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Phenological shifts of native and invasive species under climate change: insights from the *Boechera–Lythrum* model

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Warmer and drier climates have shifted phenologies of many species. However, the magnitude and direction of phenological shifts vary widely among taxa, and it is often unclear when shifts are adaptive or how they affect long-term viability. Here, we model evolution of flowering phenology based on our long-term research of two species exhibiting opposite shifts in floral phenology: *Lythrum salicaria*, which is invasive in North America, and the sparse Rocky Mountain native *Boechera stricta*. Genetic constraints are similar in both species, but differences in the timing of environmental conditions that favour growth lead to opposite phenological shifts under climate change. As temperatures increase, selection is predicted to favour earlier flowering in native *B. stricta* while reducing population viability, even if populations adapt rapidly to changing environmental conditions. By contrast, warming is predicted to favour delayed flowering in both native and introduced *L. salicaria* populations while increasing long-term viability. Relaxed selection from natural enemies in invasive *L. salicaria* is predicted to have little effect on flowering time but a large effect on reproductive fitness. Our approach highlights the importance of understanding ecological and genetic constraints to predict the ecological consequences of evolutionary responses to climate change on contemporary timescales.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

1. Introduction

Species experiencing climate change, habitat modification, translocations and other forms of global change are exposed to a suite of biotic and abiotic variables that may differ in many ways from those experienced during their evolutionary history. This environmental novelty can be conceptualized as a shift in the adaptive landscape—a change in the strength and form of natural selection favouring a change in phenotype [1]. Rapid phenotypic changes have indeed been observed in many natural populations experiencing novel or changing environments, both as a result of phenotypic plasticity [2,3] and evolutionary change (e.g. [4–6]). However, it is less clear how often these plastic and genetic changes are adaptive. Understanding limits on plasticity and adaptive evolution is important for predicting long-term persistence of natural populations in human-altered environments.

Methods from evolutionary quantitative genetics provide empirical and theoretical tools for predicting plastic and evolutionary responses to natural selection. However, until recently (e.g. [4,7–9]), studies quantifying genetic variation and constraints, natural selection and evolutionary change have tended to focus on domesticated organisms and on native populations in relatively undisturbed habitats [10]. By contrast, much less is known about natural selection and limits

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on plasticity and adaptive evolution in species experiencing novel environments. Biological invasions provide opportunities to study rapid evolution in novel environments because comparisons can be made among populations with different demographic histories and mixed genetic backgrounds, evolving for decades or centuries in novel versus native environments [11]. Plants are particularly well-suited for experiments investigating natural selection and constraints on adaptive evolution because multiple genotypes of known pedigree can be reared under common growing conditions, allowing for careful measurements of phenotypic traits and fitness components across a range of natural environments.

Many traits affect survival and reproductive fitness in plants, but flowering phenology is particularly valuable for studying natural selection and constraints on adaptive evolution in novel and changing environments, for at least two reasons. First, natural variation in flowering phenology is often strongly correlated with plant fitness [12]; determining how the timing of key phenological events interacts with climatic and biotic factors to affect survival and reproduction is therefore of fundamental interest for understanding plant adaptation. Second, flowering phenology is determined by a number of growth and life-history characteristics, which can constrain an adaptive response to selection [13,14]. Given that flowering phenology is under strong natural selection, it is not surprising that many species exhibit phenological shifts that are correlated with climate change [15,16]. Phenological shifts in response to climate warming are not consistent across plant taxa, with some species flowering earlier while others flower later or do not change significantly over time [17,18]. These differences in the magnitude and direction of phenological shifts are phylogenetically correlated, suggesting a significant genetic basis [19,20]. However, the magnitude of phenological change also differs significantly between native and introduced species, suggesting an important role for short-term ecological and evolutionary processes [21]. The relative influence of ecological and genetic constraints, phenotypic plasticity and adaptive evolution remains unclear in most species [22–24].

