Climate Change Ecology 2 (2021) 100023

Contents lists available at ScienceDirect

Climate Change Ecology

journal homepage: www.elsevier.com/locate/ecochg

Comparisons in the native and introduced ranges reveal little evidence of climatic adaptation in germination traits

Harold N. Eyster[a,b,c,*], Elizabeth M. Wolkovich[b,c,d]

[a] Institute for Resources, Environment, and Sustainability, University of British Columbia, 429-2202 Main Mall, Vancouver, BC V6T 1Z4, Canada
[b] Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, MA 02130, USA
[c] Department of Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA
[d] Department of Forest and Conservation Science, University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

ARTICLE INFO

Keywords:
Climate change ecology, Invasion ecology
Rapid evolution
Broad environmental toler- ance
Phenology
Plant–climate interactions
Growth chamber experiment
Germination
Bayesian multilevel models
Invasive plants

ABSTRACT

Plant invasions are increasing due to globalization and environmental change, including through anthropogenic climate change. Yet we lack an understanding of how some species become widespread invaders while others do not. Two competing mechanisms have been posited: post-introduction rapid evolution to the novel environments of the introduced range and broad environmental tolerance in the native population that makes invaders tolerant of diverse introduced environments. Each mechanism has implications for how invaders respond to climate change: either by evolving with future climates, or already being tolerant of diverse current/future climates. Disentangling these mechanisms requires investigating how evolution versus tolerance drive invasion traits (germination success and timing; growth rate). Here, we tested for evidence of rapid evolution in these traits by using growth chambers to provide common climates for seven herbaceous plant species sampled from multiple populations in their native (European) and introduced (North American) ranges. Chambers provided two levels of stratification—to simulate different winter lengths—and four temperature levels post-stratification—to simulate different spring conditions. We used Bayesian multilevel models to examine responses, while controlling for population and seed family. Across all species, trait responses were largely similar between native and introduced populations, except in response to particular climates representing cold winters and warm springs where introduced populations germinated later and grew faster. Our results suggest that broad environmental tolerance, not rapid evolution, likely underlies invasion success for these invaders—and may sustain their spread with continued warming—but species may evolve in response to specific combinations of winter and spring climatic regimes.

1. Introduction

Exotic plant invasions can transform biodiversity and ecosystems [5,49,54]. These invasions are increasing: globalization is facilitating extra-range plant dispersal [40], and human alteration of ecosystems may provide new niche space [7,38,42,73]. Upon dispersing to a new environment, introduced species can thrive by filling vacant niches [23] or outperforming native plants [18,19].

Changing environments, especially with anthropogenic climate change, could select for species that can take advantage of newly created temporal niches [33,81], and related resources, through shifts in the timing of flowering, fruiting, and other life history events [26]. Recent research shows invaders differ in their sensitivity to climate [61] and are able to shift their phenology more than native species in their introduced communities [61,82,86]. But whether these invaders are inherently more phenologically flexible (i.e., similar phenological responses across both their native and introduced ranges), or whether their phenology can rapidly evolve post-introduction has received less attention.

Two major biological mechanisms for how plants become widespread in novel environments are particularly relevant to understanding how phenology and invasions may intersect: 1) post-introduction rapid evolution and 2) broad environmental tolerance in the native population. A large body of literature supports this first mechanism of rapid evolution (e.g., [14,15,46,58,63]). Rapid evolution can enable introduced species to adapt to vacant niches and take advantage of variable and high-resource environments. This includes by evolving greater competitive ability when released from natural enemies ([8,11], i.e., enemy release hypothesis; though this hypothesis is likely less explanatory than is often assumed, [16]), or by evolving adaptive plasticity [64]. For example, a study found that genetic adaptation drove adaptive phenotypic variation in flowering time between high-altitude and desert populations of *Capsella bursa-pastoris*

* Corresponding author at: The University of British Columbia, Canada.
E-mail address: haroldeyster@gmail.com (H.N. Eyster).

https://doi.org/10.1016/j.ecochg.2021.100023
Received 4 November 2020; Received in revised form 15 June 2021; Accepted 21 July 2021
Available online 2 September 2021
2666-9005/© 2021 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/)

(Brassicaceae) in California [48]. Invasion can expose populations to divergent selection regimes; in one case this led to reproductive isolation and thus speciation in as few as 13 generations [41]. If post-introduction rapid evolution is this central to invader success, it would have important implications for invasive species management: managers should treat invasives not as static, homogeneous species, but as constantly adapting populations [46]. It would also suggest invaders will continually genetically evolve with climate change and thus estimates of their responses today may not forecast their future climatic responses.

Despite the support for the importance of post-introduction rapid evolution for widespread invaders, a competing body of literature suggests that invaders need not evolve to become widespread in novel environments. Instead, broad environmental tolerance, plasticity, weediness, and generalist adaptations to human-dominated environments within the native population may give invaders sufficient advantages to become widespread, obviating the necessity of post-introduction rapid evolution [3,9,62,64,69]. A meta-analysis of 117 studies found that invasion success was associated with general performance-related traits, and concluded that it may be possible to predict future invaders by these traits [76]. In contrast to the rapid evolution hypothesis outlined above, this model of invasions emphasizes invasion prevention and, for invasions that cannot be prevented, suggests treating them as a homogeneous population across their introduced range. It would also suggest that today's estimates of invaders' responses to climate can be used to forecast their future performance and, potentially, their future distributions with climate change.

While these two hypotheses—post-introduction evolution or broad environmental tolerance—are not exhaustive, they represent two major mechanisms that could explain observed differences in the phenological flexibility of invaders [61,82,86] and could be tested by exposing populations from both the introduced and native ranges to common climates. To date most research on the phenology of invaders has focused on the invaders in their introduced communities, often using observational datasets (e.g., [83]) or experimental warming in the field (e.g., [86]). But neither of these methods or even single-location common gardens (i.e., testing individuals from only one part of the range or in only one site, [17,77]) are sufficient to discriminate the two mechanisms. Reciprocal common garden experiments—with native and invader populations—can test these theories (e.g., [45,78]), but they are relatively rare and typically only include one or two species due to the immense effort they require. Growth chamber experiments are easier to control and execute, thereby enabling a larger number of species to be tested and compared simultaneously. Moreover, growth chambers can precisely vary the environments that plants experience and provide high-resolution assessment of small differences in trait responses.

Here, we report on a growth chamber experiment of seven highly invasive herbaceous plant species collected from their native (Europe) and introduced (North America) ranges, many of which appear responsive to climate [82]. Indeed, four of our seven study species (*Capsella bursa-pastoris, Chelidonium majus, Plantago lanceolata*, and *Rumex crispus*) were included in a phenology monitoring dataset (the Concord Phenology Dataset, [79]), which showed that these species flower 4.5 days earlier on average than they did in the 1800s (compared to less than a day earlier on average across all 372 species in the dataset). This suggests that these invasive species exhibit flexible phenologies—flexibility that may be key to their success.

While much work in studying invaders' phenology has focused on flowering and leaf-out (e.g., [87]), we focused on germination and growth traits here as they are some of the most important for granting invasive success [50,68]: invasive success requires the capacity to germinate in novel environments and grow rapidly enough to compete with native flora (see [32], and papers reviewed therein; [13,35]). Therefore, germination success (whether a seed germinates), germination timing (days between exposure to warm temperature and germination), and growth rate (cm/day) may represent key invasion traits. At least some of these traits appear to be sensitive to environmental differences [47,53]. In particular, they should respond strongly to two major germination cues: stratification length and spring temperature [25]. In temperate ecosystems, many species require cold stratification, which simulates winter, before their seeds can germinate, a requirement that helps ensure that seeds do not germinate during a mid-winter warm period [4,57,84]. Not surprisingly then, winter length is a key niche variable [38] that may show substantial spatial variation, independent of other climate variables [10]. Given sufficient stratification length, spring temperature dictates the appropriate germination time and growth rate [22,36].

Based on the importance of winter and spring climates, we designed a full-factorial experiment of two stratification lengths and four spring (post-stratification) temperatures, examining responses of germination success, time to germination, and growth rate of introduced (American) and native (European) conspecific populations across the eight climatic regimes. Because these invasive species have flourished and become widespread in their introduced range, we hypothesized that the seeds from the invading populations (North America) will either a) respond differently to spring temperature and stratification treatments than the native populations (Europe)—demonstrating rapid evolution, or b) both introduced and native populations will respond similarly to temperature and stratification treatments, and the most fitness-like trait, germination success, will be high and invariant across the treatments—demonstrating broad environmental tolerance.

