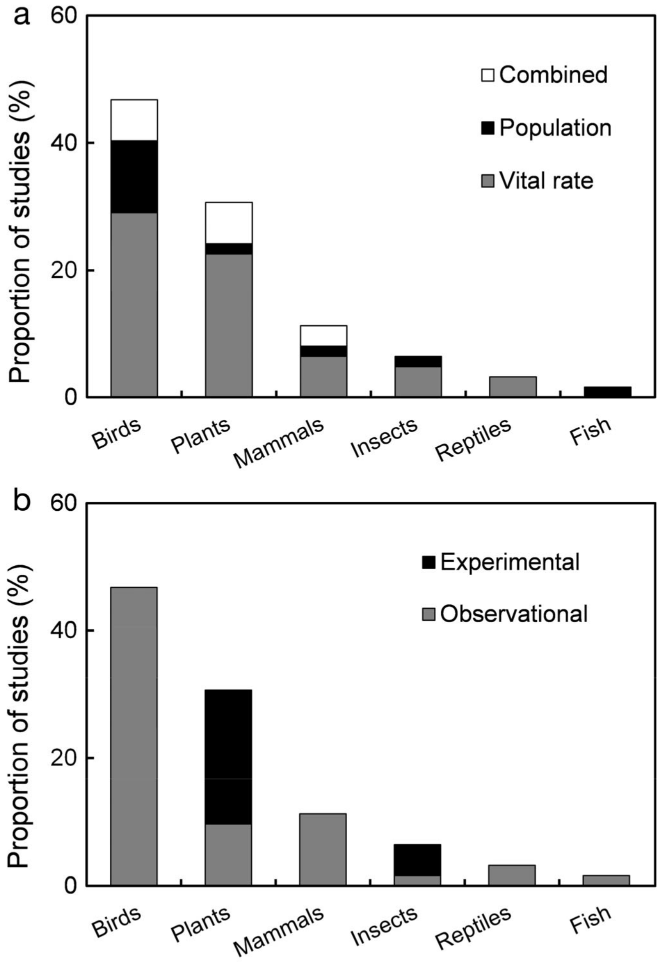

Fig. 4. The proportion of reviewed studies (n = 62) that focused on the demographic consequences of phenological shifts across taxa. Studies are separated by (a) the approach used (vital rate-based, population-based, or combined approach), and (b) the type of data collected (experimental or observational)

(Fig. 3). The vital rate-based approach was used for all taxonomic groups except for fish, and the population-based approach was applied across all taxa with the exception of reptiles (Fig. 4a). The combined approach which assessed the effects of phenological shifts on vital rates and population size was used to study birds, plants, and mammals (Fig. 4a).

Observational studies were more popular than experimental studies (74%, CI = 62–84% and 26%, CI = 16–38%, respectively), and were particularly common for birds, mammals, reptiles, and fish (Fig. 4b). Such studies frequently used a population-based approach (Table S1). By contrast, studies of plants and insects predominantly used experimental methods (Fig. 4b, Table S1).

4. DISCUSSION AND CONCLUSIONS

4.1. Linking phenological shifts to demographic change

Most studies reviewed here (66%) evaluated the consequences of phenological shifts for the vital rates of individuals (Fig. 2), sometimes reporting mixed outcomes. The advantage of studies that use this approach is that they can provide a detailed understanding of the consequences of phenological shifts for individuals through changes in their vital rates, particularly when experimental manipulations are used. However, these studies do not explicitly assess population-level impacts. As demonstrated here, changes in vital rates which are caused by phenological shifts do not necessarily reflect changes in population size (Table 1, Table S1). Therefore, future research should go beyond a focus on individuals and instead aim at a more comprehensive overview of potential consequences for population dynamics. More importantly, studies should focus on revealing the demographic mechanisms behind population-level patterns, because these mechanisms can be valuable for assessments and predictions of species abundances.