Common garden experiments using known genotypes, when combined with field observations of natural populations, offer a robust approach to investigate the genetic and ecological basis of phenological variation and potential plastic and evolutionary responses to climate change. These approaches require large sample sizes for each species, rendering multi-species comparisons impractical. We here focus on two herbaceous plant species with opposite phenological shifts in response to warmer climates—the North American native *Boechera stricta* (Brassicaeae) and Eurasian *Lythrum salicaria* (Lythraceae). We chose these species for several reasons. First, we have collectively studied them for more than 40 years and in such time have developed a detailed knowledge of their ecology, growth, life history and genetics. Second, these species have been the focus of several field surveys and common-garden studies in field and greenhouse environments measuring phenotypic plasticity, genetic variation and fitness. Third, each species has shifted its phenology in response to natural selection in warmer versus colder climates, but the evolutionary response has been in opposite directions. Finally, we have studied *L. salicaria* in both its native and introduced range, allowing for contrasts between species with different life histories and phylogenetic backgrounds and between regions with different environments and among populations that differ in genetic and demographic histories. Here, we compare the similarities and differences between these species, and between native and introduced populations of *L. salicaria*. In doing so, we develop a model of phenological change in response to changes in season length that can more generally help to explain intra- and interspecific variation in observed phenological response to climate change.

2. *Boechera stricta*

Boechera stricta (Drummond's rockcress) is a perennial forb native to the Rocky Mountains of western North America, where it inhabits subalpine meadows, river edges and forest understories [25]. This species is broadly distributed across climatic gradients from Utah to Alaska, at elevations from 700 to 3900 m [26,27]. Populations of *B. stricta* in Montana, Idaho and Colorado are locally adapted in contemporary landscapes [25,28,29], and genetically based elevational clines are present in a number of functional traits including flowering phenology and size at flowering [30]. When grown in a common garden, plants from higher altitudes flower earlier, at a smaller size and for a shorter duration than genotypes from lower elevations [30]. Phylogeographic data suggest that this species expanded and contracted its range in response to glaciation during the Pleistocene [31,32]. Specifically, genetic diversity is greatest in areas thought to have had the lowest glacial coverage, with lower genetic diversity in other areas consistent with rapid population growth following more recent deglaciation in the Northern Rocky Mountains [31,32]. Together, these data suggest that *B. stricta* has persisted in the face of historical climate change through a combination of migration and evolution of local adaptation. However, modern rates of climate change are orders of magnitude above typical historic levels [33,34], so it is not yet clear how well this species will perform under future climate change scenarios.

Coincident with a history of migration and local adaptation, *B. stricta* is predominantly self-pollinating [6] and produces simple dehiscent fruits (siliques) lacking any obvious adaptations for long-distance dispersal. These factors should reduce opportunities for gene flow and limit the potential for evolutionary rescue of populations experiencing rapidly changing environments [35]. Populations of *B. stricta* therefore provide opportunities to test whether phenotypic plasticity and standing genetic variation in natural populations are sufficient to withstand current and predicted rates of climate change.

Like many plants, flowering phenology in *B. stricta* is highly plastic in response to environmental cues, including temperature, winter length and the timing of snowmelt [36,37]. These cues are predicted to change rapidly [38], which could disrupt phenology in *B. stricta* and other species that rely on multiple cues to elicit life-history transitions. Selection favours earlier flowering in natural populations of *B. stricta* [36,37], and this is also observed in other species that flower early in spring [12]. In many plant species, flowering time in natural populations is strongly correlated with local climatic factors and can contribute to local adaptation [39,40]. For example, in reciprocal transplant experiments with recombinant inbred *B. stricta* lines, a key flowering phenology quantitative trait locus (*nFT*) displayed fitness trade-offs consistent with local adaptation to latitude: the Montana allele at this locus had elevated fitness in Montana and depressed fitness in Colorado; similarly the Colorado allele showed home-site fitness advantage [41].

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Despite clear evidence for directional selection on flowering phenology [37], several factors could constrain adaptive responses to novel climatic regimes. For one, self-fertilization in species like *B. stricta* reduces the effective population size, which can limit standing genetic variation within local populations and slow the evolutionary response to selection. Song *et al*. [32] documented high inbreeding levels in *B. stricta*, with an average $F_{IS} = 0.89$ [31]. Flowering phenology is also constrained by genetic trade-offs with other traits such as size at flowering [36] and resistance to insect herbivory ($r_G = -0.74 \pm 0.15$; $p < 0.0001$, $N = 24$ maternal families, from data available in [28,30]). As in other systems [42], these genetic correlations could restrict adaptive responses to climate change.