2. Materials and methods

2.1. Study species

Following Richardson's definition of invasive species ([65,66], see Supplement for details), seeds were collected from eight herbaceous species that originated in Europe but were introduced to the US, where they have spread and become very widespread [75]: *Alliaria petiolata* (Brassicaceae), *Capsella bursa-pastoris* (Brassicaceae), *Chelidonium majus* (Papaveraceae), *Dactylis glomerata* (Poaceae), *Plantago lanceolata* (Plantaginaceae), *P. major, Rumex crispus* (Polygonaceae), and *Taraxacum officinale* (Asteraceae) (see Haines et al. [37] for authorities). *Alliaria petiolata* exhibited minimal germination, and so was removed from the analysis. These species represent a mix of perennials, biennials, and annuals. Many were intentionally introduced for medicinal or forage uses (for additional details, including time since colonization, see Supplement). All of these species are weedy, widespread invaders in the US, with many impacting crop production and ecosystems (e.g., [27,80]).

2.2. Seed collection

We collected mature seeds from European native populations and North American introduced populations from 15 June to 5 September 2015 (see Fig. 1 for an overview of our methods). Ideally, our samples would represent the full extent of these species' native and introduced ranges. However, their native ranges span Europe, Asia, and North Africa, while their introduced ranges span North America, with some species flourishing from Florida to Alaska (see Supplement for details). Furthermore, we could visit only a limited number of sites during the time when these species would be producing seeds. Consequently, our sample was not representative of the native and introduced ranges of all species, but instead the result of a more targeted sampling effort in the likely source (Europe) of populations introduced to New England, where invaders have been well-studied [79]. European seeds thus came from a total of 63 individuals across 13 sites in nine European countries: Austria, Denmark, France, Germany, Liechtenstein, The Netherlands, Norway, Slovenia, and Switzerland. North American seeds came from a total of 21 individuals across three sites in Massachusetts, USA: Har-

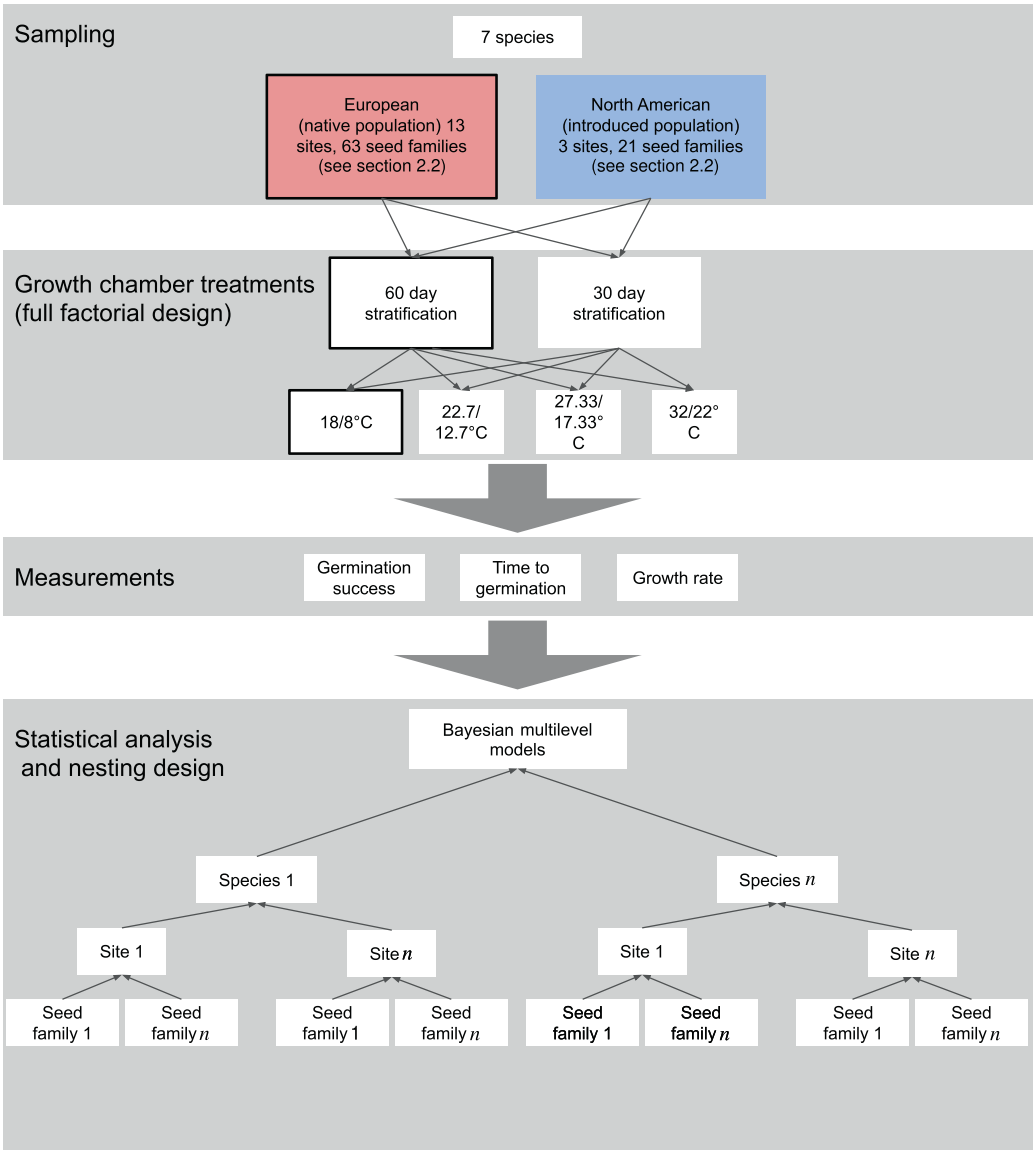

Fig. 1. Conceptual diagram showing our methods. We collected seeds from seven species of plants in both their native (pink) and introduced (blue) ranges. These colors are used in figures throughout to refer to these different ranges. We collected seeds from multiple sites and seed families. We then exposed our seeds to eight treatments in a full-factorial design, and measured whether a seed germinated, how long it took to germinate, and how fast it grew. We then modeled how these traits were affected by origin (native vs. introduced) and the eight treatments. Our model accounted for species, site, and seed family variation by using nested random effects. Boxes with bolded outlines represent the reference levels in our models.

vard Forest LTER (Petersham) Arnold Arboretum at Harvard University (Boston), and Walden Pond (Concord) (see Fig. 2). However, although more European than US sites were used, the number of sites representing *a particular species* was usually equivalent for both the US and Europe (*Plantago Lanceolata*, however, was drawn from more European sites; see 'Experimental Design,' below). Multiple seeds were collected from each parent plant (seed family). Elevation ranged from 0–1202 m in Europe and 20–300 m in USA. Seeds were collected in paper envelopes and stored at room temperature until early September 2015, when they were cleaned and returned to envelopes.

Climate: To examine how climate varied between populations and continents, the mean March, April, and May temperatures (~1 km^2 resolution) for 1970–2000 for each population location were downloaded from WorldClim Version 2 [24] and compared (see Fig. 2). Climates were similar in the native/introduced populations, but showed differences that may be sufficient to drive populations to adapt after invasion, including overall colder March temperatures and warmer May temperatures in the introduced range.

