Evolution under changing climates: climatic niche stasis despite rapid evolution in a non-native plant

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A topic of great current interest is the capacity of populations to adapt genetically to rapidly changing climates, for example by evolving the timing of life-history events, but this is challenging to address experimentally. I use a plant invasion as a model system to tackle this question by combining molecular markers, a common garden experiment and climatic niche modelling. This approach reveals that non-native Lactuca serriola originates primarily from Europe, a climatic subset of its native range, with low rates of admixture from Asia. It has rapidly refilled its climatic niche in the new range, associated with the evolution of flowering phenology to produce clines along climate gradients that mirror those across the native range. Consequently, some non-native plants have evolved development times and grow under climates more extreme than those found in Europe, but not among populations from the native range as a whole. This suggests that many plant populations can adapt rapidly to changed climatic conditions that are already within the climatic niche space occupied by the species elsewhere in its range, but that evolution to conditions outside of this range is more difficult. These findings can also help to explain the prevalence of niche conservatism among non-native species.

1. Introduction

Rapid evolution is expected to contribute to population persistence in the face of anthropogenic climate change [1] and promote the spread of invasive species [2]. Numerous studies have documented shifts in traits associated with changes in climate, and especially phenological shifts that enable organisms to synchronize key life-history events with the prevailing climate [3,4]. However, direct evidence that these involve evolution, as opposed to occurring solely through phenotypic plasticity, is still scarce [3,5], especially for plants. Indirect approaches rely on either estimates of genetic variation and selection on traits associated with responses to climate change [6], or ‘space-for-time’ studies of genetic responses in plants transplanted to sites with conditions similar to those under predicted future climates [7]. Direct comparisons of ancestral and descendent genotypes from a population that has experienced a change in climate are rare [8]. For example, Franks et al. [9] showed that Brassica rapa populations evolved advances in flowering time in response to shorter growing seasons caused by an extended drought. Other evidence comes from non-native plants, which often adapt rapidly to the changing climatic conditions that they encounter as they spread along environmental gradients [10].

While these and other studies indicate the potential of populations to evolve to changing climates, and show that evolution can be rapid, we know little about the limits to this evolutionary potential [11]. This makes it impossible to predict whether adaptive evolution will allow populations to persist over a long period [8]. For example, as the climate warms, a plant that is growing in the centre of its geographical range, or climatic niche envelope, will probably need to adapt to conditions that are already experienced by populations of the species elsewhere in its range, for example at more equatorial latitudes. By contrast, these more marginal populations might need to adapt to conditions that are outside of the climatic envelope of the species, essentially requiring evolution of the
species’s climatic niche limits [12]. Predictions about the extent to which evolution could ‘rescue’ populations experiencing changes in climate might differ crucially between these two contexts [4]. For example, in the former case, we might expect evolution to proceed rapidly because it can exploit existing genetic variation, whereas in the latter, it would be much slower, being contingent on the emergence of new beneficial mutations.

Comparative studies of native and non-native populations of invasive species present an opportunity to test this prediction [10] and to explore the conditions under which evolutionary rescue might occur [12]. This is because many non-native species rapidly evolve clines in traits, such as growth and phenology, as they spread along climatic gradients in a new region [13,14]. At the same time, population genetic processes, for instance admixture among introduced populations, could overcome some of the constraints on adaptation, such as low genetic variation or maladaptive gene flow [11], that exist in the native range [10], potentially enabling non-native species to evolve new climatic limits. Non-native species therefore present a model system to study the processes and limits of adaptive evolution to changing climates. In such a study, we should first ask whether rapid evolution of non-native populations along climatic gradients (i) produces phenotypes that transgress the variation that is already present across the native range and (ii) allows non-native populations to persist in sites that are outside of the climate envelope of the species in the native range [4,15]. However, this has not been possible until now because most studies of evolution during biological invasions have either been performed with plants from the non-native range only, or compared populations sampled from restricted parts of the native and non-native ranges [13]. Furthermore, the information on introduction history needed to make relevant comparisons of evolutionary change in non-native populations has rarely been available [16].

