Invader success and changing climate: Comparisons in the native and introduced range of seven plant species

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Abstract

Invasive plants often have large impacts on ecosystems. Yet we lack a clear understanding of how some species become successful invaders while others do not. Two competing mechanisms have been posited: 1) post-introduction rapid evolution or 2) broad environmental tolerance in the source population. Discovering the determinants of invasion success requires more information on how these two mechanisms drive essential invasion traits, including germination rate, germination timing, and growth rate. Here, we tested for evidence of evolution in these traits by using growth chambers to provide common environments for seven herbaceous plant species sampled from multiple populations in their native (European) and invasive (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). Bayesian multilevel models enabled us to examine responses for each species, as well as across the suite of all seven species. We found consistent results across all species: traits were largely insensitive to population origin, except in response to particular combinations of high-temperature and stratification. This suggests that germination and growth traits of exotic species need not evolve to become successful invaders. Instead, our results suggest that broad environmental tolerance underlies invasion success for this suite of common invaders.

1 Introduction

Exotic plant invasions can transform biodiversity (Bellard et al., 2016; Clavero & Garcia-Berthou, 2005; Walker & Steffen, 1997), and ecosystem function, services, and resilience (Daehler & Carion, 1999; Daehler & Strong, 1994; Ehrenfeld, 2003; Levine et al., 2003; Mack et al., 2000; OTA, 1993; Pejchar & Mooney, 2009; Pimentel et al., 2005; Pyšek & Richardson, 2010; Wilcove et al., 1998). To understand the drivers of these invasions, two key biological mechanisms that plants may use to invade have been identified. Understanding these mechanisms is becoming even more important because invasions may be increasing:

globalization is facilitating extra-range plant dispersal (Helmus et al., 2014; McKinney & Lockwood, 1999; Pyšek et al., 2002; Vitousek et al., 1996; Wittenberg & Cock, 2001). Upon dispersing to a new environment, invasive species can thrive by filling vacant niches (Elton, 1958) or outperforming native plants in high-resource and variable environments (Daehler, 2003; Davis & Pelsor, 2001). These invasible environments may proliferate as humans alter ecosystems (Blois et al., 2013; Harte et al., 2015; Inouye, 2008; Tilman & Lehman, 2001). This changing environment could select for species that can take advantage of the newly created temporal niches and resources through shifts in the timing of flowering and fruiting, etc. (Franks et al., 2007).

Two contrasting mechanisms have been posited to give some plants the capacity to exploit invasible environments: 1) post-introduction rapid evolution and 2) broad environmental tolerance in the source population.

A large body of literature suggests that rapid adaptive evolution is a key driver of invasion success (Clements & Ditommaso, 2011; Colautti & Lau, 2015; Cox, 2004; Fenollosa & Munné-Bosch, 2019; Lambrinos, 2004; Lee, 2002; Prentis et al., 2008; Reznick & Ghalambor, 2001; Sakai et al., 2001; Thompson, 1998; Williamson, 1997). Rapid evolution can enable nonindigenous species to adapt to vacant niches and take advantage of variable and high-resource environments, for example by evolving greater competitive ability when released from natural enemies (Blossey & Notzold, 1995; Bossdorf et al., 2005) or by evolving adaptive plasticity (Richards et al., 2006).

There are many clear examples of rapid evolution abetting plant invasions. For instance, genetic studies of two North American herbaceous goldenrods that invaded Europe, *Solidago altissima* and *S. gigantea* (Asteraceae), showed post-introduction genetic changes in flowering time in response to temperature, due to selection on source-population genetic variation and development of new mutations (Weber & Schmid, 1998). Similarly, the invasive *Centaurea solstitialis* (Asteraceae) in California evolved larger size from standing variation in the founding population (Barker et al., 2017). Also in California, a similar study found that genetic adaptation was driving adaptive phenotypic variation in flowering time of high-altitude and desert populations of *Capsella bursa-pastoris* (Brassicaceae) (Linde et al., 2001). Invasion may even produce evolution sufficient to establish reproductive isolation and trigger speciation, in as few as 13 generations (Hendry et al., 2000). If rapid evolution is so central to invader success, then managers should treat invasives not as static, homogeneous species, but as constantly adapting populations (Lee, 2002).