Climate change has brought elevated temperatures and disrupted snow dynamics to high elevation ecosystems, altering plant physiology and phenology, and ultimately transforming community composition [30,43–45]. In geographical regions with extensive winter snowpack, plant communities often rely heavily on moisture from spring snowmelt [46]. Climate change is altering snowpack and snowmelt in two ways: (i) warming winter temperatures shift precipitation from snow to rain, reducing the total winter snow bank and (ii) warming spring temperatures melt the remaining snow earlier than in the historical records [38]. Increased evapotranspiration from warming in concert with declining snowpack significantly reduces water availability [28]. For example, snowmelt at the Rocky Mountain Biological Laboratory (RMBL; Gothic, Colorado, elevation: 2900 m) has been advancing by 7.4 days/decade since 1991 [47], similar to other observed changes in the region [38,48,49]. This advancement of the growing season is associated with earlier flowering in many species at RMBL [45], consistent with phenological changes in other systems (e.g. [50–52]). In *B. stricta*, the timing of first flowering advanced by 3.4 days/decade from 1973 to 2012; this shift in flowering phenology probably results from both phenotypic plasticity and adaptive evolution in response to earlier growing seasons [37]. Indeed, in field manipulations early snowmelt induces early flowering in *B. stricta*, but the plastic response appears to lag behind the rate of change in snowmelt date [30]. In particular, *B. stricta* plants flower only 0.33 days earlier per day of snowmelt advancement in the long-term record [37] and the field experiment [30]. This lag in the plastic response could arise from environmental constraints. For example, frost can damage sensitive floral buds when snow melts prematurely [53], reducing overall fitness and delaying flowering (relative to snowmelt date). To initiate reproduction, plants integrate signals across multiple flowering time pathways that incorporate environmental cues (e.g. photoperiod, temperature and moisture) [13,54,55]. In years of early snowmelt, plants might not accumulate adequate photoperiod or temperature cues to keep pace perfectly with changing snow dynamics; thus, climate change may constrain growth and reproduction because environmental cues are changing at different rates.

In addition to frost damage and genetic constraints, other ecological constraints could limit adaptive responses to climate change. Insect herbivores in particular impose strong selection on *B. stricta* [56], and the rate of damage from herbivores can vary geographically [28]. In Colorado, across years and in common gardens in high and low elevation sites, resistance to insect herbivory declines with source elevation of transplanted genotypes [28]. This robust, consistent pattern reveals that high elevation genotypes are more vulnerable to herbivory. We hypothesize that variation in resistance to herbivores could result from selection for increased growth rates at higher elevations to complete reproduction within a shorter growing season. Traits that enable rapid growth and reproduction likely increase vulnerability to herbivory, such as high foliar nitrogen, thinner leaves and greater leaf water content [30]. Insect herbivores could respond more rapidly than plants to climate change as a result of faster *in situ* population growth rates and migration to more suitable locations at higher elevation [57]. In that case, increasing herbivory could place high elevation populations at risk of decline if they cannot adapt or adjust plastically to new herbivore stresses, and if limited gene flow does not introduce low elevation, herbivore-resistant alleles into high elevation populations.

3. *Lythrum salicaria*

The perennial herb *Lythrum salicaria* (purple loosestrife) is found in a variety of wetland habitats throughout Eurasia and North America. Its native distribution extends from southern and central Europe to northern Scandinavia and east through Siberia; it has established throughout the USA and Canada since its initial introduction to North America approximately 200 years ago [58–60]. One or several above-ground shoots are produced by each plant. They develop from winter buds formed on the rootstock in the previous year, and emerge above-ground in May–June in Sweden. Flowering begins in mid-to-late summer with purple-red flowers that are visited primarily by bumblebees, but also by honeybees, syrphid flies and lepidopterans [61,62]. In Sweden and eastern North America, *L. salicaria* flowers for six to eight weeks in July and August and the seeds mature six to eight weeks after flowering [63,64].

Individuals are self-incompatible and there are three style morphs of *L. salicaria*, which differ in the relative positioning of stigma and anthers in the flowers. As a result, full seed set is only achieved if pollen is transferred between morphs and from an anther level that corresponds to the position of the receiving stigma, resulting in disassortative mating among morphs [65,66]. Despite this limitation on seed production, the showy inflorescences of *L. salicaria* are attractive to a wide range of pollinator taxa and as a result pollen limitation is rare except in small populations with low pollinator activity and reduced abundance of compatible mates [61]. There is some evidence that pollen limitation changes seasonally: seed production is limited early in the growing season, increases as more compatible mates begin flowering, and declines later in the season as temperatures fall and pollinator activity declines [67]. Warmer temperatures are therefore expected to increase the duration of pollinator activity, favouring individuals with longer flower duration.