Here, I use a combination of molecular markers, a common garden experiment and climatic niche modelling to study the rapid evolution of phenology associated with climate across the native and non-native ranges of an invasive plant, Lactuca serriola L., a species that is both a common weed and the native and non-native ranges of an invasive plant, L. serriola. Resampling (1000 random draws) of microsatellite allelic richness within the populations with \( n \geq 20 \) retrieved 78.9 ± 6.0% (mean ± s.d.) of alleles with \( n = 10 \), indicating that the sampling effort was sufficient to capture much of the allelic variation within populations. DNA was extracted from dried leaf material of plants raised from seed from each population.

Fragment length variation was assessed for seven microsatellite loci (A001, A004, B101, B104, D106, D108 and E011) and fluorescently labelled with ATTO550, FAM or HEX. These loci are located in different linkage groups within the lettuce genome, or separated by 86 cM within a linkage group, and can therefore be considered independent [21]. Uniplex polymerase chain reactions (PCRs) were performed as previously described with minor modifications [22], and PCR products were analysed on an ABI 3730x DNA Analyzer (Applied Biosystems). Each plate included two negative and four positive controls. In total, 730 individuals were genotyped using GENEMAPPER v.4.1 software (Applied Biosystems). The error rate per reaction calculated from positive controls and repeat amplifications was 2.9%. The data were combined with a dataset collected by Alexander et al. [22] using the same primers and analysed in the same laboratory, after 32 samples were reamplified and analysed to ensure comparability.

(b) Common garden experiment
A subset of 35 populations (38 native and 17 non-native) from the population genetic analysis was included in a common garden experiment to investigate genetically based geographical variation in flowering phenology. On 26 May 2010, two batches of seeds from each seed family or bulked population were sown on seed compost. Both batches were watered in darkness and then sealed inside black polythene bags. One batch was transferred to a fridge to be vernalized at 4°C, whereas the other was stored at a constant 17°C. After four weeks [20], the seeds were removed from darkness and allowed to germinate in a climate chamber (16 L:8 D cycle, 22/16°C, 70/75% humidity). After a further 12 days, one individual of each seed family, or three per bulked population, from each batch (hereafter vernalization treatment) were potted up into individual 0.48 l plastic pots containing potting compost (Ökohum GmbH, Herberingten, Germany). The total of 303 pots (fewer than the expected 330 owing to poor germination of some populations) were randomly arranged in a grid across seven benches (hereafter ‘blocks’) in the climate chamber. To reduce positional effects on plant

— Has there been rapid evolution of flowering phenology along climatic gradients in the non-native range?
— Has L. serriola expanded its climatic niche in the non-native range?

2. Material and methods
(a) Plant material and microsatellite analyses
Achene (hereafter ‘seeds’) were collected by the author and volunteers and also obtained from the germplasm collection of the Centre for Genetic Resources (CGN; Wageningen, The Netherlands), from four regions where L. serriola has been introduced (North America, South America, South Africa and Australia) and almost across the entire native range (see electronic supplementary material, figure S1 and table S1). Wherever possible, seeds were collected from separate seed families (mother plants) within a site (hereafter ‘population’), or else seeds from on average 12 (range 1–60) families were bulked (see electronic supplementary material, table S1). In total, 75 populations (\( n = 4–24 \) per population, \( mean = 10.04 \)) were sampled from disturbed, ruderal sites, for instance roadsides, which are typical habitat for L. serriola. Resampling (1000 random draws) of microsatellite allelic richness within the populations with \( n \geq 20 \) retrieved 78.9 ± 6.0% (mean ± s.d.) of alleles with \( n = 10 \), indicating that the sampling effort was sufficient to capture much of the allelic variation within populations. DNA was extracted from dried leaf material of plants raised from seed from each population.

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— What is the source of L. serriola populations that have been introduced around the world?
growth, the pots were periodically rearranged within blocks. The benches were lined with fleece to retain moisture, and each pot was individually watered without fertilization every 2–4 days as required to prevent the compost from desiccating.

