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Opinion

Dissecting impacts of phenological shifts for performance across biological scales

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Although phenological shifts in response to climate are often assumed to benefit species' performance and viability, phenology's role in allowing population persistence and mediating species-level responses in the face of climate change remain unclear. Here, we develop a framework to understand when and why phenological shifts at three biological scales will influence performance: individuals, populations, and macroecological patterns. Specifically, we highlight three underexplored assumptions: (i) individual variability in phenology does not affect population fitness; (ii) population growth rates are sensitive to vital rates affected by phenology; and (iii) phenology mediates species-level responses to climate change including patterns of extinction, invasion, and range shifts. We outline promising methods for understanding how phenological shifts will influence performance within and across biological scales.

Consequences of shifting phenology

Phenological shifts (i.e., phenological responsiveness) (see Glossary) under climate change can affect reproduction, population persistence, and species' viability [1]. However, we have scant and mixed evidence that changes in phenology contribute positively to population persistence under climate change [1], and even fewer studies investigate the consequences of **individual variability** in phenology or how phenological shifts affect **macroecological patterns**. Since documenting changes in phenology across populations and communities and examining phenology's potential benefits to population persistence and species success are common motivations for examining phenological shifts, we need to consider mechanisms underlying how phenological shifts might influence performance across biological scales.

Most empirical work has focused on population-level shifts in phenology and effects on **vital rates** [1] or abundance [2]. This focus leaves several gaps in our understanding. For example, within-population variation among individuals in their phenological responsiveness could have important consequences for population-level processes (e.g., synchrony and species interactions) and persistence in ways that are not captured by shifts in average population phenology. Additionally, few studies have investigated whether phenological shifts influence population growth (λ) or larger-scale patterns of extinction, invasibility, or range shifts. Here we dissect the general assumption that phenological shifts affect population and species success and outline three key aspects of phenological shifts that have received less attention in the existing literature: (i) individual variability in phenology [3]; (ii) population dynamics (e.g., **demographic compensation** or lags in vital rate responses [4,5]); and (iii) effects of phenology on macroecological patterns [6–8] (Figure 1).

An overview of phenology effects at three scales
Individual variation in phenology and fitness
Most investigations of phenological shifts under climate change have focused on mean phenology of a species or population [9], but shifts in phenological variance could also have strong effects on

Highlights
Phenological shifts are commonly assumed to benefit performance of individuals, populations, and species, but few studies have linked phenological shifts to performance across biological scales despite the relevance for conservation.

Doing so will require investigating several key understudied mechanisms in the phenology literature: the effect of shifting phenological variance among individuals, the demographic consequences of phenology for population persistence, and the role of phenology in driving species' extirpation or expansion.

Future studies should use individual-based data, demographic models, and comparative approaches that leverage long-term demographic and phenological datasets paired with relevant experimental manipulations.

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Underexplored aspects

a. Does variance in individual flowering phenology affect mean fitness or λ?
b. Is λ sensitive to phenology and/or vital rates affected by phenology?
c. Does compensation between vital rates limit impacts of phenology on λ?
d. Are there lags in phenological effects on vital rates?

a. Does abundance in natural populations correlate with estimated population growth rates?
b. Do extinction and spread correspond with differences in phenological plasticity?
c. Does greater phenological plasticity favor species within the same guild?
d. How do extinction debt or lags in invasion affect inference from demographic analyses?

Individual variation → **Population dynamics** → **Macroecological patterns**

Methods

Individual to population:
1. Gather detailed individual-level data on phenological shifts and vital rates and test for individual x environment interactions
2. Quantify multiple vital rates over multiple years
3. Relate vital rates to both mean and variance in phenology directly
4. Integral Projection Models incorporating means and variances in phenological responses
5. Perturbation analyses to identify important vital rates and quantify trait elasticities
6. Combine long-term demographic studies with experimental manipulations of phenology and climate

Population to macroecology:
1. Comparative studies (e.g., invasive vs. native or extant vs. extirpated) using historical, observational, and experimental approaches
2. Resurrection studies (ancestor vs. descendant or resurrect extirpated species)
3. Parameterize population models for invasive and extirpated species
4. Reverse-engineered population viability analyses
5. Incorporate phenological shifts into species distribution models
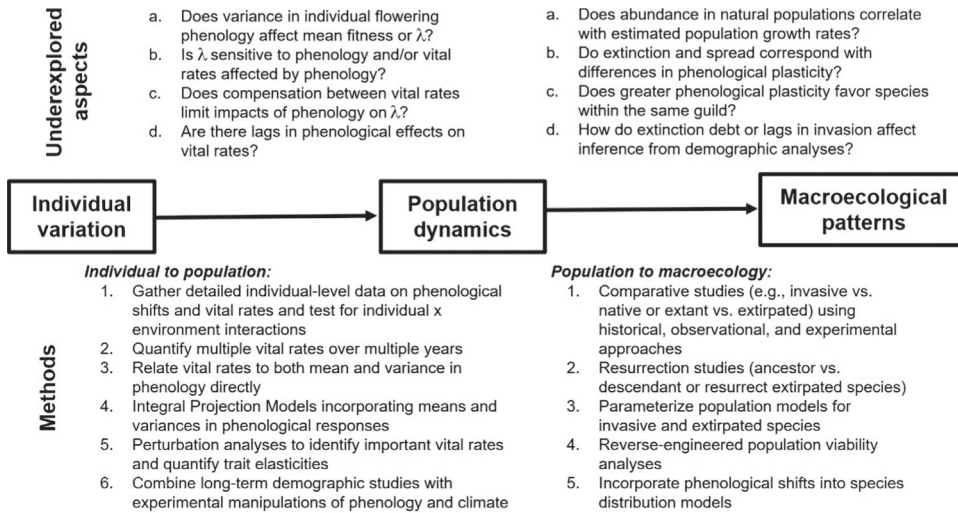
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Figure 1. Framework for the effect of phenological shifts on performance at three biological scales: individuals, populations, and macroecological patterns (i.e., invasion, extinction, and range shifts). Underexplored aspects of how phenological shifts affect performance at each scale are in lettered lists above the diagram and methods to address those aspects are in numbered lists below. Abbreviation: λ, population growth rates.