2.3. Experimental design

To test phenological responses to climate, seeds were exposed to eight treatments representing varying climates. Seeds were first subjected to either a long or short stratification treatment, and then planted in one of four spring temperature treatments. All treatments were carried out in growth chambers. For each treatment, 20 representatives of each species (with seven species this equals 140 seeds per treatment) and an additional five representatives from each site of *Plantago lanceolata* (the most heavily sampled species, with 13 populations) leading to a total of 205 seeds per treatment. Site representatives were drawn from the greatest array of seed families (ranging from 8–48 seeds/seed family; this inequality was addressed using multilevel models—see 'Statistical Analysis,' below), and seed family representation was equal across treatments. While when aggregated across all species, the total number of sample sites was greater in the native range (13), the number of sites representing each species were lower and usually similar in both ranges. Thus, sites from the native and introduced ranges were evenly sampled

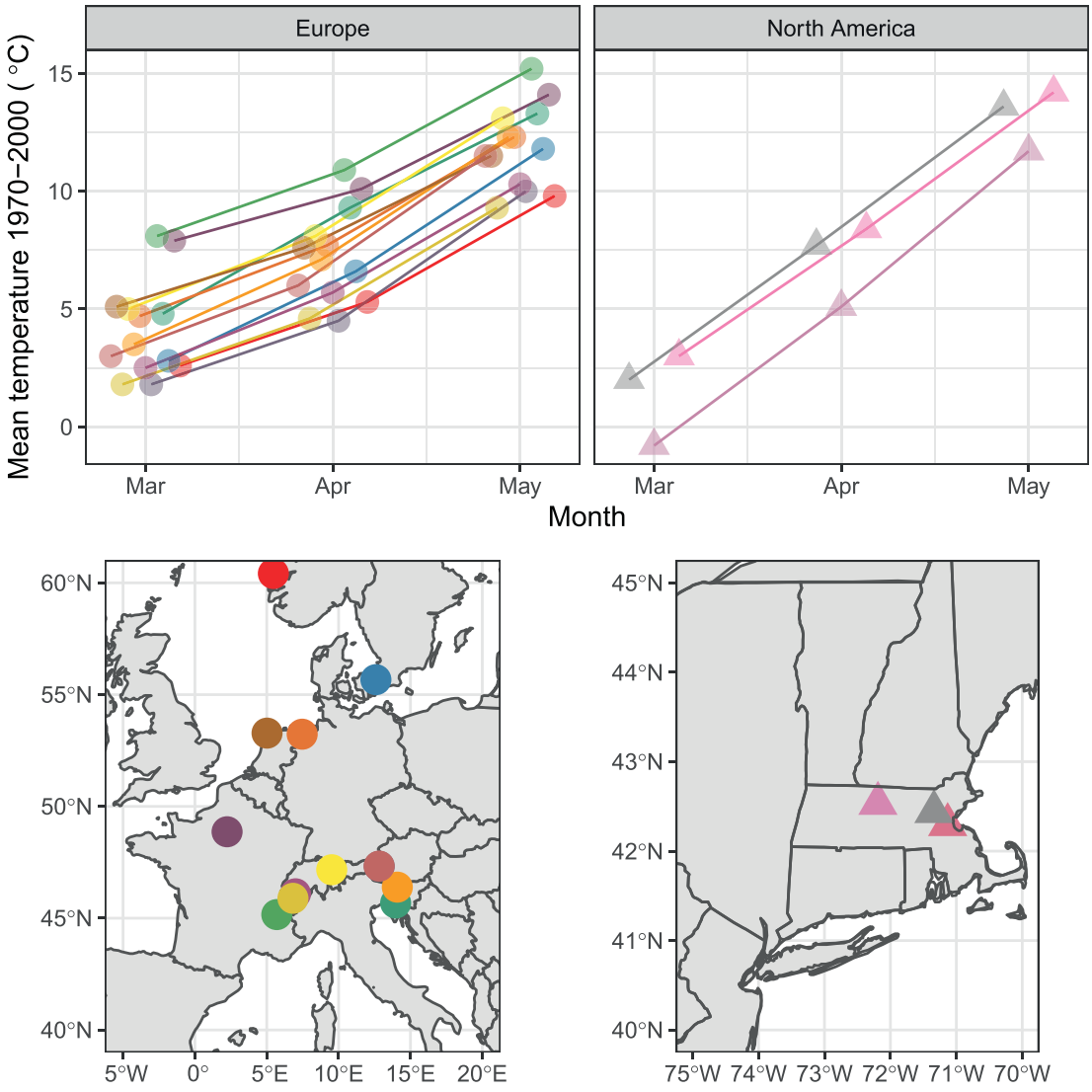

Fig. 2. Spring climates and sampling map of native European sites and introduced North American (New England) sites. Climate shows average (1970–2000) March, April, and May temperatures at each site. Note that spring temperature at native (European) sites are similar to spring temperature experienced by introduced (North American) sites, but also show key differences: introduced sites are exposed to greater increases in temperature from March to May. Data from WorldClim Version 2 [24].

for most species (except for *Plantago lanceolata*, which had more samples from the native population). For instance, a particular species may have been sampled at three invasive sites and three native sites.

2.4. Stratification

We stratified all seeds at 4°C, 70% humidity, 380 ppm of CO_2 (e.g., [51,57]) on moistened Whatman 1 qualitative filter paper in sterile, vented, light-version Greiner bio-one 94 × 16 petri dishes in darkness [4,57] in a single Biochambers TPC-19 Reach-In Growth Chamber for either 30 days (reference level) or 60 days. These two stratification treatments represent intermediate stratification lengths for our species: studies show that our species require stratification lengths between 16 days [57] and 120 days [51]. We began the 60-day stratification treatment in late September 2015; other seeds remained in paper envelopes at room temperature until they were stratified in late October 2015. Water was added to petri dishes every 30 days.

2.5. Germination

On November 23, 2015, seeds from both stratification treatments were transferred into individual pots with soil (see 'Experimental Design' above), which were placed into four different growth chambers (three Biochambers TPC-19 and one Biochambers LTCB-19 Reach-In Growth Chamber) and subjected to four different germination treatments. Temperature varied across treatments—all other measured variables were kept constant, and treatments were rotated through growth chambers to control for unmeasured chamber effects. (Seeds that germinated during stratification were not included in the analysis, but this was a small number and unlikely to affect results.)

Germination Temperature: Our four treatments used four temperatures between 18 and 32°C (explained in 'Thermoperiocity' directly below). Optimal weed germination typically occurs at 20–30°C [39,57,71,84]. We used this sightly broader spectrum to ensure a sufficient variance in germination response.

Thermoperiocity: Our treatments employed daily fluctuations in temperature (thermoperiocity) of 10°C (see e.g., [43,71,74]), translating to treatment temperatures of: 18/8°C (reference temperature), 22.67/12.67°C, 27.33/17.33°C, and 32/22°C. For conciseness, in the following figures and text, we refer to temperature treatments by the high temperature value. All treatments were subjected to 8 hours at the high temperature and the remaining 16 hours at the low temperature [4,57,59,67].

Light type, period, & luminance: We used T5HO fluorescent lights [74], which have a high R:FR ratio as exposure to a high R:FR ratio generally increases germination success (though some studies find germination requires high R:FR ratio or is insensitive, [56,57,84]). We exposed all treatments to eight hours (coinciding with the higher temperature, [4]) of 75 micromol/m2/second, which yielded a daily photon dosage of 2.16 mol/m2. This amount of light should be sufficient to evoke germination response in all species [55]. Because none of our species are known to exhibit high-irradiance response and growth chambers provide less light than normal natural conditions, we erred on the side of high light (see Supplement for additional details).

Planting substrate & water: We planted each seed in its own tray cell, on top of Fafard Growing Mix (a mixture of fine peat moss, fine perlite, and vermiculite) soil. This planting arrangement ensures light availability [72] and provides higher germination success than filter paper [1]. Every two days, seeds were watered until all of the soil had become wet [71]; but not so much that a film of water covered the seeds [2].

Germination and growth rate monitoring: Collection of germination and growth data was masked to population. Seeds were checked during the light period for germination every two days. Germination was defined as the growth of shoot or radical through the seed coat [4,57]. Germination date for each seed was recorded. Germination was monitored until 29 Jan 2016, for a total observation length of 67 days (this is longer than the typical two-week germination trials according to [4,84]). Aboveground linear height of each seedling was measured five times: 7 Dec 2015, 15 Dec 2015, 21 Dec 2015, 4 Jan 2016, and 29 Jan 2016. On 1 Jan 2016, the plants were moved from the growth chambers to a greenhouse subject to the following conditions: natural photoperiod (approximately 10 hours of light/day), 20 to 25°C, and 65% humidity.

2.6. Statistical analysis

To test for evidence of post-introduction rapid evolution across seven species, while accounting for variation due to population and seed family, we used a Bayesian multilevel modeling framework [12]. These multilevel models are robust and generally provide high power and unbiased estimates, especially for fixed effects [52]. This approach yielded estimated (fixed) effects that fully incorporate these multiple levels of variance to produce overall estimates both for each species and generalized across species.