Plants were checked every 2–4 days to determine the dates of bolting (the first date on which sections of elongated stem were visible between the rosette leaves) and seed set (first capitulum dehisced and seeds visible), the total number of leaves when a plant bolted (correlated with total biomass; \( r = 0.81, \) d.f. = 39, \( p < 0.001 \)), and plant height at seed set (maximum stem length to the top of the inflorescence). Flowering plants were covered with perforated plastic sheaths (Lehle Seeds, Round Rock, TX) to collect seeds. All plants were harvested on 30 November 2010, when the majority had senesced. The seeds were collected and the remaining aboveground plant parts were dried at 60°C for 3 days to determine biomass. Both the common garden and microsatellite datasets were deposited in the Dryad Repository (doi:10.5061/dryad.nr916).

(c) Statistical analyses

(i) Inferring invasion history

The population genetic structure across the native and non-native regions was examined to generate testable hypotheses about the source of non-native plants. A principal components analysis (PCA) was performed using the R package ‘adegenet’ [23,24] on a matrix of allele frequencies that had been centred, scaled and had missing data replaced by the mean allele frequency. This revealed substantial differentiation in the native range between individuals from Asia and Europe (figure 1), and differentiation in the non-native range between individuals from North America (including the three populations from Argentina and Tenerife; hereafter ‘America’), and South Africa and Australia. Therefore, to concentrate computing power on a manageable set of competing hypotheses, individuals from America, and individuals from Australia and South Africa, were grouped for subsequent analyses; Europe and Asia were considered as potential native source regions.

Competing hypotheses about the introduction history of *L. serriola* in the two non-native groups were compared within an approximate Bayesian computing (ABC) framework using the software DIYABC [25,26]. The 14 scenarios (see electronic supplementary material, table S2) considered all four possible combinations of Europe and/or Asia as putative source regions, plus five scenarios in which at least one non-native group arose through admixture between Asia and Europe. A further five scenarios considered the possibility that at least one non-native group was founded from an unsampled ‘ghost’ population [27]. Datasets \((n \approx 14 \times 10^6)\) were simulated according to the different scenarios by drawing demographic and mutation model parameter values from prior distributions that were based on knowledge of the biogeographic history of this and similar species (see electronic supplementary material, table S3) [28]. The observed and simulated datasets were summarized and compared using a set of nine statistics. These were: for each region, the mean number of alleles, mean gene diversity, mean allele size variance and mean \(M\) index (the ratio of the number of alleles to the range in allele sizes) across loci; and for each pair of regions, the mean number of alleles, gene diversity and allele size variance across loci, pairwise \(F_{ST}\) and the mean index of classification [25]. The total number of summary statistics was 52.

The posterior probability of each scenario was calculated as (i) its frequency among the 500 simulated datasets that were closest in terms of summary statistics to the observed data (‘direct estimate’) and (ii) using a logistic regression-based estimate of this proportion for the closest 1% of simulated datasets [25]. The latter is considered a more robust estimate of the posterior probability of a given scenario [26]. Confidence in the choice of scenarios was assessed by estimating type I and type II error rates (i.e. the probability of rejecting the true scenario or accepting a false scenario, respectively) among 500 pseudo-observed datasets (PODs) simulated with each of the two most probable scenarios [25]. Finally, the goodness-of-fit of the most probable scenario was assessed by comparing the observed data with the posterior predictive distribution of 1000 PODs generated under that scenario, based on a different set of summary statistics than that used for scenario selection (see electronic supplementary material, table S4) [27]. The observed dataset was plotted together with the PODs in a PCA of the summary statistics, and the probability of the observed data being more extreme than the simulated data was calculated for each summary statistic.

(ii) Genetically based variation in flowering phenology

The macroclimate at the locations from which populations were sampled was summarized as scores from the first two axes of a PCA on eight bioclimatic variables (see ‘Climatic niche modelling’ below). PC1 explained 46.0% of variation in climate and was mainly associated with temperatures ranging from cold, dry, seasonal to warm, wet, aseasonal climates (see electronic supplementary material, table S5). For the populations included in the common garden experiment, PC1 was most strongly correlated with the absolute value of population longitude in the native range \((r = -0.75, \) d.f. = 36, \( p < 0.001 \)) and latitude in
the non-native range \( (r = -0.65, \text{ d.f.} = 15, p < 0.01) \). PC2 explained a further 30.5% of variation, mainly capturing an aridity gradient from dry, hot sites with seasonal precipitation to wet, cool sites with annual precipitation. PC2 was correlated with latitude across both ranges \( (r = 0.64, \text{ d.f.} = 53, p < 0.001) \).