individual fitness and λ (Figure 2). Changes in variance of a trait can directly influence population mean fitness under **nonlinear selection** due to **Jensen's inequality** [10]. Greater variance decreases mean fitness under **concave selection** (Figure 2C) but increases mean fitness under **convex selection** (Figure 2D). **Phenological variability** (i.e., individual variability) among individuals can also indirectly affect absolute fitness (Figure 2E,F) by altering the availability of mates, patterns of gene flow, inbreeding, and overlap with food resources, predators, pathogens, and mutualists (reviewed in [11–13]). However, few studies have rigorously linked phenological (a) synchrony within or between species to changes in λ or persistence (reviewed in [1,13]).

Despite potentially strong direct and indirect effects on fitness, few studies have tested for changes in phenological variance with climate change. For short-lived species, phenological shifts are often at least partially due to **evolutionary change** [14] and strong selection should erode variance in phenology over time. In contrast, phenological shifts in longer-lived species largely reflect **phenotypic plasticity** [15], and thus changes in variance will depend on **individual × environment interactions (I×E)** [3] (Figure 2A,B). However, few study systems are able to quantify individual variability in phenological plasticity in wild populations, which requires repeated measurements of the same set of known individuals across a range of environmental conditions [3]. The best tests for I×E come from long-term vertebrate studies, which highlight several methodological and biological complexities. For example, the extent of I×E can differ dramatically among populations of a given species [16–18], choice of environmental driver [16,19], or the way residual error is modeled [20]. Some studies fail to detect I×E [21,22]. However, strong I×E increases variance in breeding phenology with warming in gulls (*Larus canus*; [23]), while in blue tits (*Cyanistes caeruleus ogliastrae*) I×E was associated with age such that middle-aged females are most plastic in their breeding phenology [24]. Alternatively, nonlinear effects of climate could impose hard limits on phenological responsiveness that reduce variance among individuals [25,26]. While I×E should occur in many populations due to genetic, environmental, and demographic effects on plasticity [3,27], it may be difficult to detect even with extensive long-term datasets and even more difficult to generalize across populations, much less species.

Glossary

Concave selection: nonlinear selection wherein quadratic regression coefficients are positive (i.e., populations are locally adapted).

Convex selection: nonlinear selection wherein quadratic regression coefficients are negative (i.e., populations are maladapted and the phenotype is far from the optimum).

Demographic compensation: opposing vital rate trends in response to environmental conditions, wherein the positive effects of one vital rate can potentially cancel out the negative effects of another.

Evolutionary change: genetic and phenotypic shift in the optimal trait value of a population that occurs when individuals with favorable traits in a particular environment have greater fitness than those with unfavorable traits.

Extinction debt: local extinction with a substantial delay wherein a species' abundance might still be relatively high prior to the extinction event.

Individual × environment interactions (I×E): when individuals within a population vary in their phenotypic responses to environmental conditions.

Integral Projection Model (IPM): size-structured population model that uses integrodifference equations to predict population growth in discrete time using continuous functions of size-dependent vital rates.

Jensen's inequality: the property of a function, $y = f(x)$, in which $\overline{y} \leq f(\overline{x})$ if the function is concave and $\overline{y} \geq f(\overline{x})$ if the function is convex. For example, if fitness (y) is a convex or concave function of a phenological trait (x), then the mean fitness ($\overline{y}$) will increase or decrease, respectively, with greater variance in the phenological trait (x).

Leading versus trailing edge population: populations residing at the current margin of a species' distribution that is predicted to become more climatically suitable under climate change, potentially facilitating range expansion (often more poleward or high elevation populations) versus populations residing at the current margin of a species' distribution that is predicted to become less climatically suitable under climate change, potentially leading to range contraction or extirpation (often more equatorial or low elevation populations).