Yet, despite the support for the importance of rapid evolution, a competing body of literature suggests that invaders need not evolve. Instead, broad environmental tolerance, plasticity and generalist adaptations to human-dominated environments (i.e., weediness) within the source population may give invaders sufficient advantages, obviating the necessity of rapid evolution (Baker, 1965; Bock et al., 2015; Rejmanek & Richardson, 1996; Richards et al., 2006; Schwartz, 1994). Some studies have shown that weediness in the native range is the best predictor of invasiveness (e.g., Maillet & Lopez-Garcia, 2000), while other studies have not found this relationship (Mack, 1996; Perrins et al., 1992). Seeking a unified answer, a meta-analysis of 117 studies found that invasive plants were associated with performance-related traits, and concluded that it may be possible to predict future invaders by those traits

(van Kleunen et al., 2010). However, this reasoning ignores the possibility (as argued by the rapid evolution theory) that these performance-related traits only evolve post-introduction.

One reason why the importance of rapid evolution remains contested is because few experimental designs allow unambiguous discrimination between the two claims. Neither observational datasets (e.g., Wolkovich et al., 2013) nor experimental common gardens (Conner & Hartl, 2004; Vitasse et al., 2009) are sufficient to discriminate. And while genetic studies can identify the existence of rapid evolution, they do not demonstrate the prevalence of this invasion mechanism. Instead, reciprocal common garden experiments with native and invader populations can test these theories (e.g., Lamarque et al., 2015; Williams et al., 2008). For example, a reciprocal common garden experiment of two invasive maple species (*Acer*, Sapindaceae) demonstrated that rapid evolution was important for one species, but plasticity was important for the other (Lamarque et al., 2015). This and other studies show the promise of reciprocal common garden experiments for testing invasion mechanisms. However, despite their utility, they are quite rare and typically only include one or two species due to the immense effort required. Growth chamber experiments offer an attractive alternative: they are easier to control and execute, thereby enabling a large swath 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. Testing such a multitude of species with growth chambers could help identify the mechanism(s) important for invasion success.

Another reason why these claims are contested may be because different mechanisms may underlie different traits. Some traits, such as flowering time, may be under rapid selection (Weber & Schmid, 1998), while others may be broadly tolerant and stable. This may be partly because some traits are known to evolve faster than others (Weiss-Lehman et al., 2017). The importance of rapid evolution vs. broad environmental tolerance should thus be couched in specific traits, rather than overall effects. Thus, understanding invasions requires understanding the mechanisms driving traits most essential for invasion.

Germination and growth traits are some of the most important for granting invasive success (Maillet & Lopez-Garcia, 2000; Sattin & Sartorato, 1997). Invasive success requires the capacity to germinate in novel environments and grow rapidly enough to compete with native flora (Grime et al., 1988). Therefore, germination rate, germination timing, and growth rate may be key to granting invasive success. At least some of these traits appear to be sensitive to environmental differences (Leger & Rice, 2007). Across multiple species, testing how invasive and native population germination and growth traits respond to the environment could test if rapid evolution or broad environmental tolerance drives invasion.

Seeking this more general appraisal of the importance of rapid evolution and broad environmental tolerance of germination and growth traits in invasive plants, this paper reports on a growth chamber experiment of the native and introduced ranges of seven highly invasive herbaceous plant species. We test the degree to which rapid evolution has occurred since the species colonized North America from Europe. This work follows a long history of studies on invaders and phenology (Wolkovich & Cleland, 2014). Our growth chamber experiment enabled us to test the degree to which phenologies in native and invasive populations differ in their response to climate. Specifically, we measured how germination rate, time to germina-

tion, and growth rate of invasive (American) and native (European) conspecific populations responded to an array of temperature and stratification treatments. This study manipulates two key climate elements: temperature and stratification length. These variables act as important phenological cues for plants (Finch-Savage & Leubner-Metzger, 2006). Responding appropriately to these cues may be essential for invasive species. In temperate ecosystems, a cold stratification simulates winter. A minimum period of winter must often pass before seeds can germinate to ensure that seeds do not germinate during a mid-winter warm period (Baskin & Baskin, 1998; Popay & Roberts, 1970; Wulff et al., 1994). Winter length is a key niche variable (Harte et al., 2015) and may show substantial spatial variation, independent of other climate variables (Bonan, 2003). Once the necessary stratification length has been achieved, temperature can cue that it is the appropriate time for a seed to break dormancy. Temperature also plays an important role in controlling plant growth rate (Egli & Wardlaw, 1980; Guilioni et al., 2003). Thus, a range of temperature and stratification treatments will simulate the driving features of the diverse environments in which invasive species thrive.

If rapid evolution is of generalizable importance to invasive plants, we expect to find that seeds from the invading populations (North America) will respond very differently to temperature and stratification treatments than the indigenous populations (Europe) for all or nearly all species. Here we use growth chambers to isolate effects of stratification and temperature, combined with Bayesian multilevel models to test for evidence that rapid evolution drives changes in germination rate, timing and growth rate across a suite of North American invader species. These study species included seven highly-invasive species, many of which have been shown to be responsive to climate.