The log of the number of days between germination and the onset of bolting was analysed with a mixed-effects model as a function of origin (non-native range, Europe or Asia), climate (separate models for PC1 and PC2), vernalization treatment (vernalized or not) and all interactions as fixed effects. The model was fitted using maximum likelihood with the ‘lme4’ package in R [24], and contained the random effects of population and experimental block to account for the nested structure of the data, as well as initial seed size as a fixed effect to control for potential differences in maternal investment (i.e. maternal effects). After checking that the full model satisfied the assumptions of homoscedasticity and normality of errors, it was compared with the 18 possible reduced models fitted according to the principle of marginality. These contained different combinations of the fixed effects (except seed size, which was retained in all models) but the same random effects, including a null model containing only seed size and the random effects. The minimum adequate model was selected using the Akaive information criterion with a correction for small sample sizes (AICc) as the most parsimonious model within 2 AICc units of the lowest AICc value [29]. Additionally, support for each model was assessed by calculating its Akaive weight (\( w_2 \)), which represents the probability that a model is the best, given the set of competing models [29]. Support for individual terms, \( w_{2i} \), across the whole set of models was derived by summing \( w_i \) across the models in which a particular term appeared. The evidence ratio, \( ER \), was also calculated for each term as \( \frac{w_H}{1 - w_H} \) [30]; an \( ER > 2.7 \) corresponds to \( \Delta = 2 \) and indicates strong support in favour of a particular term. Three-way interactions were investigated further by fitting separate models for plants from each origin using the same model selection procedure. Similar models were fitted with the time between germination and first seed production. In this case, only vernalized plants were considered, because only 62% of non-vernalized plants that bolted had set seed by the end of the experiment, compared with 96% of vernalized plants. Finally, correlations were examined between bolting phenology and size at bolting across all plants, and with the final biomass and reproductive output (total seed mass) of plants that set seed. The effect of delayed bolting on these traits was quantified in mixed effects models after controlling for initial seed size, and block and population as random effects.

(iii) Climatic niche modelling

Global occurrence data for \( L. \) serriola were obtained from several sources (see electronic supplementary material, figure S1). For each location, bioclimatic data were extracted from the WORLDCLIM database of climate interpolations for the years 1950–2000 [31]. Following Keller et al. [32], eight variables were selected that represent biologically relevant variability in temperature and precipitation at each locality and are assumed to be important for growth of \( L. \) serriola (electronic supplementary material, table S5) [33]. Additionally, global climate data were extracted at 0.5° intervals across the native (Palaearctic) and non-native (Nearctic, South Africa, Lesotho, Swaziland, Australia and New Zealand) ranges [34]. The species occurrence data were then aggregated to a resolution of 0.5° to make them more comparable with the global climate data, giving in total 3572 native and 1614 non-native occurrences.

The climatic niche in the native and non-native ranges was modelled using the framework proposed by Broennimann et al. [35] and Petitpierre et al. [34]. The first two axes from a PCA of bioclimatic variables, including both species occurrences and the global climate, are projected as smoothed densities of occurrence in gridded (resolution = 100 x 100 cells) environmental space using a kernel function [35]. Niche dynamics were assessed by calculating the proportion of the densities in the non-native range that occur in environments that are also occupied in the native range (‘stability’), the proportion of non-native densities that occur in environments that are not occupied in the native range (‘expansion’) and the proportion of densities in the native range that occur in environments that are not occupied in the non-native range (‘unfilling’) [34]. The global climate data were used to delimit the total climate space present in each range. Niche dynamic indices were only calculated for environments that occur in both ranges, but restricted to the 75 or 95 percentile of the global climate in each range to exclude any bias caused by marginal habitats and artefacts of the kernel smoother [34]. Separate analyses were performed using native species occurrences from the entire native range and for the European subset of the native range (Eurasia, west of Russia and Turkey).