Plant height was roughly linear with time (see Fig. S1), so growth rate was defined as β in the linear model: $height = \alpha + \beta * day + error$, where *error* is normally distributed. This growth rate was calculated for each seed that germinated. The four temperature treatments were recoded as three indicator binary factors, allowing non-linear responses to temperature. For all models (growth rate, germination success, and germination timing), stratification length, continental origin, and temperature were treated as binary fixed effects, with the full suite of 2- and 3-way interactions included. Europe, 18/8°C, and 30 days were reference levels for origin, stratification length, and temperature, respectively (see Fig. 1). Seed family was treated as a random effect, nested within sampling population, nested within species (with both random slopes and intercepts). Growth rate was modeled with a normal error distribution:

$$y_i \sim N(\mu_i, \sigma) \tag{1}$$

$$\begin{aligned}\mu_i = {} & \alpha + \beta_1 \times origin + \beta_2 \times strat \\ & + \beta_3 \times 22.7°C + \beta_4 \times 27.3°C + \beta_5 \times 32°C \\ & + \beta_6 \times origin \times strat + \beta_7 \times origin \times 22.7°C \\ & + \beta_8 \times origin \times 27.3°C + \beta_9 \times origin \times 32°C \\ & + \beta_{10} \times strat \times 22.7°C + \beta_{11} \times strat \times 27.3°C \\ & + \beta_{12} \times strat \times 32°C + \beta_{13} \times origin \times strat \times 22.7°C \\ & + \beta_{14} \times origin \times strat \times 27.3°C + \beta_{15} \times origin \times strat \times 32°C)\end{aligned} \tag{2}$$

Where the α (intercept) and β (slope) coefficients were all specified with the same normally-distributed nested random effects (γ): seed family nested within sampling population, nested within species—$sp[pop[sfamily[i]]]$ (not shown above). Thus, for each γ in [α, β1: β15]:

$$\gamma_{sp[k]} \sim N(\mu_\gamma, \sigma_\gamma) \tag{3}$$

$$\gamma_{sp[pop[j]]} \sim N(\mu_{\gamma_{sp[k]}}, \sigma_{\gamma_{sp[k]}}) \tag{4}$$

$$\gamma_{sp[pop[sfamily[i]]]} \sim N(\mu_{\gamma_{sp[pop[j]]}}, \sigma_{\gamma_{sp[pop[j]]}}) \tag{5}$$

Where *sp* = species, indexed with *k*, *pop* = sampling population, indexed with *j*, *sfamily* = seed family, indexed with *i*, and *strat* = stratification. Germination success was modeled similarly to growth rate, but using a binomial error distribution and logit link function, while germination timing was modeled with a Poisson error distribution and log link function.

All models were estimated using four chains, each with 2000 iterations (1000 devoted to warm-up), and wide priors. All models were built with Stan [12] using `rstanarm` version 2.17.4 [34] in R (R [60]). Chain convergence was confirmed using the Gelman–Rubin statistic/$\hat{R}$ close to one [30]. Model implementations were validated using simulated data; model fits were assessed using posterior predictive checks [28].

Average predictive comparisons: The interactions of treatments (stratification and temperature) and random effects (species, population and seed family) make this model complex, and can make clear interpretations of parameter estimates difficult. To address this, we calculated average predictive comparisons [29] for each stratification and temperature level. These estimates average over interaction terms and the full mixed (fixed and random) effects, to provide a single estimate per level that includes all modeled uncertainty. Additionally, unlike model output from Poisson and Binomial models, which are given in transformed units, average predictive comparisons yield estimates that are in the units of the dependent variable (but always positive, [29]) and thus allow comparisons across effects. Average predictive comparisons can be complicated to implement in certain designs; because we have a full-factorial experiment, our stratification and temperature variables are appropriately balanced (i.e., every temperature occurs at every stratification level) and independent (i.e., every combination of input values is equally likely to co-occur), we calculated average predictive comparisons without any weighting requirement, thus simplifying the computation. See Supplement for equations and details.

3. Results

Germination success: Germination success was high: across all species, populations, and seed families, 76% of seeds germinated. Multiple seeds from every species germinated in every treatment combination. Overall, germination success was insensitive to stratification, temperature, or origin—95% credible intervals (henceforth, 'CrI') for all effects were clustered around zero (Figs. 4, S2; Table S2). Regardless of the climatic conditions, seeds germinated at fairly constant, high levels. Seeds from the introduced and native ranges germinated at similar levels and responded similarly to treatments (see 'origin,' 'strat,' '22.7°C,' '27.3°C,' '32°C,' 'origin × strat,' 'origin × 22.7°C,' 'origin × 27.3°C,' 'origin × 32°C,' 'strat × 22.7°C,' 'strat × 27.3°C,' 'strat × 32°C,' 'origin × strat × 22.7°C,' 'origin × strat × 27.3°C,' 'origin × strat × 32°C' labeled in red in Fig. 4 and in Table S2). Seeds from different local populations of *Plantago lanceolata* also germinated at similar levels (see Fig. S5).

Germination timing: The mean time to germination across all species, populations, and seed families was 12.33 days. Overall, stratification and seed origin had no noticeable effect (see 'origin' and 'strat' in Fig. 4 and Table S3). All species showed advanced germination at the higher temperatures (see '27.3°C,' and '32°C' in Figs. 4, S3; Table S3). However, *Plantago lanceolata* did show advanced germination in

response to temperature × stratification interaction (see Fig. S5). Moreover, all species showed a significant positive interaction effect of origin, stratification and the highest temperature (95% CrI: 0.33–0.85 days; see 'origin × strat × 32˚C' in Fig. 4 and Table S3). That is, the introduced population showed advanced germination at the short stratification/highest temperature combination (Fig. 5). Populations showed fairly homogeneous responses, though temperature × stratification interactions did show some inter-population variability (see Fig. S5).

Growth rate: The mean growth rate was 1.2 mm/day. Overall, growth rate was the most sensitive response variable to treatments, though it was still unaffected by population origin and stratification alone (see 'origin' and 'strat' in Figs. 4, S4; Table S4). Growth was slower at warmer temperatures for all species, but especially *Dactylis glomerata* (see '22.7˚C', '27.3˚C', and '32˚C' in Fig. 4; negative effects indicate slower growth). This effect was larger for each higher temperature; this is in contrast to germination timing, where the change with temperature was more constant (see comparison in absolute change displayed in Fig. 3). However, this decreased growth rate at high temperatures was not uniform across all treatments: in response to one of the higher temperatures (27.3˚C) seeds of all species from North America grew 0.56mm faster per day (95% CrI: 0.14–0.98) (see 'origin × 27.3˚C' in Fig. 4 and Table S4). However, this effect was erased in seeds stratified for 30 days (see Fig. 5, and 'origin × strat × 27.3˚C' in Fig. 4 and Table S4).

4. Discussion

This study leveraged the power of a multi-species growth chamber experiment of native and introduced populations to investigate the importance of post-introduction rapid evolution for widespread plant invasions across a range of winter-to-spring climatic regimes. All seven widespread, weedy, highly invasive plant species responded similarly to climate treatments across the subset of populations we studied, suggesting that broad tolerance underlies these invasive species rather than post-introduction rapid evolution. Across all species, we found only isolated support for post-introduction rapid evolution (when winters were long and springs were warm) of key invasion traits—germination success, timing, and growth rate. Instead, our results suggest that these traits do not need to evolve for these species to invade: wide environmental tolerance in the native populations may instead provide sufficient capacity to exploit novel environments [3]. Post-introduction rapid evolution may provide a helping hand, but—at least for these traits and for these widespread invaders—rapid evolution does not appear essential for invasion success. This is an encouraging result for forecasts of invader responses to climate change as it suggests we may be able to use current estimates to extrapolate to future responses (up to a point).

4.1. Variation across invasion traits

Our results varied somewhat across traits, highlighting the potential benefits of conditioning biological invasion mechanisms on specific invasion traits [50]. We found that post-introduction rapid evolution appeared to play no role in germination success, but may play a role in germination timing and growth rate—under certain treatment conditions (see Fig. 5). This suggests that research and theory may be more productive by aiming to identify which traits are a) broadly tolerant of environmental conditions or b) more likely to rapidly evolve under specific conditions in the introduced range.