2 Methods

2.1 Study species

Following Richardson's definition of invasive species (Richardson et al., 2011; Richardson et al., 2000, see Supp. for details), seeds were collected from eight herbaceous species that originated in Europe but were recently introduced to the US, where they have spread and produced substantial populations (Uva et al., 1997): *Alliaria petiolata*(ALLPET), *Capsella bursa-pastoris* (CAPBUR), *Chelidonium majus* (CHEMAJ), *Dactylis glomerata* (DACGLO), *Plantago lanceolata* (PLALAN), *P. major* (PLAMAJ), *Rumex crispus* (RUMCRI), and *Taraxacum officinale* (TAROFF). *A. 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, see Supp.). All of these species have proven prodigious invaders in the US, with many impacting crop production and transforming ecosystems (e.g., Froese & Acker, 2003; Wolfe et al., 2008). Furthermore, those of our study species that are included in the Concord Phenology Dataset (CITE) (CAPBUR, CHEMAJ, PLALAN, and RUMCRI), are on average flowering 4.5 days earlier than they did in the 1800s (compared to less than a day earlier for all 372 species in the dataset). This suggest that these invasive species exhibit flexible phenologies—flexibility that may be key to their success. Although this paper focuses on a different set of phenologies, the flexible flowering phenolgoy suggests that these species may

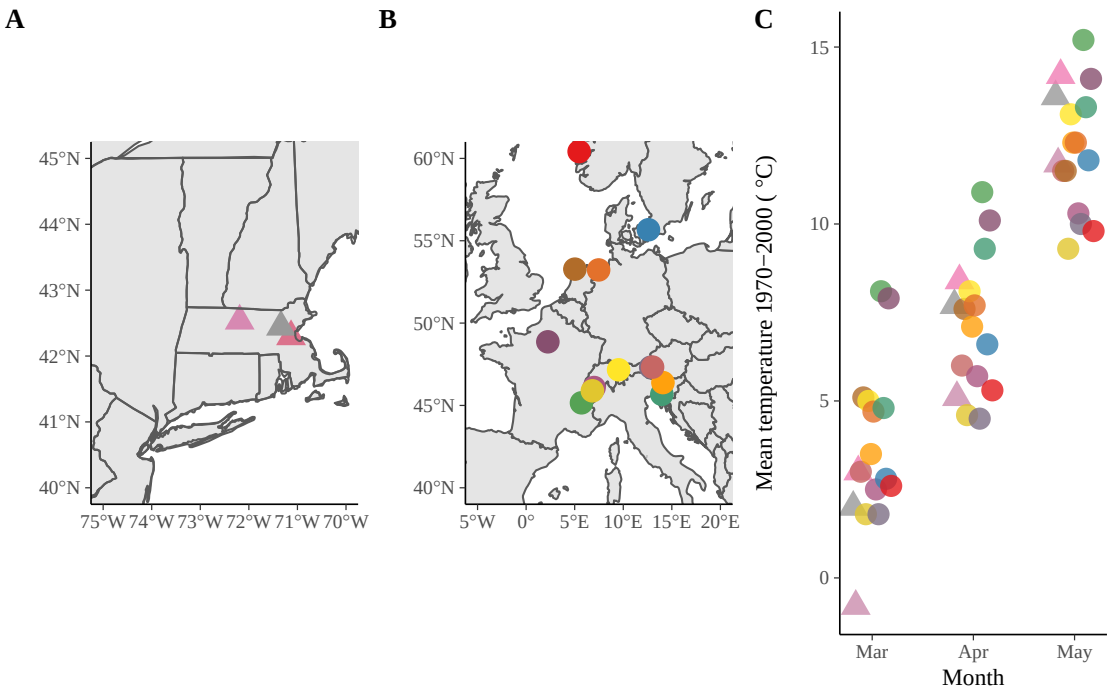

Figure 1: Map of collection sites of (A) invasive populations in New England and (B) native populations in Europe and (C) average March, April, and May temperatures at each site. Note that spring temperature at native populations (circles) are comparable to spring temperature experienced by invasive populations (triangles)

also exhibit flexible germination or growth rate traits. If so, this work will be able to identify whether this flexibility is due to rapid evolution. Thus, these species offer apt subjects to test the importance of rapid evolution in invader germination and growth traits.