In Sweden, *L. salicaria* is mainly attacked by the specialist leaf beetles *Galerucella pusilla* and *G. calmariensis* (Coleoptera: Chrysomelidae), and a seed predator, the weevil *Nanophyes marmoratus* Goeze (Coleoptera: Curculionidae). Herbivory by *G. calmariensis* and *G. pusilla* can cause extensive damage to the host plant in the native range [68,69], and in the introduced range where the beetles have been widely introduced as biological control agents [70]. The number of herbivore species decrease with increasing latitude in the native range [71], but it is not clear if the same is true in North America. More generally, evolutionary responses of *L. salicaria* to the introduced specialist herbivores are not well studied, but this could be a

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good system for examining coevolutionary dynamics in an eco-evolutionary framework.

(a) Evidence for a genetic trade-off between flowering time and size

As a consequence of poor cold tolerance and reliance on pollinators, short growing seasons should favour rapid growth early in the season and early initiation and rapid completion of reproduction in *L. salicaria*. Indeed, common-garden studies of several late-season perennial herbs have documented heritable latitudinal clines in phenological traits that are consistent with local adaptation to different season lengths [63,72,73]. In *L. salicaria* in particular, early vegetative growth rates are positively correlated with latitude of origin, whereas flowering start, duration of flowering and size at the end of the growing season are negatively related to latitude of origin in both the native [63] and introduced populations [64]. Early flowering reduces the time available for vegetative growth and accumulation of resources before reproduction, resulting in the classic life-history trade-off between size and timing of reproduction. In *L. salicaria*, early flowering is indeed associated with reduced size at onset of flowering in genotypes sampled in both the native [74], and introduced range [75]. Northern genotypes are smaller than southern genotypes when raised in common-garden experiments and many of them do not flower in their first year [63,76]. Significant phenotypic plasticity in flowering time has been observed in common-garden experiments in glasshouse versus field environments [64,74,77] and at different latitudes [10], however, the rank-order of flowering times among genotypes is highly conserved [77]. In a common-garden experiment conducted in northern Sweden, local populations had a clear fitness advantage with strong selection against populations from central and southern Europe [74]. Similarly, reciprocal transplant experiments demonstrated that populations are locally adapted along a climatic gradient in eastern North America [10]. Local adaptation along a latitudinal gradient in season length evolved quickly in North America (less than 50 years) as a consequence of (i) colder climates imposing stronger directional selection for earlier flowering and (ii) a trade-off between size at flowering and time to first flower, limiting seed production in early flowering genotypes [10]. Warmer temperatures are predicted to increase the length of the growing season, thereby favouring the evolution of later-flowering genotypes that grow larger and produce more seeds.

(b) Interactions with specialist herbivores with regards to size and phenology

Specialist insect herbivores strongly affect the demographic structure and seed production of *L. salicaria* populations in its native range [68,69,78]. Both resistance and tolerance to herbivore damage vary with latitude, which may be related both to divergent selection on resistance traits as well as pleiotropic effects of growth and phenology [76]. The number of herbivore species [71], the intensity of damage and the negative effects of herbivory on plant fitness tend to decrease with latitude in Sweden [68,76]. In common-garden experiments, the main herbivores (*G. calmariensis* and *G. pusilla*) have been found to preferentially feed on genotypes from northern populations, even though they are smaller than southern genotypes [76]. This is consistent with stronger selection for increased resistance in the south, where the risk and negative effects of damage are larger. The early developing northern populations may also be more attractive to insect herbivores, because they are larger at the time when herbivores emerge in late spring to early summer, and because their rapid early growth may be associated with higher leaf nutrient concentrations. Differences in vegetative phenology may explain why tolerance to damage increases with latitude. When insect herbivores emerge, northern populations have completed a larger proportion of their total growth compared with southern populations and opportunity costs caused by damage to leaves and meristems are thus not as large [76]. It is therefore likely that similar clines in herbivory and tolerance exist in the introduced range, but to our knowledge this has not been tested explicitly. A warming climate is expected to result in selection for increased resistance to herbivory, both because it will likely be associated with increased herbivory [76], and because a longer period of vegetative growth should result in stronger negative effects of a given level of damage [68,76].