The evidence for broad environmental tolerance in our results was especially pronounced in germination success, where all species germinated well, with little regard for climatic conditions. This result suggests that, rather than evolving upon invasion, these widespread invaders drew on the broad environmental tolerance in their native populations. Given the relationship between germination success and fitness (e.g., [20]), this invariant and high germination across climates may be consistent with adaptive phenotypic plasticity [3]. Some have suggested that, while initially species may not need to evolve, they may evolve once achieving a foot-hold [45]. However, many of the study species (e.g., *Dactylis glomerata*) have occupied their introduced range for centuries, yet still show little sign of an evolving, or evolved, germination success in our experiment (i.e., overall, seeds from native and introduced ranges respond similarly to environmental treatments).

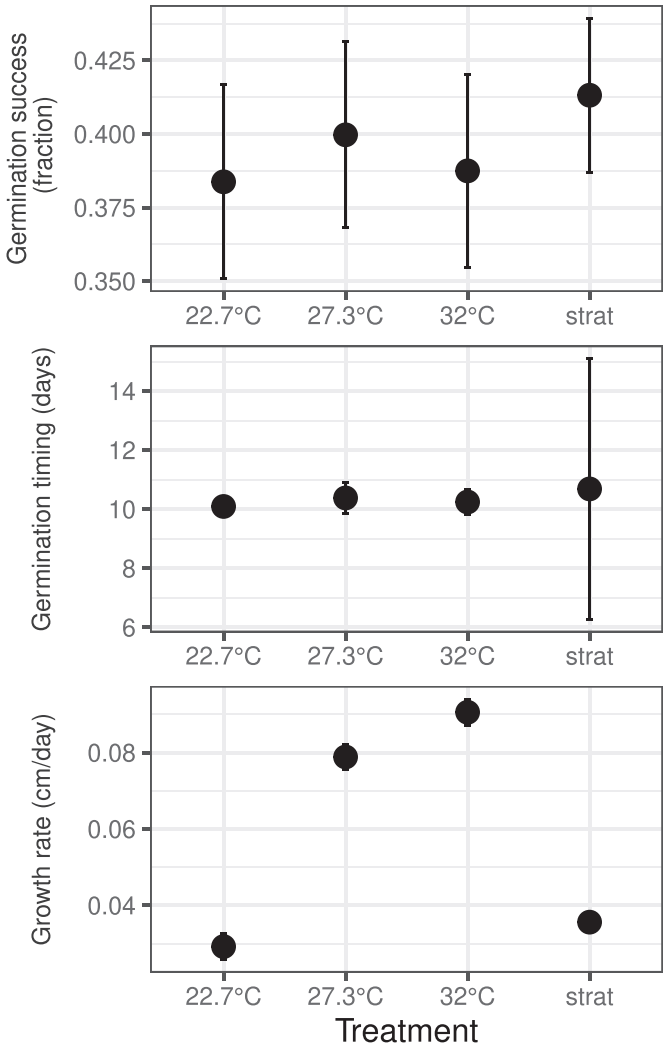

Fig. 3. Average predictive comparisons (± standard error) indicating absolute value differences of germination success (top), germination timing (middle), and growth rate (bottom) show how much change in the dependent variable results from a one unit change in the predictor variable while at once integrating over uncertainty from other effects in the model (including population origin). `strat` refers to the stratification treatment, while `22.7°C`, etc., refer to each temperature binary indicator variable. Higher temperatures had indistinguishable effects on germination timing (middle), but sequentially bigger effects on growth rate (bottom). These calculations include all species from both native and introduced populations. See Supplement for further explanation.

Overall, germination timing and growth rate showed few signs of post-introduction evolution. However, there was some evidence that particular responses have evolved: North American (introduced) populations germinated later and grew faster under longer winter/higher spring temperature combinations (Fig. 5). Taking the climate of North American populations into account (Fig. 2), this rapid post-introduction evolution of growth rate may be adaptive. North American populations experience climates with longer winter stratification (lower mean March temperatures) and hotter spring temperatures (higher mean May temperature). Thus, the capacity to grow faster after being exposed to a long stratification treatment and high temperatures may provide fitness advantages. Furthermore, germinating later after long winters might help

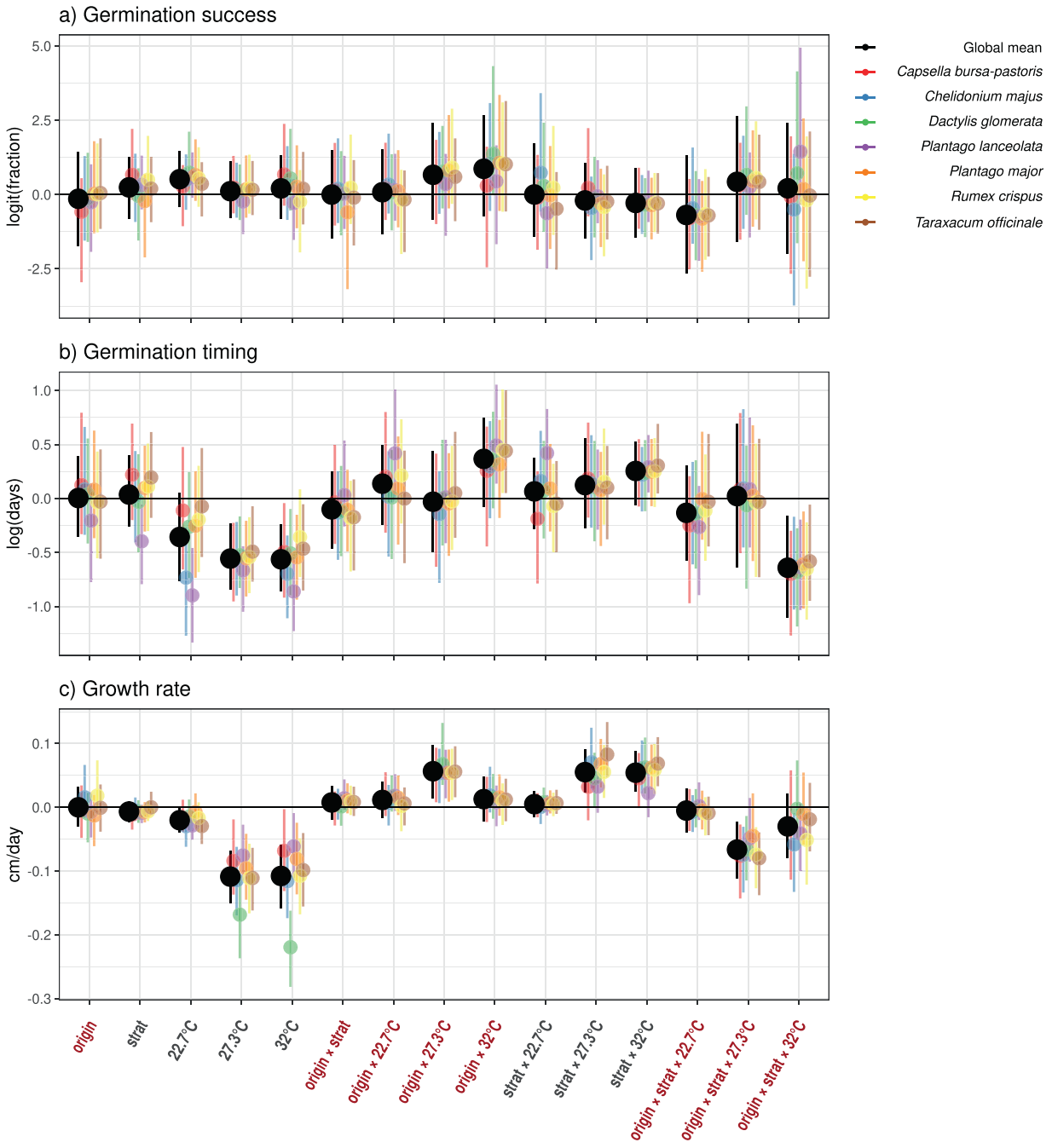

Fig. 4. Multilevel model coefficients with means (circles) 95% credible intervals (lines) for a) germination success, b) germination timing and c) growth rate, showing overall effects across species (black circles, 'global mean') and species-specific random effects (colored circles, for intercept coefficients, see Tables S2, S3, S4). The reference level for temperature is a high of 18°C, sixty days is the reference level for stratification and Europe is the reference level for population origin. Parameters testing for effects only of stratification or temperature are in black, while parameter testing for rapid evolution vs. broad environmental tolerance (i.e., those parameters containing 'origin') are in red.

avoid harsh spring conditions (e.g., frosts), which could have costs for later growth and reproduction. Our sampling and modeling framework accounted for variation across seed family, which suggests that our results are not due to maternal effects. Future work designed to estimate maternal effects, as well as consider residual founder effects [70] and genetic drift [21], could provide important insight into the mechanisms of this potential evolution.