2.2 Seed collection

We collected mature seeds from native European populations and invasive North American populations from June 15th to September 5th 2015. European seeds came from 63 individuals across 13 sites in nine European countries: France, The Netherlands, Germany, Denmark, Norway, Austria, Slovenia, Liechtenstein, and Switzerland North American seeds came from 21 individuals across three sites in Massachusetts, USA: Harvard Forest, Arnold Arboretum at Harvard University, and Walden Pond (see 1). Elevation ranged from 0–1202 m in Europe and 20–300 m in USA. Seeds were collected in paper envelopes and stored at standard 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 (Fick & Hijmans, 2017) and compared (see Figure 1). Climates did not differ substantially between native/introduced populations.

2.3 Experimental Design

To test phenological responses to climate, seeds were exposed to eight treatments representing varying climates. Seeds were first subjected either a long or short stratification treatment, and then planted in one of four temperature treatments. All treatments were carried out in growth chambers. For each treatment, ten representatives of each species (with seven invasive species this equals 140 seeds per treatment) and an additional five representatives of each local population of *Plantago lanceolata* (the most heavily sampled species, with 13 populations) leading to a total of 205 seeds per treatment. Germination, time to germination, and aboveground linear height were recorded. Local population representatives were drawn from the greatest diversity of seed families, and seed family representation was equal across treatments.

2.4 Stratification

We stratified all seeds at 4°C, 70% humidity, 380 ppm of CO_2 (e.g., Meekins & McCarthy, 1999; Popay & Roberts, 1970)) on moistened Whatman 1 qualitative filter paper in sterile, vented, light-version Greiner bio-one 94x16 petri dishes in darkness (Baskin & Baskin, 1998; Popay & Roberts, 1970) in a single Biochambers TPC-19 Reach-In Growth Chamber for either 30 days or 60 days. These two stratification treatments represents intermediate stratification lengths for our species: studies show stratification of our species vary from 16 days (Popay & Roberts, 1970) to 120 days (Meekins & McCarthy, 1999). We began the 60-day stratification treatment in late September 2015; other seeds remained in paper envelopes at room temperature until they were in turn 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 the unmeasured effects. Seeds that germinated during stratification were discarded.

Germination Temperature: Our four treatments used temperatures between 18 and 32°C. Optimal weed germination typically occurs at 20-30°C (Hartmann & Kester, 2010; Popay & Roberts, 1970; Steinbauer & Grigsby, 1957; Wulff et al., 1994). 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., International Seed Testing Association, 1954; Steinbauer & Grigsby, 1957; Toole, 1963), translating to treatment temperatures of: 18/8°C, 22.67/12.67°C, 27.33/17.33°C, and 32/22°C. All treatments were subjected to 8 hours at the high temperature and the re-

maining 16 hours at the low temperature (Baskin & Baskin, 1998; Popay & Roberts, 1970; Probert, 2000; Roberts & Totterdell, 1981).

Light type: We used T5HO fluorescent lights (Toole, 1963), which have a high R:FR ratio as, generally, exposure to a high R:FR ratio increases germination rates (though across studies, some find successful germination requires high R:FR ratio or no effect Pons, 2000; Popay & Roberts, 1970; Wulff et al., 1994).

Period/luminance of light: We exposed all treatments to eight hours (coinciding with the higher temperature(Baskin & Baskin, 1998)) of 75 micromol/m^2/second, yielding a daily photon dosage of 2.16 mol/m^2. This amount of light should be sufficient to evoke germination response in all species (Pons, 1991). Because none of our species are known to exhibit high-iradiance response (HIR) (except perhaps an unsampled population of DACGLO (Probert et al., 1986)), we erred on the side of too much light (see Supp. for additional details).

Planting substrate: 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. We planted seeds on top of soil to ensure light availability (Tester & Morris, 1987) and because some species germinate poorly on filter paper (Andrews & Burrows, 1974).

Water: Every two days, seeds were watered until all of the soil had become wet (Steinbauer & Grigsby, 1957); but not so much that a film of water covered the seeds (of Official Seed Analysts., 1960).

Germination and growth rate monitoring: Collection of germination and growth data was blind 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 (Baskin & Baskin, 1998; Popay & Roberts, 1970). Germination date for each seed was recorded. Germination was monitored until January 29, 2016-01-29, for a total observation length of 67 days (this is longer than the typical two-week germination trials (Baskin & Baskin, 1998; Wulff et al., 1994)). Aboveground linear height of each seedling was measured five times: 2015-12-07, 2015-12-15, 2015-12-21, 2016-01-04, and 2016-01-29. Plant height was roughly linear with time (see Figure S1), so growth rate was defined as β in the linear model: $height = \alpha + \beta * day$. This growth rate was calculated for each seed that germinated. On 2016-01-01, 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

Testing for evidence of rapid evolution in complex multispecies, multi-population designs can be challenging with classic frequentest approaches without balanced sampling and high replication. Thus we used a Bayesian multilevel modeling framework to enable fitting a model including full effects, and estimated variance, of species, population and seed family (Carpenter et al., 2017). This yielded estimated (fixed) effects that transcend this variability in species, populations, and seed families to reveal generalized patterns.