Macroecological patterns: patterns of abundance, distribution, and diversity

Finally, the degree to which individuals express plastic versus genetic variation in phenology under climate change will have important consequences for the longer-term ability of populations to adapt to new climates [14]. Although phenotypic plasticity generally weakens the efficacy of selection, it also plays an important role in allowing populations to track adaptive phenotypes, and thus avoid extinction, long enough to enable evolutionary adaptation [28,29]. However, although phenological plasticity is often adaptive [14], the evidence that plasticity itself is under selection with climate change is surprisingly sparse [30].

Population dynamics

Phenology is often associated with vital rates. Most plant studies detect earlier leaf emergence and increased growth in response to warm temperatures or earlier snowmelt, and earlier reproductive phenology under climate change associated with increased fecundity (references in [1]; but see [31,32]). Shifting phenology can also expose plants to novel conditions, potentially counteracting any benefits: cold temperatures, frost damage [33], shorter photoperiods [34], drought and altered soil conditions [35,36], or altered species interactions (reviewed in [11,12]). In animals, advancing timing of emergence and reproduction can increase body weight and reproduction or result in an extra generation (references in [1]). The effects of earlier phenology on animal vital rates often depend not only on climate but on how food sources respond to climate [37,38]. For instance, warming temperatures advance caterpillar phenology twice as much as great tit (*Parus major*) laying dates [39].

Despite evidence for effects on vital rates, studies linking phenology to subsequent population dynamics are relatively rare (reviewed in [1]; Figure 2G,H). Among animals, multiple studies correlate shifts in phenology with population fitness: insufficient migration advancement correlates with decreased abundance in birds [40,41], earlier emergence increases λ in butterflies and yellow-bellied marmots (*Marmota flaviventris*) [42,43], and mismatched timing between snowshoe hare (*Lepus americanus*) molt and snowmelt increases predation and projected population declines [44]. Only one study to date has explicitly incorporated plant phenological shifts into projections of λ [4].

Macroecological patterns

Differences in species' ability to shift their phenology in response to novel environmental conditions may correlate with species success under climate change, including invasibility, high abundance, low extinction risk, and rapid range shifts (Figure 2I–L). First, invasive species are more likely to shift their phenology than native species [6,45–47]. However, 85% of studies examining phenological shifts in response to experimental warming are on only native species [48]; even fewer test for native versus invasive differences in phenological responses to other environmental factors. Second, if phenological shifts correlate with increasing abundance and invasiveness, then failures to shift phenology should be associated with decreasing abundance and extirpation [49]. Yet evidence for this is mixed, with phenological shifts correlated with increasing abundance [2,40,50], decreasing abundance [50,51], or no change [52]. Only one study [7] has linked phenological shifts to a reduced risk of local extinction; extirpated prairie species demonstrated idiosyncratic phenological responses in herbarium records, while closely-related extant species consistently advanced flowering in response to warmer spring temperatures. Comparisons of extirpated versus extant or native versus invasive species provide powerful tests of these hypotheses but remain rare [48]. Finally, phenological plasticity will likely influence range shifts under climate change (reviewed in [8]), but only one study to date, in partridge pea (*Chamaecrista fasciculata*), has found that phenology benefits persistence beyond the range edge [53].

(e.g., extinction, invasion, and range shifts).

Nonlinear selection: changes in not the mean (i.e., linear selection) but the distribution (i.e., variance, skew, or number of modes) of a quantitative trait. Nonlinear selection is measured using second-order polynomial regression and can be either be concave or convex (Figure 2).

Perturbation analyses: demographic analyses exploring how population growth rates (λ) respond to changes in vital rates. Types of perturbation analyses include (but are not limited to): (i) prospective analyses (sensitivity and elasticity), which test how much λ depends on vital rates independently of previous variability; (ii) retrospective analyses (Life Table Response Experiments), which decompose variance in λ as a function of variance in vital rates; and (iii) trait elasticities, which investigate effects of trait variation on vital rates by incorporating selection gradients across vital rates and their proportional contributions to λ.