The convergence between experienced climate and the observed change in growth rate, consistent with adaptive post-introduction rapid evolution, suggests that there is an interdependent relationship between trait responses and multivariate environments (i.e., seasonal combinations of winter length and temperature). Considering such interdependencies in the introduced range may be crucial for predicting how plants evolve post-introduction. Not only can these trait–evolution/environment relationships be useful for understanding invasions, they can also help characterize plant capacities to adapt to the multifaceted effects of anthropogenic climate change.

4.2. Implications for invader responses to climate change

Our evidence for broad environmental tolerance suggests that these widespread invasive species may continue to perform well with contin-

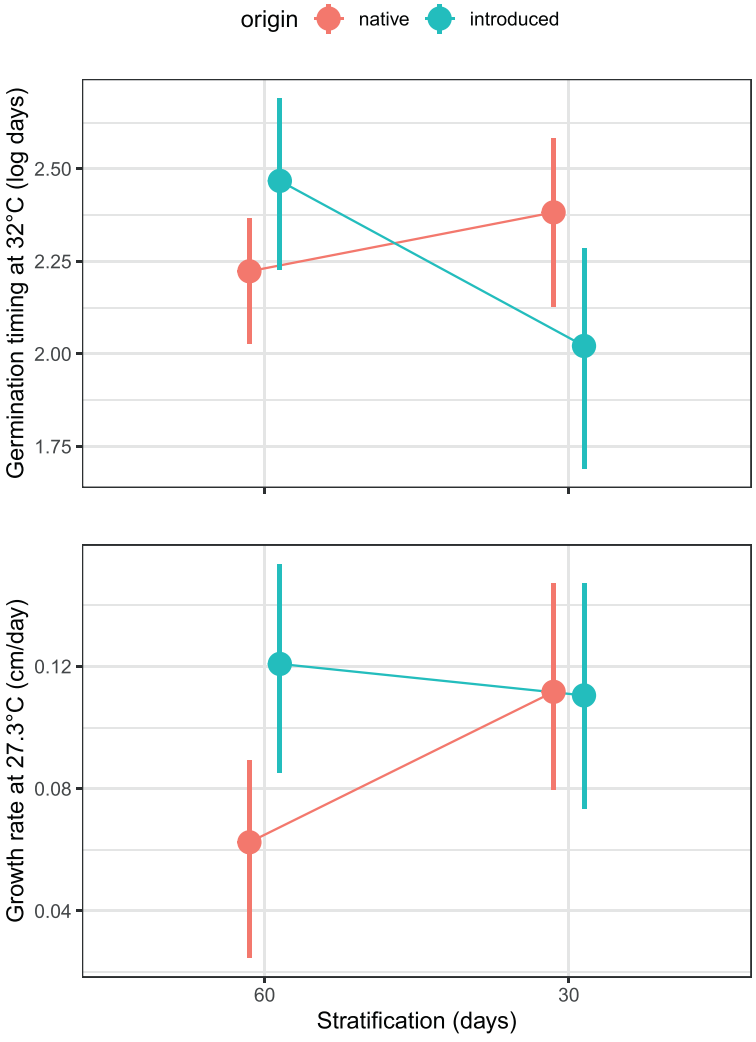

Fig. 5. Significant interaction effects of native vs. introduced origin on germination timing (top) and growth rate (bottom). There were no significant effects of origin on germination success. Uncertainty intervals represent posterior predictions across all species (showing 50% credible intervals). For all coefficient estimates, see Fig. 4 and Tables S3, S4).

ued climate change, without any evolution in these traits. This inference may hold for other widespread species, too. Plant invasions have long been used as a natural experiment for studying plants more generally (e.g., [85]). In that light, these results can be seen as a test of how widespread species may react to rapid climatic change, where the climate change experienced when a plant colonizes a new environment (i.e., introduced range) is a proxy for the anthropogenic climate change that plants are experiencing now. Our results showing that all species germinated earlier at the three higher temperatures, combined with the invariability of germination success, suggests the prevalence of broad environmental tolerance. These results indicate that widespread plants may have the capacity to maintain their germination success and germinate/grow rapidly despite the changing climate. While our study focused on widespread invaders, future research should test if temperate plant species with small range sizes share this broad environmental tolerance, or if these localized species may become inferior competitors as the climate changes. If the latter case is true, then climate change may increase the dominance of widespread species.

Our findings that species may adapt their growth rate under certain conditions suggests that invasive species may have the capacity to adapt to the changing winter and spring temperature regimes that are expected under anthropogenic climate change [44]. If species are adapting to specific combinations of winter × spring climatic regimes, then forecasters would need to consider evolutionary responses to multivariate or seasonal environments. Our results also echo the importance of designing experiments that vary both winter length and spring temperature in order to observe responses to climate change (e.g., [6]).

4.3. Study limitations & extensions

Our results come from a limited number of individuals and populations collected from the introduced range (see Fig. 2; Table S1). The small amount of geographic variation captured in the introduced range may have introduced bias. Our sampling sites show substantial climate variation (Fig. 2), highlighting potentially important climatic differences, but additional sampling across the introduced range would provide insights into whether our results generalize to other regions or if context- (or climate-) dependency is the norm in the introduced range. To this aim, we suggest future research could build upon our findings by sampling across distinct introduced-range climates to help understand which traits evolve where, post-introduction.

We harnessed the benefits of growth chambers to provide a common set of precisely controlled multivariate environments for seven species; however, the benefits of this design trade off with a lack of realism. In contrast to reciprocal field common garden experiments, which can integrate many important factors [7,31], our approach lacked most biotic interactions and natural climatic variation. Yet our approach let us tease apart the multivariate nature of climate (stratification × temperature) and examine evidence for post-introduction rapid evolution across a large range of introduced climates. We believe combining simi-

lar growth chamber designs with Bayesian modeling approaches, which integrate across multiple levels of variance (species, population, seed family), provides a tractable approach for other populations, other traits, and other combinations of climate factors (including precipitation). Such future small-scale growth chamber studies could enable robust meta-analyses capable of identifying the traits and climate responses for which post-introduction rapid evolution is, or is not, essential for invasion success, and may guide where best to invest the intensive resources required for reciprocal field common garden experiments.

5. Conclusions

Our results show that post-introduction rapid evolution of germination and growth traits is unlikely to be essential for all plant invasions and that current phenological flexibility seen in invaders was likely present in their native ranges. This suggests that broad environmental tolerance may be important for invasion success in these seven widespread invaders. Post-introduction rapid evolution may still play a role, especially in more extreme or different environments. For example, Linde et al. [48] found that *Capsella bursa-pastoris* evolved to colonize high-altitude and desert environments in California. In contrast, our temperate population comparisons showed little sign of rapid evolution, suggesting the tolerance traits contained in temperate native populations may be suitable as long as the introduced environment is not too different [3]. Our findings provide support for the speculation by van Kleunen and colleagues (2010) that future invasions can be predicted by species' characteristics (such as broad environmental tolerance), but perhaps only for specific traits (such as germination success). Consequently, managers can perhaps best guard against future invasions by targeting widespread weedy species and preventing them from dispersing beyond their native ranges. Likewise, our results suggest that current estimates of invaders' responses to diverse climates may forecast their future responses under continued climate change.

Authors' contributions

HNE and EMW conceived the study and designed the methods; HNE led the data collection, analysis, and writing, with assistance from EMW. HNE and EMW contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Thanks to E. Forrestel for mentorship to HNE. Thanks to J. Williams and H. Branch for fruitful discussions. Thanks also to D. Flynn, S. Gee, J. Samaha, and T. Savas for help transplanting, collecting, and measuring. Thanks to F. Rosin, K. Woodruff, and J. Gard for help with collection and growing logistics. Thanks to S. Fritz for help with data input. Thank you to A. Acosta, D. Buonaiuto, C. Chamberlain, A. Delgado, A. Ettinger, N. Gilbert, C. Husic, and M. Rucinski for comments on earlier drafts of this paper. Thanks to J. Eyster, S. Stalhandske, and G. Barbone for assistance with and camaraderie during field sampling. This field work was supported by the Harvard College Undergraduate Research Fund and the Harvard University Center for the Environment Undergraduate Summer Research Fund. We also thank two anonymous reviewers.