4. Model of phenological response to climate change

Using methods from evolutionary quantitative genetics, we have studied native populations of *L. salicaria* in Europe, introduced populations in North America, and native populations of *B. stricta* from North America. Our study species and populations encompass a broad range of demographic histories, mating systems, growth forms, life histories, phenologies and biotic/abiotic environments. Despite this variation, our research on phenological and life-history traits reveals striking similarities in plasticity, selection gradients and genetic constraints in both species and in populations of *L. salicaria* on two continents (table 1). Below we implement a simple resource allocation model to evaluate how relatively small changes in moisture, temperature and herbivory can lead to large changes in growth, phenology and reproductive fitness. We use our knowledge of *B. stricta* and *L. salicaria* to parametrize the model, and explain how our approach can be generalized to a wide range of study systems.

As noted in our review above, selection gradients of *B. stricta* and *L. salicaria* confirm that both species are under strong directional selection to grow larger and reduce herbivory. However, two core trade-offs constrain adaptive evolution in both species. First, vegetative growth halts during reproduction and this in turn limits resources available for reproduction. In *B. stricta*, rosette growth ends when bolting is initiated, whereas in *L. salicaria* the apical meristem stops producing new leaves when flowering production is initiated. More generally, a switch from producing resource gathering structures (e.g. roots and leaves) to resource sinks (i.e. seeds and tubers) may vary across species, but these structures nonetheless compete for available resources. The second core trade-off occurs between growth rate and susceptibility to herbivory. As summarized above, there is evidence that genotypes with faster growth rates experience more damage from herbivores. This is particularly important for populations experiencing shorter growing seasons, which could otherwise increase growth rates to flower earlier at a larger size. Moreover, we assume there is an upper limit on growth rate that is determined by physiological factors such as net photosynthesis rates and enzyme kinetics. As a result, genotypes that are under

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Table 1. Summary of key ecological and evolutionary parameters in native *Boechera stricta* populations, and populations of *Lythrum salicaria* in Europe (native) and North America (introduced).

	B. stricta	*L. salicaria* (native)	*L. salicaria* (introduced)
genetic correlations (trade-offs)			
growth rate versus herbivore defence	−	−	−[a]
size versus time to reproduction	+	+	+
selection gradients			
size at first flower	+	+	+
herbivore defence	+	+	+
ecological factors affecting seed production			
pollinator activity	0	+	+
snowpack (moisture)	+	0	0
herbivory	high	high	low[a]

[a]Predicted, but not empirically tested.

stronger selection to flower earlier cannot simply evolve faster growth rates.

We modelled how climate change affects reproductive fitness and the evolution of phenology using a variant of the classic resource allocation models (reviewed in [79]), which has been used to model reproductive timing in plants (e.g. [80]) and animals (e.g. [81]). Details of our model and its parameters are provided as the electronic supplementary material and briefly summarized here. Growth initially follows an exponential curve with a base vegetative growth rate (r) from an initial seed size (V_0) until a threshold size at reproduction (θ). At the time of reproductive maturity, vegetative size remains constant and seed production increases following a saturation curve with an upper limit determined by θ. The optimum size at reproduction for a given growing season is a balance of time between adding additional vegetative growth and maximizing seed production before the end of the growing season.

The growing season is defined in our model as the period of time over which air temperature and soil moisture are above minimum threshold values that differ for each species (*B. stricta*: 8°C, 10% VWC; *L. salicaria* 12°C, 18% VWC). Temperature and moisture are modelled separately for each habitat, using sine functions to account for seasonal fluctuations in moisture and temperature, with values chosen to approximate high and low altitude populations of *B. stricta* or high and low latitude populations of *L. salicaria* (figure 1). In alpine habitats, *B. stricta* experiences cooler temperatures on average, but also lower moisture levels in mid to late summer (figure 1*a*). By contrast, *L. salicaria* typically occupies wetland and shore habitats at lower altitudes where temperatures are warmer and moisture generally is not limited throughout the season (figure 1*b*). We then consider a trend of anthropogenic climate forcing that increases temperature by up to 5°C and decreases moisture by up to 40% (figure 1*c*,*d*), similar to moving from higher to lower altitudes or latitudes and consistent with a range of climate warming scenarios [38,82]. Minimum temperature and moisture values for the two species therefore determine the growing season in each environment (shaded bars in figure 1).

In order to explore the effect of climate variation on plastic and genetic changes in phenology, we assume that each species begins growth as soon as conditions are favourable and flowers at the time that will maximize reproductive fitness at the end of the growing season (see the electronic supplementary material). The plastic response of flowering time in our model is determined by a shift in the initiation of growth and development in response to altered climate conditions. The plastic response is adaptive if it tracks the onset of the growing season. Therefore, the plastic response is equal in magnitude and direction to the shift in the onset of the growing season. By contrast, the optimum genetic response of flowering time is proportional to the duration, rather than onset, of the growing season in our model. This is because the threshold size at flowering is an evolvable and canalized trait in the model. The time from initiation of growth to onset of flowering determines the Julian day of first flower, and ultimately the total reproductive output at the end of the growing season.