Phenological shifts (i.e., phenological responsiveness): changes in the mean phenology (i.e., the timing of life-history events) of a population in response to an environmental cue.
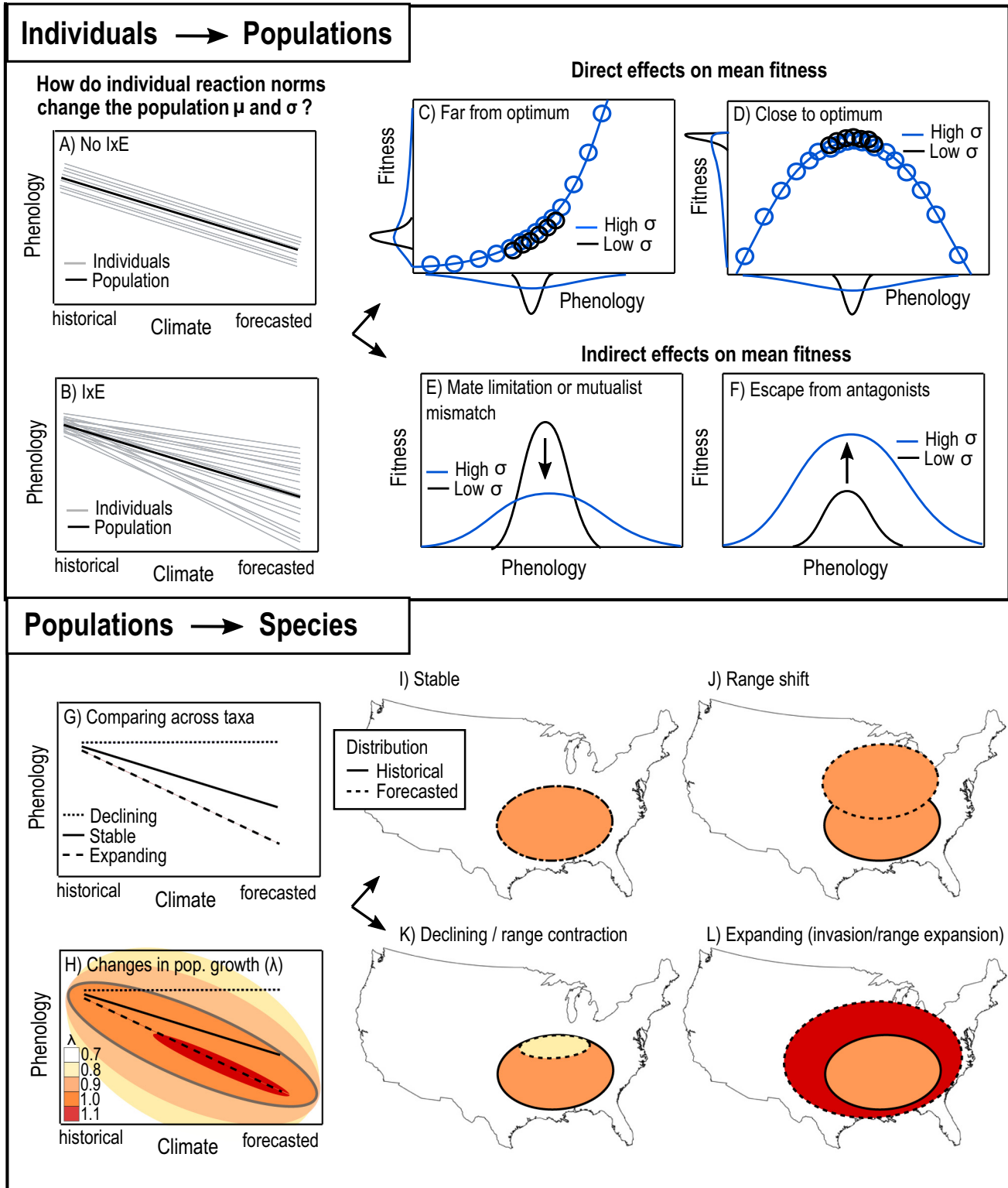
Phenological variability (i.e., individual variability): variation in phenology and/or phenological responses across individuals; the variance around a population's mean phenology.

Phenotypic plasticity: the ability to vary in phenotype under different environmental conditions.

Population viability analyses (PVA): demographic analysis predicting future extinction risk (or the probability that a population will persist for some time into the future).

Process-based species distribution models: mechanistic models predicted species' geographical occurrence using mathematical functions representing environmental effects on ecological processes (e.g., physiology and demography).

Vital rates: rates corresponding to particular life-stages or progression across an organism's development (e.g., birth/germination, survival, growth, reproduction, and senescence). Vital rates may depend on size (e.g., plant height or body size) or be classified into age-based classes.

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(See figure legend at the bottom of the next page.)

Linking phenology to performance across scales

Linking vital rates to population persistence

Given that phenology often influences individual vital rates, we need to account both for how individual variability and mean vital rates affect λ.

Individual variability

Many studies focus on shifts in mean phenology without considering the potential for changes in phenological variance to also influence population dynamics. Addressing this challenge requires (i) individual-level data on phenology across a range of environmental conditions; and (ii) experimental and statistical approaches to link changes in the distribution of phenology to mean vital rates and ultimately λ.

Most study systems lack repeated measurements of phenology for the same known individuals. Quantifying changes in phenological variance over time or with respect to climate is still possible in these systems by fitting models that allow for nonconstant variances, although attributing any change in variance to biological versus other causes may be difficult. Where feasible, we encourage the collection of repeated individual-level data on phenological responses, allowing rigorous tests for I×E with random regression models [3,54; Box 1A]. Although these models are data-hungry, simulation studies have yielded recommendations and statistical packages to optimize sampling and experimental designs [55,56].

If shifts in phenological variance are supported, several approaches can test for (in)direct effects of phenological variance on vital rates. The degree of nonlinearity in the relationship between phenology and a vital rate (e.g., nonlinear selection [57]; Box 1B) can indicate the potential for phenological variance to influence mean performance [58]. Demographic models such as **Integral Projection Models (IPMs)** offer a flexible approach to account for such effects by integrating among-individual trait variability and nonlinear vital rate functions into projections of λ [59]. IPMs have demonstrated strong effects of phenotypic variance on population dynamics for growth and body size [60,61]. Finally, experiments could manipulate variance in phenology to test for effects on mean fitness, while statistical approaches can be used to compare the explanatory power of phenology itself (i.e., absolute timing) versus phenological synchrony for variation in vital rates.