3. Results

(a) Introduction history

The microsatellite analysis retrieved 173 alleles across the seven loci (mean 24.7, range 14–34). Only five alleles were found uniquely in non-native populations (frequency 0.018 ± 0.018, mean ± s.d.), suggesting that their potential source regions in the native range were adequately sampled. Of the 60 alleles found in Asian populations but not in European populations (0.031 ± 0.023), only eight (13%) were found in non-native populations, whereas 10 of the 24 alleles (42%) found in European but not Asian populations (0.035 ± 0.049) were also found in the non-native range.

Plants from Europe and the non-native regions clustered closely together in the PCA of allele frequencies, on the margin of a broad cluster formed by plants from Asia (figure 1). The inference of introduction history using DIYABC confirmed that \( L. \) serriola in the non-native range originated primarily from Europe, with admixture rates from Asia of 0.30 [0.07, 0.67] (median and 95% credible interval of the posterior distribution) and 0.17 [0.04, 0.48] in Australia/South Africa and America, respectively (scenario 9; electronic supplementary material, table S6). Although no single scenario was clearly supported using the direct estimate, scenario 9 was selected with high probability (0.64 [0.31, 0.98]; 95% credible interval) using the logistic regression approach (see electronic supplementary material, figure S2). The next best scenario, scenario 10 (0.30 [0.00, 0.65]), hypothesized that all non-native plants were introduced from an unsampled native lineage. These scenarios could be distinguished with a high degree of confidence; across 500 PODs, scenario 9 always had a higher posterior probability than scenario 10 when it was the true scenario (type I error \( P < 0.002 \) for the logistic regression estimate) and only once had the higher posterior probability when PODs were simulated according to scenario 10 (type II error \( P = 0.002 \)). The comparison of the observed dataset with 1000 PODs generated under scenario 9 also indicated a good fit between the data and the model. The observed dataset was in the tail of the posterior predictive distribution for only two out of 28 summary statistics (the ratio of number of alleles to range in allele sizes in Asia and Europe; electronic supplementary material, table S4), and the observed dataset was located centrally within the posterior predictive distribution of the PODs in a PCA on summary statistics,
although it was more marginal along PC2 (see electronic supplementary material, figure S3).

(b) Clines in phenoology along climatic gradients

Non-native L. serriola plants bolted on average 9.4 (vernalized) and 39.6 (non-vernalized plants) days faster than plants from Europe, and some bolted faster than any European plant (figure 2c). However, the shortest bolting times were recorded for certain populations from the native range in Asia. These differences were explained by a combination of genetically based clines along climate gradients and additional differences between origins. Responses to PC1 differed among origins (origin × PC1 vernalization treatment $w_{11} = 0.79$, ER = 3.69; electronic supplementary material, table S7); both vernalized and non-vernalized plants from warm, wet climates in Asia bolted faster (PC1 vernalization treatment, non-native plants bolted 12.1 and 21.6 days faster than plants from Asia and Europe, respectively (figure 2). Clines were weaker but still well supported in models fitted with non-native plants only (PC2 vernalization treatment $w_{21} = 0.75$, ER = 3.02).

Plants produced approximately an additional leaf for every 2 days of delay in bolting ($r = 0.78$, d.f. = 282, $p < 0.001$). Similarly, time to bolting was positively related to biomass at the end of the experiment ($r = 0.32$, d.f. = 221, $p < 0.001$, including only plants that produced seed), with plants adding approximately 0.06 g for every day that bolting was delayed; however, reproductive output was negatively related to time to bolting ($r = -0.42$, d.f. = 222, $p < 0.001$). Across all vernalized plants, the time to bolting was correlated with time to the first seed production ($r = 0.70$, d.f. = 223, $p < 0.001$). Plants from arid climates also set seed earlier than those from wet, cool climates (PC2 $w_{21} = 0.85$, ER = 5.49), although there were no differences between origins and no cline along PC1 (PC1 $w_{11} = 0.31$, ER = 0.46; electronic supplementary material, figure S4 and table S7).