Finally, we consider the effect of herbivory on flowering time and reproductive output. We assume that the loss of vegetative and reproductive growth to herbivores (L) is proportional, ranging from 0 (no herbivory) to 1 (complete herbivory). Furthermore, an individual genotype can reduce its herbivore load by reallocating resources from growth to defence. As the intensity of herbivory (h) increases (e.g. a larger herbivore population), more resources must be reallocated to maintain the same level of protection (1-L), reducing the relative growth rate. We assume that h and L are constant throughout the growing season, but we consider the effects of reduced herbivory in introduced populations of *L. salicaria* in two ways. First, we consider a reduction in the overall intensity of herbivory (h); this reduces the loss to herbivory (L) for the same level of investment in defence (*ecological release model*). Second, we consider the effect of herbivory as a relaxed constraint by allowing a small increase in relative growth rate (r); this would occur if defences were less costly, allowing for an increase in growth and reproduction (*relaxed constraint model*).

5. Model results and discussion

Initial temperature and moisture profiles of *B. stricta* and *L. salicaria* (figure 1*a*,*b*) ultimately determine how the timing

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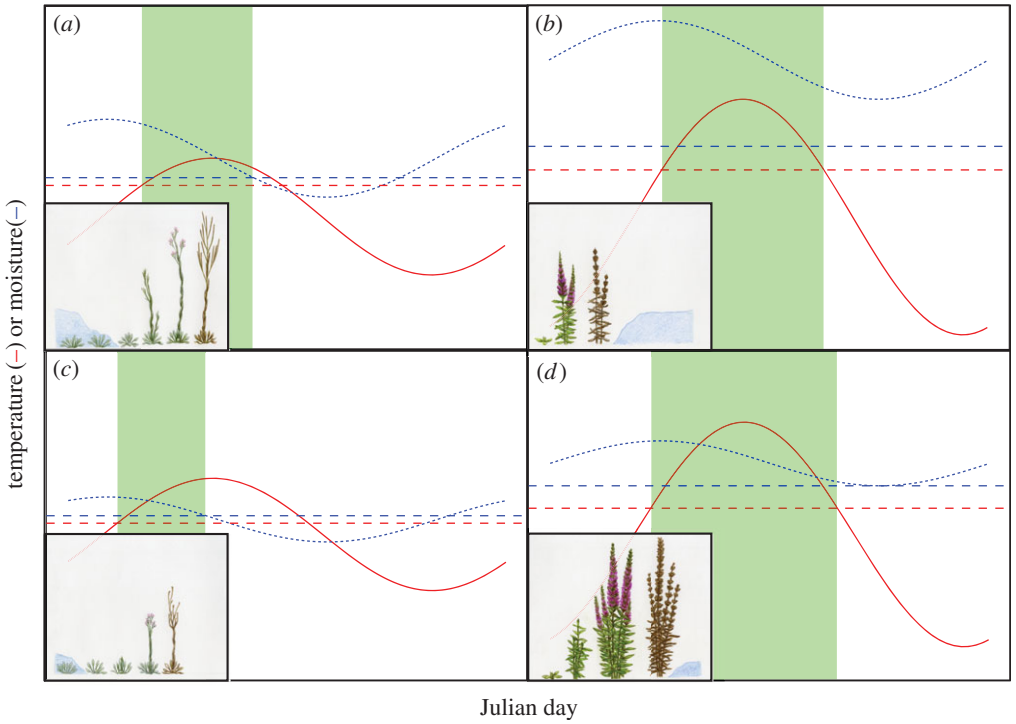