Mean vital rates

When phenological shifts affect vital rates, we often assume that λ will also be affected. However, several mechanisms can buffer λ from the effects of phenology.

Phenology's effects on a vital rate will only influence population persistence if λ is strongly sensitive to that vital rate (Box 2A). Additionally, many studies relate climate to changes in phenology

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Figure 2. Understudied effects linking individual phenological shifts to impacts on populations and species. (A) Climate change affects mean phenology (μ), but (B) variance in phenology (σ) may also shift if individuals differ in their plasticity to climate (individual environment interactions, or I×E). Changes in σ among individuals (circles; black = low versus blue = high variance) can directly alter the distribution and mean of fitness if selection is nonlinear: higher σ (C) increases mean fitness when populations are far from optimal phenology and (D) decreases it when populations are close to optimal phenology. Changes in σ can also indirectly alter the pattern of selection on phenology: higher σ could (E) reduce fitness by reducing synchrony, increasing inbreeding, or driving mismatches with mutualists or resources, or (F) increase fitness by allowing escape from antagonists. (G) Stable (solid line), declining (dotted line), and expanding (dashed line) populations or species might demonstrate different degrees of phenological plasticity (i.e., a shift in phenology between historical and forecasted climates). (H) Greater phenological plasticity in novel environments may increase population growth (λ; darker colors indicate higher λ). λ then influences macroecological patterns: orange indicates λ~1, so even as stable populations advance their phenology, λ remains consistent. In these cases, populations will be stable (I) or shift their ranges poleward to track appropriate temperatures (J). If static phenology correlates with λ<1 (yellow), species might experience range contraction or even extirpation (K). Finally, greater phenological plasticity might increase λ>1 (red), allowing invasion or range expansion (L). Abbreviation: λ, population growth rates.

Box 1. Case studies linking phenological shifts to individual-level consequences

(A) Individual variation in phenology

Variation among individuals in their phenological responsiveness to climate change could drive changes in both phenological means and variances. In common gulls (*Larus canus*; Figure IA), individual differences laying date responses to spring temperature (i.e., individual × environment interactions or I×E) result in greater variance in laying-date with warming (Figure IB,C) [23].
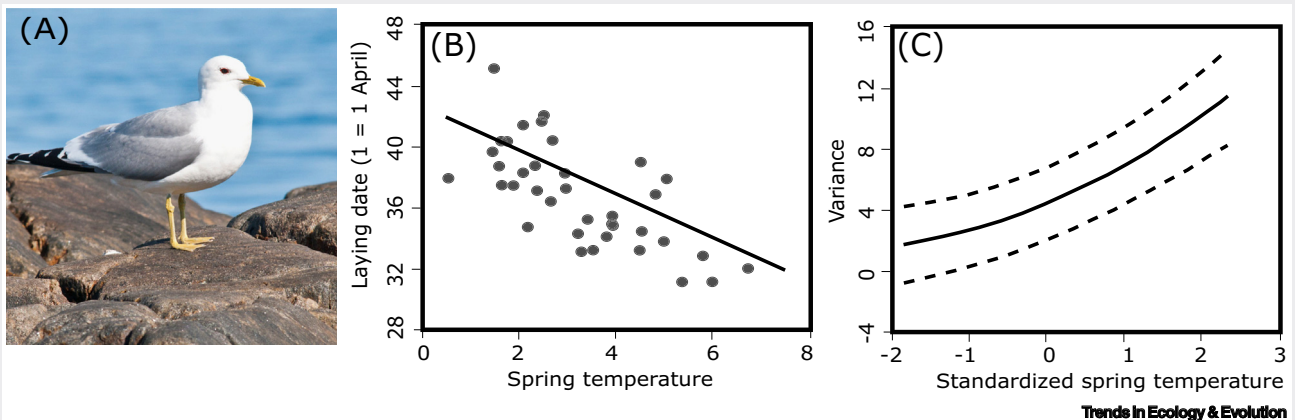
Figure I. Individual x environment interactions in common gulls. (A) *L. canus* (Creative Commons, licensed under CC BY-SA-NC). (B) Annual mean laying dates from 1968–2006 plotted against the annual mean temperature (°C) that had the highest correlation with mean laying date, fitted using a restricted maximum-likelihood (REML) mixed model. (C) Variance in laying date (and 95% confidence interval) due to non-genetic individual causes (I×E). Recreated from Figures 1 and 2A in [23].