(c) Climatic niche limits of non-native plants

Lactuca serriola in the non-native range has expanded its climatic niche considerably relative to populations from Europe (figure 3). Of the climatic niche in the non-native range, 31% lies outside of environments occupied by populations from Europe, whereas only 0.001% of the European climatic niche lies outside of the climatic niche of populations from the non-native range. By contrast, when
introduced to its non-native range primarily from Europe, with low levels of admixture from Asia. Overall, there was strong support for this scenario, which provided a close fit to the data, and there was sufficient power using the ABC approach to distinguish between competing introduction scenarios with a high degree of confidence. Therefore, support for this scenario is robust, even if based on a relatively small number of microsatellite loci. Including more data might help to pin down the origin of non-native genotypes in Europe more precisely, although previous analyses also reported weak population structure in Europe [21,36]. This is probably owing to the ephemeral nature of L. serriola populations, the species’s high dispersal potential and its recent history of range expansion in Europe [37,38]. However, even without more precise information, insights from comparisons among plants from Europe, Asia and the non-native range have a number of implications for understanding and predicting the extent of biological invasions, as well as of rapid evolutionary responses to changing climate.

4. Discussion

The expansion of non-native species along climatic gradients can provide a model for understanding the potential of populations to adapt to changing climates and the limits to this capacity. The data presented here show that L. serriola was considering the entire native range of the species, the native and non-native portions of niche space overlap by 93%, with only a 7% expansion in the non-native range. Similar results were obtained when these indices were calculated considering environments within the 95% percentile of the global climate in each range (expansion 32% relative to Europe and 9% relative to Eurasia).

(a) Rapid evolution of flowering phenology

Non-native L. serriola plants flower earlier than ancestral European plants and in some cases bolted faster than any plant from Europe, providing strong evidence for selection-driven evolution following introduction [16]. The presence of parallel clines across both ranges also suggests that non-native plants have evolved in response to changing climate along environmental gradients. However, where native and non-native plants had overlapping flowering phenologies, these clines could potentially also result from the introduction and sorting of different preadapted genotypes. Clinal patterns of trait variation can also occur owing to neutral processes as a consequence of range expansion [32], but this can be ruled out in this case, because the non-native populations were sampled from different continents and do not represent a single invasion event.

Advanced flowering phenology and a weak vernalization response in plants from more arid climates in both ranges are consistent with genetic adaptation to growing seasons that are cut short by the onset of summer drought [39,40]. Comparable data on season length at each sampling site are not available, but an estimate based on Walter climate diagrams for each site correlates closely with PC2 (r = 0.66, d.f. = 53, p < 0.001), supporting this interpretation, which is also consistent with the conclusions of similar studies with a range of different species [18,40]. The increasing requirement for vernalization to hasten bolting is also an expected adaptation to prevent flowering during winter [20]. Lactuca serriola has recently expanded its range in northern Europe (e.g. it was first recorded in Britain in 1632) [37], and so the requirement for vernalization in these populations might also have evolved rapidly. Although advanced bolting is often found in wet, cool sites at high latitude [17,18], L. serriola transplanted beyond its northern limit in Britain sets seed well within the growing season, and so this limit is unlikely to be controlled by phenology [33]. In these populations, delayed bolting correlates with large size at flowering, which confers higher fitness under field conditions [41], although not in this experiment, probably because it ended before all plants had senesced. Except in Asia, the climate gradient captured by PC1 did not exert strong selection on flowering phenology.
These various lines of evidence suggest that *L. serriola* has adapted rapidly to the local climates that it has encountered after introduction to new geographical regions, but reciprocal transplants are needed to demonstrate this definitively. It is also possible that the faster phenology of non-native plants partly constitutes an adaptation to aspects of the invasion process other than climate; for example, securing reproduction in ephemeral habitats [42], which could explain the advance in phenology that was observed after controlling for climate.