Figure 1. Model of temperature (solid red curve) and moisture (dotted blue curve) effects on season length (green shaded area) and growth and phenology (insets) of two species: (*a*,*c*) *Boechera stricta*, which is native to North America; (*b*,*d*) the North American invasive species *Lythrum salicaria*. Each species has minimum temperature (red dashed line) and moisture (blue dashed line) thresholds necessary for growth and reproduction. (*a*) *Boechera stricta* is a subalpine plant that overwinters as a rosette and flowers early in the spring following snowmelt, completing reproduction before warm summer temperatures limit available moisture. (*c*) As the climate warms, the growing season begins sooner but also lasts for a shorter duration as lower snowpack and higher temperatures reduce soil moisture, especially in hot and dry subalpine elevations. The adaptive plastic response and genetic responses both act to flower at an earlier Julian date (*b*). By contrast, *L. salicaria* typically occupies habitats where moisture is not limiting, and it has evolved to flower later in the growing season before pollinators and low temperatures limit reproduction. (*d*) Warmer temperatures increase both the onset and the duration of the growing season, resulting in an adaptive plastic shift to begin to develop earlier but an adaptive genetic response to flower later at a larger size, resulting in a net delay in the Julian date of first flower.

of favourable growing conditions change with rising temperature and lower moisture. Increasing temperatures shift the beginning of the growing season (*B*) to earlier Julian days in both species (figure 2*a*). By contrast, reduced moisture availability decreases the season length of *B. stricta* but does not affect the season length of *L. salicaria* because moisture levels remain above the threshold necessary for growth and reproduction (figure 1*c*,*d*). Length of the growing season determines the optimum size at flowering, which combines with the onset of favourable growing conditions to cause earlier flowering dates in *B. stricta* but delayed flowering dates in *L. salicaria* (figure 2*b*). Thus, despite constraints (table 1), initial environmental differences between *B. stricta* and *L. salicaria* are predicted to cause opposite phenological shifts in response to a warming climate.

Changes in the length of the growing season determine the optimum flowering time and the threshold size of reproduction, which ultimately determine total seed production in our model (figure 2*c*). Importantly, these changes are all adaptive in the model because the flowering time and threshold size in each species tracks its optimum. We therefore assume that evolution is immediate and unimpeded by genetic drift, gene flow or a lack of standing genetic variation. These factors can constrain evolutionary responses to selection (e.g. [83–85]) and may favour invasive species over native species with sparse populations [11]. Thus, incorporating delayed evolutionary responses would potentially slow the evolution of flowering time and reduce reproductive fitness in native populations more than introduced populations. However, even under our ideal assumption of no evolutionary time lag, seed production in *B. stricta* is predicted to decline with warming temperatures. This demonstrates how life-history trade-offs can reduce population viability, even as a species adapts rapidly in response to climate change. For this reason, the rate of phenotypic or evolutionary change in response to climate change may not be a good predictor of long-term viability. Instead, empirical studies should quantify fitness components under current and projected climates to model population growth rates.

Escape from natural enemies has no effect on flowering time under the ecological release model, and delays flowering time only slightly under the relaxed constraint model (figure 2*b*). In the ecological release model, herbivory does not affect flowering time, because it acts like a constant tax on growth throughout, reducing reproductive output (figure 2*c*) but not affecting the optimal flowering time or threshold size. In the relaxed constraint model, flowering time is delayed only slightly despite a higher relative growth rate. This slight delay allows a much larger threshold size at flowering, and therefore an exponentially higher reproductive output (figure 2*c*). Seasonal variation in the intensity of herbivory could shift the optimal flowering time in both models, but the magnitude and direction of the shift would depend on the specific function characterizing herbivory over the growing season. Such a complicated analysis is beyond the scope of our study, but it may be relevant that latitudinal and altitudinal clines in flowering time observed among introduced species often parallel those observed in the native range (reviewed in [86,87]). This

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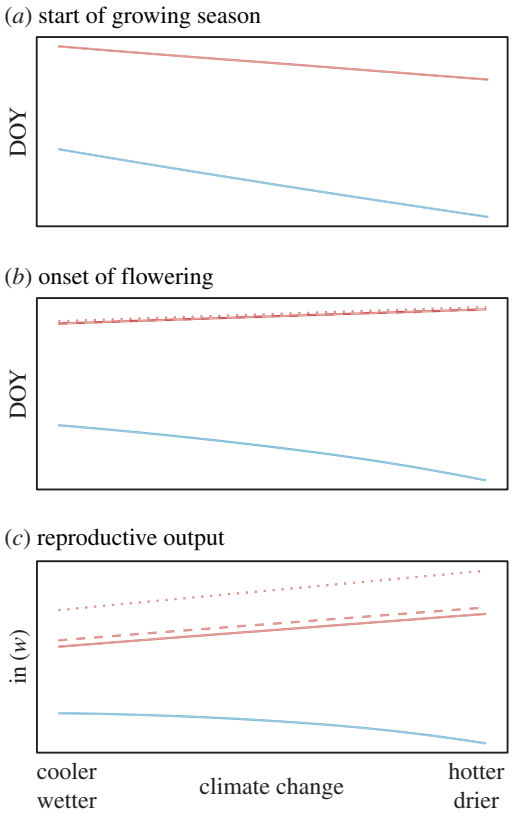