The population-based approach, which examines phenological shifts in relation to population trends, is explicitly focused on the consequences of such shifts for population size. However, this approach is usually based on correlations, making it difficult to draw rigorous conclusions about causation, as multiple factors may coincide with changes in population size (Cordes & Thompson 2013). For example, changes in bird population sizes, although correlated with phenological shifts, might be ultimately driven by the resources available at wintering sites rather than by climate *per se* (Knudsen et al. 2011). Unsurprisingly, the relationship between phenological advances and population size varied from positive to negative among the studies reviewed here. Moreover, the population-level approach requires records of annual population sizes or population growth rates over many years, which may limit its use for some organisms. As an example, for plants, demographic observations tend to cover just a few years (reviewed by Menges 2000). A better mechanistic understanding of the consequences of phenological shifts for population dynamics can be achieved using the combined approach, in which observed phenological shifts are linked to population dynamics through vital rates (Fig. 1) with the help of statistical methods and/or demographic models. The combined approach can be based on data from only a few years or up to decades (see, e.g. Griffith & Loik 2010, Ozgul et al. 2010, Wesolowski 2011) and is thus able to utilise and integrate different types of data.

Demographic models, such as structured population models, are particularly useful for addressing the links between changes in vital rates and population size (e.g. Jenouvrier & Visser 2011). For example, Ozgul et al. (2010) coupled phenological shifts with vital rates and population size in a study which used both demographic and statistical models. They determined that phenological shifts increased the population growth rate of the yellow-bellied marmot *Marmota flaviventris* because earlier emergence from hibernation in spring led to an increase in body mass during summer and, consequently, higher survival (Ozgul et al. 2010). Although demographic models are a standard and widely used tool in population ecology across a variety of taxa (e.g. Silvertown et al. 1993, Heppell et al. 2000, Sæther & Bakke 2000, Crone et al. 2011), they are less frequently applied in a phenological context (but see e.g. Griffith & Loik 2010, Ozgul et al. 2010). However, together with demographic analyses, demographic models can reveal patterns that are not necessarily detected by using standard statistical methods for individual vital rates (Ehrlén 2003, Ramula 2008).

4.2. Problems in extrapolating from individuals to populations

Studies that used the combined approach (i.e. examining changes in phenology, vital rates, and population size) showed that the consequences of phenological advances for population dynamics varied, from positive in certain cases to negative in others (Table 1). Among the studies reviewed here, the most noticeable mismatch between changes in vital rates and population size occurred in the perennial orchid *Ophrys sphegodes*, in which survival and flowering probability declined over time, while annual recruitment increased, leading to an increase in population size (Hutchings 2010 in Table 1). Why do phenological shifts not necessarily translate into changes in population size? At least 4 non-mutually exclusive factors might explain this discrepancy. (1) The population growth rate is more sensitive to changes in some vital rates than in others (Caswell 2001). Survival is known to be important for the population dynamics of long-lived organisms (Silvertown et al. 1993, Heppell et al. 2000, Sæther & Bakke 2000, Oli & Dobson 2003, Ramula et al. 2008) and therefore, we cannot necessarily expect a change in annual fecundity to result in a change in population size; multiple vital rates need to be examined simultaneously. In the present review, changes in survival were positively associated with changes in population size in 86 %, (CI = 42–97 %) of the studies (6 out of 7), while changes in fecundity and population size were positively associated in 50 %, (CI = 16–84 %) of the studies (4 out of 8; Table 1). This greater correspondence between survival and population size is probably due to the prevalence of longer-lived organisms in the data set, i.e. mammals, birds and perennial plants rather than insects (Fig. 4a). (2) The discrepancy between changes in vital rates and those in population size can be partly caused by mechanisms of density dependence. For example, Ådahl et al. (2006) showed theoretically that an increase in annual fecundity can result in a reduction in population size because of over-compensating density dependence (see also Åström et al. 1996). This necessitates an understanding of how vital rates vary with population density. Still, few of the 10 phenological studies that used the combined approach (Table 1) explicitly addressed the relationship between vital rates and population density (but see Lane et al. 2012). (3) Individuals interact with the individuals of other species and the consequences of phenological shifts for a population may depend on these interactions (e.g. the phenology or abundance of enemies or food sources) more than the absolute magnitude of the shifts (Visser 2013). (4) Reed et al. (2013b) argued that the demographic consequences of phenological shifts might be difficult to detect due to high environmental stochasticity. In other words, short-term measures of vital rates may not accurately capture the long-term effects of those rates, which might explain some of the contrasting responses between vital rates and population sizes in the studies reviewed here (Table 1). Of course, the 4 factors listed above are not limited to the field of phenology, but apply to any study that extrapolates from vital rates to population size.