(B) Nonlinear selection

The degree of nonlinearity in the relationship between phenology and a fitness component can indicate whether phenological variance will influence mean population performance. Lustenhouwer *et al.* (2018) [57] tested whether rapid evolution assists recent range expansion in a native annual, *Dittrichia graveolens* (Figure IIA), by examining the relationship between fitness and individual-level phenology using nonlinear fitness splines in a generalized additive model. Fitness declined as plants flowered later and earlier-flowering plants had a fitness advantage at range edges, suggesting that rapid evolution of earlier phenology could promote range expansion (Figure IIB).
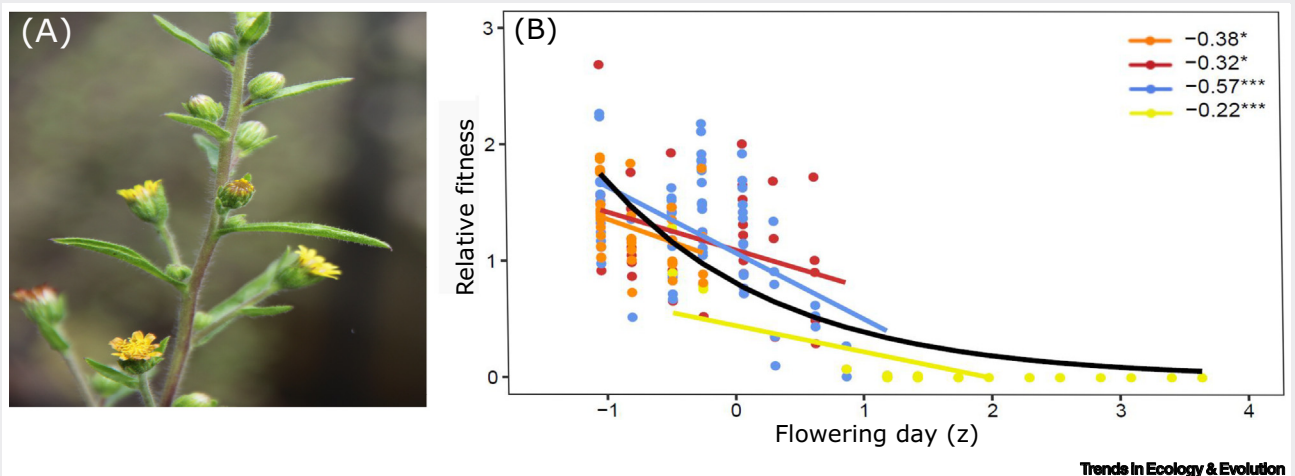

Figure II. Nonlinear selection in a range-expanding species. (A) *D. graveolens* (Credit: N. Lustenhouwer). (B) Selection on phenology in the Zurich common garden. Flowering day was standardized such that z = 0 corresponds to September 18th and a z-score of 1 = 12–13 days. The curved black line represents nonlinear fitness over all individuals, while straight lines represent regressions for plants from four regions across the range. Values are standardized selection differentials (regression slopes); ***$P < 0.001$, *$P < 0.05$. Recreated from Figure 3B in [57].

and vital rates separately; we join calls for researchers to relate climate-driven shifts in phenology to vital rates directly [1]. IPMs, which again require individual-level data, can integrate effects of environmental drivers and phenological shifts across vital rates into projections of λ. Importantly, **perturbation analyses** quantifying which vital rate(s) affect λ most strongly can be applied to IPMs [62]. Similarly, **trait elasticities** can estimate the sensitivity of λ to phenology by multiplying the sensitivity of vital rates to phenology by the sensitivity of λ to vital rates [63]. For example, flowering phenology has differing effects on λ in annual versus perennial monkeyflower (*Mimulus guttatus*) in part due to differences in the sensitivity of λ to reproductive vital rates [64].

Demographic compensation [5] can dampen overall effects of phenology on λ as organisms compensate for losses in one vital rate by allocating resources to another. Laying dates of great tits (*P. major*) are mismatched with caterpillar phenology under warmer springs, which reduces annual fledgling production but also relaxes competition, increasing survival and buffering

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Box 2. Case studies linking phenological shifts to population-level and macroecological consequences