Figure 2. Relationship between intensity of climate change (*x*-axis) and phenology or fitness in *Boechera stricta* (blue) and *Lythrum salicaria* (red) in its native range (solid red lines), or in its introduced range with either an ecological release from herbivory (dashed red lines) or a relaxed constraint resulting from enemy release (dotted red lines). (*a*) Start of the growing season—the first day of the year (DOY) on which environmental conditions allow growth. (*b*) Initiation of flowering (DOY). (*c*) Natural log of total reproductive fitness at the end of the growing season.

observation is consistent with our model of an average reduction in herbivory throughout the season, rather than a major shift in the intensity of herbivory at particular time periods, as the latter could alter flowering phenology significantly. Moreover, the minimal effect of herbivory on flowering time in our model emphasizes that robust tests for ecological release and relaxed constraints in invasive species require careful consideration of local adaptation to season length.

Our model is based on parameters for *B. stricta* and *L. salicaria*, but it can be generalized to a range of environmental conditions and taxa, including animals. For example, snowmelt affects emergence time of mammals, which may be analogous to the start of the growing season in our *Boechera–Lythrum* model. Our model would predict that early snowmelt should result in earlier emergence times, and indeed this seems to be the case in, for example, Columbian ground squirrels (*Urocitellus columbianus*) [88] and yellow-bellied marmots (*Marmota flaviventris*) [89]. However, the effect on fitness will depend on the length of the growing season, which is determined not only by snowmelt but also resource availability.

The key environmental variables are those that limit growth and development, which in turn determine the onset and duration of favourable conditions for growth, maturation and offspring production. For any given season length, the initiation of growth, the threshold size of reproduction, the timing of reproduction and total reproductive fitness all depend on the growth rate prior to maturity. Future models could explore ecological constraints on growth rate. For example, competitive interactions may alter the relative strength of selection on growth versus survival and reproduction [90]. The allocation of resources from growth to reproduction could also be altered to account for growth that occurs after reproductive maturity.

We modelled an average growth rate (r), with the simplifying assumption of a constant rate throughout the growing season. However, r can be affected by changes in productivity throughout the growing season (e.g. temperature, nutrient availability), and this in turn could affect optimal flowering time. For example, Wadgymar *et al.* [91] found that artificial warming compressed the entire phenology of both early and late-flowering genotypes into a shorter time window. Incorporating productivity and non-constant r is not straight-forward as the effects on flowering time depend on the specific shape of the productivity function over the growing season [80]. Empirical studies characterizing the specific fitness function of flowering time (e.g. [92]) can help to clarify how seasonal changes in productivity affect the evolution of flowering time, and ultimately determine fitness in novel environments.

There are reasons to expect that invasive species may respond more rapidly than native species to climate change [11]. Additionally, we found that interspecific differences in habitat and life history had strong effects on phenological shifts under climate change—much stronger than enemy release. Escaping natural enemies had little effect on flowering time but a large fitness benefit, especially when lower herbivory relaxed constraints on relative growth rate. By contrast, relatively small changes in climate led to very different phenological shifts in both species, with strong effects on reproduction. A general prediction of our models is that species experiencing shorter growing seasons should evolve a more rapid phenology, maturing earlier at a smaller size and producing fewer offspring. By contrast, species experiencing longer growing seasons should evolve delayed reproduction to grow larger and produce more offspring, but the phenotypic shift in phenology could be masked by an earlier onset of favourable growing conditions. These predictions could be manifested in a simple log–linear relationship between (i) a species' phenological shift in response to climate change—measured as the change in flowering time from the start of the growing season, rather than the change of Julian date *per se* and (ii) the change in relative reproductive fitness. Researchers have extensively characterized phenologies of reproduction, migration and emergence in a diversity of organisms. Our modelling framework could be applied to existing eco-evolutionary datasets to predict vulnerability of natural populations to climate change, and to help prioritize populations and species for conservation actions.

Authors' contributions. All authors contributed to the conceptual development, writing and revising of the manuscript. R.I.C. initiated and coordinated the project.

Competing interests. We have no competing interests.

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