Data and code

All R code and data necessary to reproduce these results have been archived with the Open Science Foundation (OSF): http://doi.org/10.17605/OSF.IO/DNGHW.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100023.

References

[1] C.J. Andrews, V.D. Burrows, Increasing winter survival of dormant seeds by a treatment inducing secondary dormancy, Can. J. Plant Sci. 54 (1974) 565–571.
[2] Association of Official Seed Analysts, *Rules for testing seeds* (tech. rep.), Proc. Assoc. Off. Seed Anal. (1960).
[3] H. Baker, Charateristics and modes of origin of weeds, in: H. Baker, G. Stebbins (Eds.), The genetics of colonizing species, Academic Press, 1965, pp. 147–168.
[4] Baskin, C. C., & Baskin, J. M. (1998). Seeds: ecology, biogeography, and evolution of dormancy and germination. San Diego.
[5] C. Bellard, P. Cassey, T.M. Blackburn, Alien species as a driver of recent extinctions, Biol. Lett. 12 (2) (2016) 20150623.
[6] G. Bernareggi, M. Carbognani, A. Mondoni, A. Petraglia, Seed dormancy and germina- tion changes of snowbed species under climate warming: the role of pre- and post-dispersal temperatures, Ann. Botany 118 (3) (2016) 529–539.
[7] J.L. Blois, P.L. Zarnetske, M.C. Fitzpatrick, S. Finnegan, Climate change and the past, present, and future of biotic interactions, Science 341 (6145) (2013) 499–504.
[8] B. Blossey, R. Notzold, Evolution of increased competitive ability in invasive nonindige- nous plants: a hypothesis, J. Ecol. 83 (5) (1995) 887–889.
[9] D.G. Bock, C. Caseys, R.D. Cousens, M.A. Hahn, S.M. Heredia, S. Hübner, K.G. Turner, K.D. Whitney, L.H. Rieseberg, What we still don't know about invasion genetics, Mol. Ecol. 24 (9) (2015) 2277–2297.
[10] G.B. Bonan, Ecological Climatology, Cambridge University Press, 2003.
[11] O. Bossdorf, H. Auge, L. Lafuma, W.E. Rogers, E. Siemann, D. Prati, Phenotypic and genetic differentiation between native and introduced plant populations, Oecologia 144 (1) (2005) 1–11.
[12] B. Carpenter, A. Gelman, M.D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. Brubaker, J. Guo, P. Li, A. Riddell, Stan: a probabilistic programming language, J. Statis. Software 76 (1) (2017).
[13] T. Chrobock, A. Kempel, M. Fischer, M. van Kleunen, Introduction bias: cultivated alien plant species germinate faster and more abundantly than native species in Switzerland, Basic Appl. Ecol. 12 (3) (2011) 244–250.
[14] D.R. Clements, A. Ditommaso, Climate change and weed adaptation: can evolution of invasive plants lead to greater range expansion than forecasted? Weed Res. 51 (3) (2011) 227–240.
[15] R.I. Colautti, J.A. Lau, Contemporary evolution during invasion: evidence for differ- entiation, natural selection, and local adaptation, Mol. Ecol. 24 (9) (2015) 1999–2017.
[16] R.I. Colautti, A. Ricciardi, I.A. Grigorovich, H.J. MacIsaac, Is invasion success explained by the enemy release hypothesis? Ecol. Lett. 7 (8) (2004) 721–733.
[17] J.K. Conner, D.L. Hartl, A Primer of Ecological Genetics, Sinauer Associates Incorporated, 2004.
[18] C.C. Daehler, Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration, Annu. Rev. Ecol. Evol. Syst. (2003) 183–211.
[19] M.A. Davis, M. Pelsor, Experimental support for a resource-based mechanistic model of invasibility, Ecol. Lett. 4 (5) (2001) 421–428.
[20] A.I. Domic, J.M. Capriles, G.R. Camilo, Evaluating the fitness effects of seed size and maternal tree size on polylepis tomentella (rosaceae) seed germination and seedling performance, J. Trop. Ecol. 36 (3) (2020) 115–122.
[21] C.G. Eckert, D. Manicacci, S.C.H. Barrett, Genetic drift and founder effect in native versus introduced populations of an invading plant, Lythrum salicaria (Lythraceae), Evolution 50 (4) (1996) 1512–1519.
[22] D.B. Egli, I.F. Wardlaw, Temperature response of seed growth characteristics of soybeans, Agron. J. 72 (3) (1980) 560–564.
[23] C.S. Elton, The Ecology of Invasions by Animals and Plants, 2000th Ed., University of Chicago Press, 1958.
[24] S.E. Fick, R.J. Hijmans, Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas, Int. J. Climatol. (2017).
[25] W.E. Finch-Savage, G. Leubner-Metzger, Seed dormancy and the control of germination, New Phytol. 171 (3) (2006) 501–523.
[26] S.J. Franks, S. Sim, A.E. Weis, Rapid evolution of flowering time by an annual plant in response to a climate fluctuation, PNAS 104 (4) (2007) 1278–1282.
[27] N.T. Froese, R.C.V. Acker, Distribution and interference of dandelion (Taraxacum officinale) in spring canola, Weed Sci. 51 (2003) 435–442.
[28] A. Gelman, J.B. Carlin, H.S. Stern, D.B. Rubin, Bayesian Data Analysis, Hall, Chapman, 2004.
[29] A. Gelman, I. Pardoe, Average predictive comparisons for models with nonlinearity, interactions, and variance components, Sociol. Methodol. 37 (1) (2007) 23–51.
[30] A. Gelman, D.B. Rubin, Inference from iterative simulation using multiple sequences, Statis. Sci. 7 (1992) 457–511.
[31] R.M. Germain, M.M. Mayfield, B. Gilbert, The 'filtering' metaphor revisited: competition and environment jointly structure invasibility and coexistence, Biol. Lett. (8) (2018) 14.
[32] M. Gioria, P. Pyšek, Early bird catches the worm: germination as a critical step in plant invasion, Biol. Invasions 19 (4) (2017) 1055–1080.
[33] O. Godoy, J.M. Levine, Phenology effects on invasion success: insights from coupling field experiments to coexistence theory, Ecology 95 (3) (2014) 726–736.
[34] Goodrich, B., Gabry, J., Ali, I., & Brilleman, S. (2018). rstanarm: {Bayesian} applied regression modeling via {Stan}. R package version 2.17.4.