(A) Population dynamics

Understanding how phenology influences population dynamics requires estimating the sensitivity of (i) individual vital rates to phenology; and (ii) of population growth rates (λ) to those vital rates. Earlier flowering does not influence λ in *Helianthella quinquinervis* (Figure IA) because snowmelt affects λ via decreased survival rather than reproductive losses (Figure IB) [4]. This study demonstrated that phenology can be an unreliable indicator of population persistence if λ is insensitive to the vital rate(s) influenced by phenology.
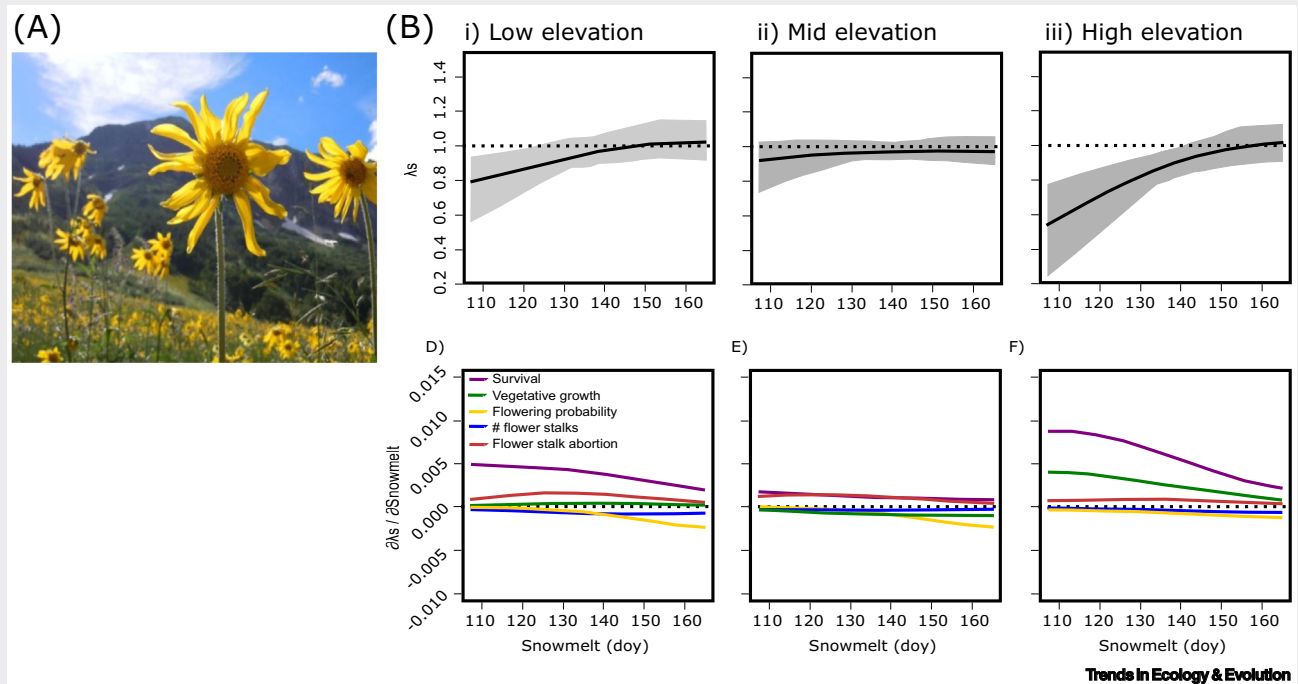

Figure I. Effects of phenology on population dynamics in a subalpine sunflower. (A) *H. quinquenervis* (Credit: A. Iler). (B) (Top) Stochastic population growth rates (λ$_s$) at three elevations and (bottom) the magnitude by which each vital rate influences the response of λ$_s$ to snowmelt date. Positive values indicate that the vital rate caused λ$_s$ to increase with later snowmelt. Recreated from Figure 5 in [4].

(B) Macroecological patterns

Comparative studies can link phenological patterns to macroecological patterns of invasion and extinction. Historical records and herbarium specimens reveal that extirpated versus extant species from Michigan prairies and savannas (Figure IIA) differ in their phenological responses to spring temperatures over the past century [7]. While extant species consistently advanced flowering, extirpated species demonstrated idiosyncratic responses to warmer spring temperatures, resulting in the

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appearance of no overall response to spring temperature among extirpated species (Figure IIB,C). This comparative approach provided the capacity to test the hypothesis that phenology not only influences abundance but local extinctions.
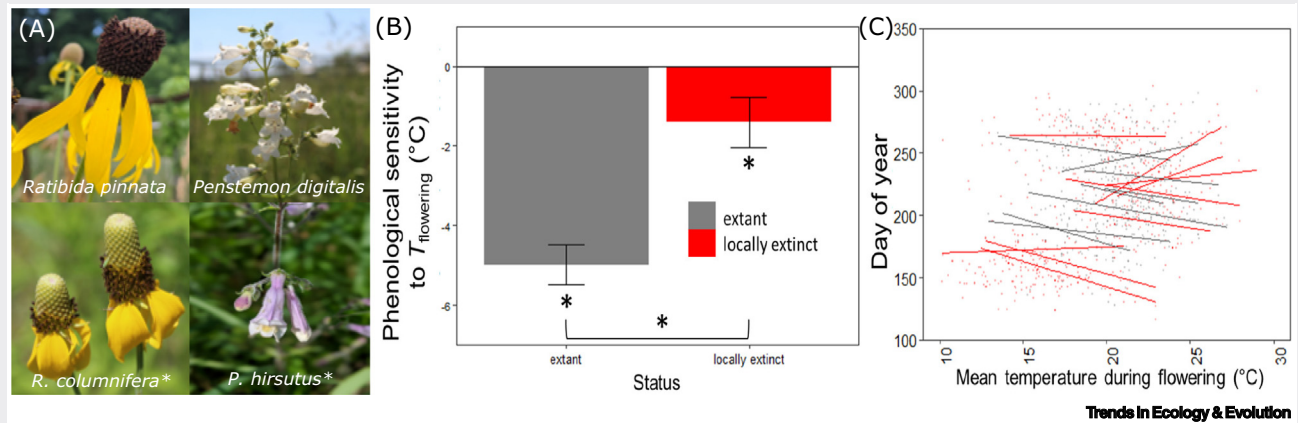

Figure II. Potential role of temperature-dependent phenology in extirpation. (A) Two confamiliar pairs (bottom*: extirpated species) (Credit: M. Zettlemoyer). (B) Left: Phenological sensitivity (days °C^{-1}) of locally extinct (red) versus extant (grey) species to mean temperatures experienced during flowering (T$_{flowering}$, °C). (C) Effect of T$_{flowering}$ on flowering phenology (day of year) of all species included in the study. Recreated from Figure 2 in [7]. Abbreviations: *P., Penstemon*; *R., Ratibida*.

populations from decline [39]. To test for demographic compensation, studies must integrate multiple vital rates rather than examining individual fitness components.