An additional challenge in phenological studies is the degree of uncertainty and observational bias that may be contained in phenological data sets. Reported phenological shifts might be based on the most extreme observations, such as the first individuals to arrive or reproduce in populations. These observations do not necessarily describe the average phenology of individuals (Miller-Rushing et al. 2010) and can be sensitive to the number of sample sites (van Strien et al. 2008), thoroughness of sampling activity, and population size (Lindén 2011). For example, Tøttrup et al. (2006) found that the data based on the first arrivals of songbird populations in northern Europe suggested a stronger phenological advance than the data based on 50% of the individuals arriving (0.42 vs. 0.16 d yr^{-1}). It is also possible that reports of phenological shifts and their effects on vital rates may be based only on a small proportion of a population that has changed its phenology, despite the fact that the majority of individuals may not have done so. This might overestimate the total demographic consequences of phenological shifts for populations and species.

Overall, to quantitatively assess the demographic consequences of phenological shifts for populations and species abundances, for instance using a meta-analysis, more research is needed on the links between vital rates and population size, particularly for taxa that are currently underrepresented (e.g. insects). The fact that birds and mammals are overrepresented in phenological studies, while insects are underrepresented, is hardly surprising as a similar trend has been previously reported in conservation studies (Clark & May 2002). Such biases might reflect the taxonomic distribution of ecological research as a whole, as well as the general interests of citizen science.

4.3. Utilising different types of data

Our review revealed that the studies on phenological shifts and demography were primarily conducted based on observational data, probably because of the availability of long-term phenological and demographic records for vertebrates (mainly birds and mammals). We note that, although numerous studies have reported phenological shifts for plants (Fitter & Fitter 2002, Feehan et al. 2009), these shifts have not necessarily been linked to plant demography, as indicated by the lower relative frequency of plant studies included in this review compared to, for example, studies of birds (Fig. 4b). A clear benefit of observational studies is that they are based on actual environmental change(s). However, due to the correlative nature of observational studies, causalities between different variables are often difficult to demonstrate. Therefore, experimental studies conducted under controlled conditions may shed more light on the consequences of phenological shifts (Rutishauser et al. 2012). Interestingly, climate conditions were most often experimentally manipulated in studies of plants and insects (Fig. 4b), even though such manipulations could be possibly carried out also for other organisms, such as small mammals, reptiles, and fish. The drawbacks of experimental studies are their small spatial scale (Cleland et al. 2007, Forrest 2015) and the fact that they may not correctly predict the responses of organisms to real environmental change (Wolkovich et al. 2012, Forrest 2015), which makes generalisation challenging. To increase the realism of experimental studies, it is important to jointly manipulate multiple (preferably all) species in a community rather than only a single species (Forrest 2015). For example, an examination of the effects of climate-induced phenological shifts on a given plant species necessitates simultaneous manipulations of coexisting plant species, pollinators, and herbivores.

When no detailed demographic data of vital rates in relation to environmental change are available, a demographic model with simulated vital rates can still be used to explore alternative scenarios for population dynamics. Although this approach contains a lot of uncertainty, it is valuable particularly when the potential consequences of phenological shifts for population dynamics need to be assessed urgently. For example, by constructing hypothetical populations with different fruiting scenarios, Picó et al. (2002) discovered that an extended flowering and fruiting season would have only a minor effect on a Mediterranean perennial herb, *Lobularia maritima*, because its population growth rate is not sensitive to changes in fecundity.

4.4. Conclusions

One of the key concerns related to climate-induced phenological shifts is their consequences for wild populations. Our review revealed that phenological advances (or delays) do not consistently have the same consequences across taxa; however, there are some weaknesses and knowledge gaps in existing phenological research. Since the consequences of phenological shifts are typically assessed for a single or a few vital rates of individuals, this may not be enough to reveal the consequences for population size. Such an understanding is necessary to enable quantitative assessments of the consequences of phenological shifts for species abundances. Moreover, the existing literature is taxonomically biased towards terrestrial vertebrates, such as birds and mammals, while studies on the most abundant taxonomic group, insects, are underrepresented. A more systematic collection of demographic data, including multiple vital rates, would enable changes in individuals' life-cycles to be linked to populations and then to species abundances with the help of demographic models. Such systematic data collection is laborious, but we still encourage researchers to adopt this approach in phenological studies in order to better reveal the mechanisms at work, and to increase the predictive power of such research.

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