(b) Climatic niche limits

The climatic niche of *L. serriola* has expanded by over 30% in the non-native range compared with Europe, its principal source region, primarily into arid regions (figure 3). Together with the evolution of flowering phenology, this suggests that some non-native *L. serriola* populations have adapted to climates that are more arid than those experienced by ancestral populations. These results must be interpreted cautiously, because there is no direct evidence that the evolution of phenology is causally linked to the observed expansion in climatic niche. Nonetheless, it is known that flowering phenology constrains the distribution of other species [17,18,43], and this is especially likely for annual species that must complete their life cycle within a single growing season [9,39,40]. Furthermore, in other species, it is also possible, within a few generations, to artificially select flowering phenology to exceed the extremes present in a base population [44]. The source of variation for this evolution is unclear, but could come from standing genetic variation within non-native populations or novel mutation, and could have an epigenetic basis [45]. It is also plausible that admixture with plants from arid parts of Asia provided the genetic variation necessary to evolve faster phenology [16].

This study shows that, when introduced to a new range, a subset of native plants are able to evolve traits that allow them to rapidly refill the native climatic niche of the species as a whole. However, while non-native *L. serriola* plants have evolved phenologies and occupy climatic niches that are more extreme than in their principal source region, they do not exceed the range of phenological variation or niche breadth observed across the native range as a whole, such as in parts of western and central Asia. This might be because non-native *L. serriola* is not yet in equilibrium with its climatic limits. However, it is well dispersed and has been present in the non-native regions for hundreds of generations, so has plausibly had time to establish stable climate limits. The earliest record of the species in North America is 1863 [38], whereas the DIYABC analysis suggested introduction dates in the mid-seventeenth century. However, there was large uncertainty in these estimates, which do not account for ongoing gene flow among regions owing to multiple introduction events [28]. The weaker clines observed across the non-native range might also imply that local adaptation is ongoing. Furthermore, niche dynamics might be different in other regions (e.g. South America) where *L. serriola* is present but that were not included in the niche model owing to a scarcity of data.

Assuming that non-native *L. serriola* is no longer expanding its climatic range, and again that phenology and distribution are functionally linked [43], the observed niche conservatism could be explained by constraints on evolution that apply to the species across its entire geographical range. These assumptions can only be tested by transplant experiments beyond the current climatic limits [15]. What these constraints may be remains unclear, but they could be the consequence of trade-offs among traits, such as size and time to flowering, that are inherent to the biology of the species [7,17]. Indeed, the majority of plants conserve their climatic niche limits when introduced to new regions [34], despite the fact that many also evolve rapidly as they spread along climatic gradients [10], suggesting that this finding is likely to be general.

(c) The potential for rapid evolution to changing climates

These findings suggest that, for this species at least, many populations might have the capacity to adapt genetically to climatic conditions that are within the species’s climate envelope. However, the conservatism of the phenological and climatic limits across the native and non-native ranges as a whole suggest that adaptation to climates outside this envelope is much less likely [15]. This suggests that predictions of the extent of biological invasions will be robust based on knowledge of a species’s climatic niche in the native range, even when they evolve rapidly. However, it will be crucial to distinguish between these different scenarios when considering the potential of native populations to adapt *in situ* to changing climates. For example, evolution might be possible for populations that are near the centre of the species’s climatic envelope, but not for those that are near the trailing edge of the species’s distribution [4]. Given that most species ranges have tracked climate during previous episodes of rapid climate change, this evolution presumably happens only very rarely [4].

There are, however, several reasons why non-native populations might poorly represent expected responses to changing climates in many native species. One is that non-native populations are often composed of genotypes from different native source populations [16], providing increased genetic variation and novel genetic combinations for selection to act upon, as indeed might have occurred in *L. serriola*. Gene flow can enhance the adaptive potential of native populations in a similar way [46], but opportunities for admixture might be more limited in species that are not widely dispersed. Another possible reason is that widespread weedy species are, by definition, successful at coping with climatic variation [42], whereas more specialized native species might lack suitable genetic variation to adapt to changing conditions [47].

This study also highlights the usefulness of comparisons of native and non-native populations for studying climate adaptation, and points to promising avenues for future research. For example, examining the genetic basis of traits such as phenology that are well characterized at the molecular level could reveal the extent to which evolution occurs based on standing genetic variation and novel mutation or the contribution of epi-genetic variation. Quantitative genetic experiments [8] using native and non-native populations could also enlighten the role of genetic trade-offs in determining limits to climate adaptation, such as at range margins.

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