Finally, climate can have lagged effects on both phenology and vital rates [4,37,65]. Bud phenology in *Picea mariana* does not influence height because shoot extension depends on environmental conditions in the previous growing season [66]. We need to measure multiple vital rates and phenological responses across more than one year. Long-term demographic studies in natural populations could inform experimental climate manipulations quantifying phenological and demographic responses over multiple years.

Linking population dynamics to macroecological patterns

While some species exhibit limited phenological shifts, others respond strongly to climate change. Comparative approaches relating the magnitude of phenological shifts to species' guilds (e.g., invasive versus native, stable versus declining, or early- versus late-flowering), especially when made between closely-related species, can highlight how phenological differences between taxa drive responses to global change. Within a given guild, species with greater phenological plasticity are expected to be more successful. However, a recent meta-analysis found that 70% of experimental warming studies include a single guild [48]. Comparative observational and experimental studies will further our understanding of how phenological shifts affect patterns of invasion and extinction. For example, historical datasets and herbarium specimens provide valuable records of extirpated species' phenology that can test whether extirpated species demonstrated weaker phenological shifts than extant species (Box 2B). Researchers can also 'resurrect' populations of locally-extirpated species using seeds sourced from elsewhere in their range or from historical seed collections to test for shifts in phenology [67]. Such reintroductions, especially under relevant experimental manipulations, can link demographic and phenological responses to macroecological patterns across species.

Yet several processes could confound our ability to link effects of phenology on population dynamics to larger-scale patterns of invasion, extinction, or range shifts. While some invasive

species expand quickly, others spread slowly so λ is not high compared to residents [68]. Similarly, species en route to extirpation often demonstrate **extinction debt**. Considerable time might pass before declining populations disappear [69], which may confound results based on percent cover or abundance. Therefore, demographic models that quantify extinction risk or invasive species' spread by explicitly incorporating phenological shifts are particularly powerful. For example, experimental warming and artificially-advanced phenology increased annual (relative to biennial) reproduction and λ by 15% in *Carduus nutans*, indicating that compressed phenology under warming benefits λ in an invasive species [70]. **Population viability analyses (PVA)** can also be applied to extinct species using reference subspecies. A 'reverse-engineered' PVA examined drivers of extinction for cave bears, using demographic data on Marsicano brown bears, and revealed that climate change drove cave bears' dramatic population decline [71]. PVAs could incorporate phenology estimates from historical datasets for recently extinct species to test whether phenological shifts affect extinctions.

Lastly, empirical evidence for phenology's role in range shifts is limited [8]. Although a majority of studies detect adaptive phenological plasticity, few detect more plastic phenology in **leading edge populations** relative to more central or **trailing edge populations**. Fewer studies test whether phenology can promote not only expansion but persistence beyond contemporary range edges, which requires beyond-the-edge transplants. Finally, **process-based species distribution models** represent another powerful method for predicting range shifts, invasion, and extinction risk by parameterizing underlying mechanisms (e.g., effects of climate on functional traits like phenology that might affect demography and distributions) [72,73]. Models predicting species distributions should include not only local adaptation in phenological traits [74,75] but also phenological shifts in response to novel environments.

Concluding remarks

Phenological shifts may yet serve as an indicator of species' success under climate change. However, not only is there limited evidence that phenological shifts affect population persistence, but few studies link phenological shifts to performance across biological scales. Here we highlight three key aspects of phenological shifts that have received less attention: (i) individual variability in phenology; (ii) demographic mechanisms that might negate the effects of phenology on population dynamics; and (iii) effects of phenology on macroecology (see Outstanding questions). Incorporating phenological shifts, including changes in variability, into demographic and distribution models will be critical for predicting whether and how phenological shifts affect species performance under climate change.

Outstanding questions

Individual variation

- To what extent is the variation in phenology also shifting with climate change?

- How important are fitness effects of phenological variance (e.g., synchrony) relative to fitness effects of mean phenology for wild populations?

- Will genetic variation in phenological plasticity play an important role in adaptation to future climates?

Population dynamics

- How often does phenology truly affect population growth rates?

- What are the vital rate trade-offs (e.g., costs of reproduction or demographic compensation) associated with shifting phenology?

- Under what conditions might vital rates demonstrate lagged responses to climate or phenological shifts in the previous year?

Macroecological patterns

- Do invasive species consistently demonstrate greater phenological plasticity than native species?

- When do static phenology or inappropriate phenological responses correlate with population declines and extirpations?

- How do rapid evolution or plastic responses in phenology influence species' expansions (for both invasive and range-expanding native species)?

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