[35] J. Grime, J.G. Hodgson, R. Hunt, Comparative Plant Ecology: A Functional Approach to Common British Species, Unwin Hyman, 1988.
[36] L. Guilioni, J. Wéry, J. Lecoeur, High temperature and water deficit may reduce seed number in field pea purely by decreasing plant growth rate, Funct. Plant Biol. 30 (11) (2003) 1151–1164.
[37] A. Haines, E. Farnsworth, G. Morrison, New England Wild Flower Society's Flora Novae Angliae: A Manual for the Identification of Native and Naturalized Higher Vascular Plants of New England, Yale University Press, 2011.
[38] J. Harte, S.R. Saleska, C. Levy, Convergent ecosystem responses to 23-year ambient and manipulated warming link advancing snowmelt and shrub encroachment to transient and long-term climate–soil carbon feedback, Global Change Biol. 21 (6) (2015) 2349–2356.
[39] H.T. Hartmann, D.E. Kester, Plant Propagation: Principles and Practices, Prentice-Hall, 2010.
[40] M.R. Helmus, D.L. Mahler, J.B. Losos, Island biogeography of the Anthropocene, Nature 513 (2014) 543–546.
[41] A.P. Hendry, J.K. Wenburg, P. Bentzen, E.C. Volk, T.P. Quinn, Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon, Science 290 (5491) (2000) 516–518.
[42] D.W. Inouye, Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers, Ecology 89 (2) (2008) 353–362.
[43] International Seed Testing Association, International rules for seed testing, Proc. Int. Seed Testing Assoc. (1954) 3–79.
[44] IPCC*Climate Change 2014: Synthesis Report* (tech. rep.), Intergovernmental Panel on Climate Change, Geneva, 2015.
[45] L.J. Lamarque, C.J. Lortie, A.J. Porté, S. Delzon, Genetic differentiation and phenotypic plasticity in life-history traits between native and introduced populations of invasive maple trees, Biol. Invasions 17 (4) (2015) 1109–1122.
[46] C.E. Lee, Evolutionary genetics of invasive species, Trends Ecol. Evol. 17 (8) (2002) 386–391.
[47] E.A. Leger, K.J. Rice, Assessing the speed and predictability of local adaptation in invasive California poppies (Eschscholzia californica), J. Evol. Biol. 20 (3) (2007) 1090–1103.
[48] M. Linde, S. Diel, B. Neuffer, Flowering ecotypes of Capsella bursa-pastoris (L.) Medik. (brassicaceae) analysed by a cosegregation of phenotypic characters (qtl) and molecular markers, Ann. Bot. (Lond.) 87 (1) (2001) 91–99.
[49] R.N. Mack, D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, F.A. Bazzaz, Biotic invasions: causes, epidemiology, global consequences, and control, Ecol. Appl. 10 (3) (2000) 689–710.
[50] J. Maillet, C. Lopez-Garcia, What criteria are relevant for predicting the invasive capacity of a new agricultural weed? The case of invasive American species in France, Weed Res. 40 (1) (2000) 11–26.
[51] J.F. Meekins, B.C. McCarthy, Competitive ability of Alliaria petiolata (garlic mustard, Brassicaceae), an invasive, nonindigenous forest herb, Int. J. Plant Sci. 160 (4) (1999) 743–752.
[52] O. Paccagnella, Sample size and accuracy of estimates in multilevel models, Methodology 7 (3) (2011) 111–120.
[53] S. Paudel, L.L. Battaglia, Germination responses of the invasive triadica sebifera and two co-occurring native woody species to elevated salinity across a gulf coast transition ecosystem, Wetlands 33 (3) (2013) 527–535.
[54] L. Pejchar, H.A. Mooney, Invasive species, ecosystem services and human well-being, Trends Ecol. Evol. 24 (2009) 497–504.
[55] T.L. Pons, Induction of dark-dormancy in seeds: its importance for the seed bank in the soil, Funct. Ecol. 5 (1991) 669–675.
[56] T.L. Pons, Seed responses to light, Seeds (2000) 237–260.
[57] A.I. Popay, E.H. Roberts, Factors involved in the dormancy and germination of Capsella bursa-pastoris (L.) Medik. and Senecio vulgaris L, J. Ecol. (1970) 103–122.
[58] P.J. Prentis, J.R. Wilson, E.E. Dormontt, D.M. Richardson, A.J. Lowe, Adaptive evolution in invasive species, Trends Plant Sci. 13 (6) (2008) 288–294.
[59] R.J. Probert, The role of temperature in the regulation of seed dormancy and germination, Seeds 2 (2000) 261–292.
[60] R Development Core Team, *R: A Language and Environment for Statistical Computing* (tech. rep.), R Foundation for Statistical Computing, Vienna, Austria, 2015 URL.
[61] R.A. Reeb, I. Acevedo, J.M. Heberling, B. Isaac, S.E. Kuebbing, Nonnative old-field species inhabit early season phenological niches and exhibit unique sensitivity to climate, Ecosphere 11 (8) (2020).
[62] M. Rejmanek, D.M. Richardson, What attributes make some plant species more invasive? Ecology 77 (6) (1996) 1655–1661.
[63] D.N. Reznick, C.K Ghalambor, The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution, in: P. Hendry, M.T. Kinnison (Eds.), Microevolution Rate, pattern, Process, Springer, 2001.
[64] C.L. Richards, O. Bossdorf, N.Z. Muth, J. Gurevitch, M. Pigliucci, Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions, Ecol. Lett. 9 (8) (2006) 981–993.
[65] D.M. Richardson, P. Pyšek, J.T. Carlton, A compendium of essential concepts and terminology in invasion ecology, Fifty Years Invasion Ecol. (2011) 409–420.
[66] D.M. Richardson, P. Pyšek, M. Rejmánek, M.G. Barbour, F.D. Panetta, C.J. West, Naturalization and invasion of alien plants: concepts and definitions, Diversity Distribut. 6 (2) (2000) 93–107.
[67] E.H. Roberts, S. Totterdell, Seed dormancy in Rumex species in response to environmental factors, Plant Cell Environ. 4 (2) (1981) 97–106.
[68] M. Sattin, I. Sartorato, Role of seedling growth on weed-crop competition, in: Proceedings of the 10th EWRS (European Weed Research Society) Symposium, Poznań, Poland, 22-26 June 1997, European Weed Research Society, Doorwerth, Netherlands, 1997, pp. 3–12.
[69] M.D. Schwartz, Monitoring global change with phenology: the case of the spring green wave, Int. J. Biometeorol. 38 (1) (1994) 18–22.
[70] R.Y. Shirk, J.L. Hamrick, C. Zhang, S. Qiang, Patterns of genetic diversity reveal multiple introductions and recurrent founder effects during range expansion in invasive populations of Geranium carolinianum (Geraniaceae), Heredity 112 (5) (2014) 497–507.
[71] G.P. Steinbauer, B. Grigsby, Interaction of temperature, light, and moistening agent in the germination of weed seeds, Weeds 5 (1957) 175–182.
[72] M. Tester, C. Morris, The penetration of light through soil, Plant, Cell, Environ. 10 (1987) 281–286.
[73] D. Tilman, C. Lehman, Human-caused environmental change: impacts on plant diversity and evolution, Proc. Natl. Acad. Sci. 98 (10) (2001) 5433–5440.
[74] V.K. Toole, Light control of seed germination, Ass. Official Seed Anal. 53 (1963) 124–143.
[75] R.H. Uva, J.C. Neal, J.M. DiTomaso, Weeds of the Northeast, Cornell University Press, 1997.
[76] M. van Kleunen, E. Weber, M. Fischer, A meta-analysis of trait differences between invasive and non-invasive plant species, Ecol. Lett. 13 (2) (2010) 235–245.
[77] Y. Vitasse, S. Delzon, C.C. Bresson, R. Michalet, A. Kremer, Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden, Can. J. For. Res. 39 (7) (2009) 1259–1269.
[78] J.L. Williams, H. Auge, J.L. Maron, Different gardens, different results: Native and introduced populations exhibit contrasting phenotypes across common gardens, Oecologia 157 (2) (2008) 239–248.
[79] C.G. Willis, B. Ruhfel, R.B. Primack, A.J. Miller-Rushing, C.C. Davis, Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change, PNAS 105 (44) (2008) 17029–17033.
[80] B.E. Wolfe, V.L. Rodgers, K.A. Stinson, A. Pringle, The invasive plant Alliaria petiolata (garlic mustard) inhibits ectomycorrhizal fungi in its introduced range, J. Ecol. 96 (4) (2008) 777–783.
[81] E.M. Wolkovich, E.E. Cleland, The phenology of plant invasions: a community ecology perspective, Front. Ecol. Environ. 9 (5) (2011) 287–294.
[82] E.M. Wolkovich, E.E. Cleland, Phenological niches and the future of invaded ecosystems with climate change, AoB Plants 6 (2014).
[83] E.M. Wolkovich, T.J. Davies, H. Schaefer, E.E. Cleland, B.I. Cook, S.E. Travers, C.G. Willis, C.C Davis, Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change, Am. J. Bot. 100 (7) (2013) 1407–1421.
[84] R.D. Wulff, A. Caceres, J. Schmitt, Seed and seedling responses to maternal and offspring environments in Plantago lanceolata, Funct. Ecol. (1994) 763–769.
[85] T. Yoshida, K. Goka, F. Ishihama, M. Ishihara, S.-I. Kudo, Biological invasion as a natural experiment of the evolutionary processes: introduction of the special feature, Ecol. Res. 22 (6) (2007) 849–854.
[86] M.A. Zettlemoyer, E.H. Schultheis, J.A. Lau, Phenology in a warming world: differences between native and non-native plant species, Ecol. Lett. (2019).
[87] C.M. Zohner, B.M. Benito, J.D. Fridley, J.-C. Svenning, S.S. Renner, Spring predictability explains different leaf-out strategies in the woody floras of north america, europe and east asia (H. Maherali, Ed.), Ecol. Lett. 20 (4) (2017) 452–460.