For all models (growth rate, germination rate, 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, temperature, and stratification length, respectively; temperature was recoded as three dummy binary factors, allowing non-linear responses to temperature. Seed family was treated as a random effect, nested within sampling population, nested within species (with random slopes and intercepts). Growth rate was modeled with a normal error distribution:

$$
\begin{aligned}
y_i =& N(\mu_i, \sigma) && (1)\\
\mu_i =& \alpha_{sp[pop[sfamily[i]]]} + \beta 1_{sp[pop[sfamily[i]]]} \times origin + \beta 2_{sp[pop[sfamily[i]]]} \times strat && (2)\\
&+ \beta 3_{sp[pop[sfamily[i]]]} \times temp1 + \beta 4_{sp[pop[sfamily[i]]]} \times temp2 + \beta 5_{sp[pop[sfamily[i]]]} \times temp3\\
&+ \beta 6_{sp[pop[sfamily[i]]]} \times origin \times strat + \beta 7_{sp[pop[sfamily[i]]]} \times origin \times temp1\\
&+ \beta 8_{sp[pop[sfamily[i]]]} \times origin \times temp2 + \beta 9_{sp[pop[sfamily[i]]]} \times origin \times temp3\\
&+ \beta 10_{sp[pop[sfamily[i]]]} \times strat \times temp1 + \beta 11_{sp[pop[sfamily[i]]]} \times strat \times temp2\\
&+ \beta 12_{sp[pop[sfamily[i]]]} \times strat \times temp3_+ \beta 13_{sp[pop[sfamily[i]]]} \times origin \times strat \times temp1\\
&+ \beta 14_{sp[pop[sfamily[i]]]} \times origin \times strat \times temp2 + \beta 15_{sp[pop[sfamily[i]]]} \times origin \times strat \times temp3)
\end{aligned}
$$

Where the α and each β coefficient were specified with nested random effects. For each γ in $[\alpha, \beta 1 : \beta 15]$:

$$
\begin{aligned}
\gamma_{sp[pop[sfamily[i]]]} =& N(\mu_{\gamma_{sp[pop[j]]}}, \sigma_{\gamma_{sp[pop[j]]}}) && (3)\\
\gamma_{sp[pop[j]]} =& N(\mu_{\gamma_{sp[k]}}, \sigma_{\gamma_{sp[k]}}) && (4)\\
\gamma_{sp[k]} =& N(\mu_\gamma, \sigma_\gamma) && (5)
\end{aligned}
$$

Where sp = species, indexed with k, pop = sampling population, indexed with j, $sfamily$ = seed family, indexed with i, and $strat$ = stratification. Germination rate 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 (Carpenter et al., 2017) using `rstanarm` version 2.17.4 (Goodrich et al., 2018) in R (R Development Core Team, 2015). Chain convergence was confirmed using the Gelman-Rubin statistic/$\hat{R}$ close to one (Gelman & Rubin, 1992). Model implementations were validated using simulated data; model fits were assessed using posterior predictive checks (Gelman et al., 2004).

Average predictive comparisons The interactions and random effects make this model complex, and frustrate clear interpretation of parameter estimates. Average predictive comparisons can increase interpretability of variables in complex models (Gelman & Pardoe, 2007). Across interaction terms and mixed effects, this method is capable of providing a single point estimate and associated uncertainty of the impact of a given parameter. 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) (Gelman & Pardoe, 2007). Average predictive comparisons translate the variability in parameter draws directly into uncertainty in estimates (Gelman & Pardoe, 2007). This makes average predictive comparisons well-suited for complex Bayesian models. However, despite being theoretically introduced more than a decade ago, they remain complicated to implement. However, our stratification and temperature variables are balanced and independent (i.e., every combination of input values is equally likely to co-occur), so we can ignore average predictive comparison's weighting requirement, thus simplifying the computation. Thus we calculated average predictive comparisons for stratification and each temperature factor.

Data, code Data and R code is available on github at XXX

3 Results

Germination rate Germination rate was high: 76% of seeds germinated. Overall, germination rate was insensitive to temperature, stratification, or origin—95% credible intervals (CrI) for all effects were clustered around zero (Figures 2, S2; Table S2). Regardless of the climatic conditions, they germinated at fairly constant, high rates. Seeds from the invasive and native ranges germinated at similar rates and responded similarly to treatments. Seeds from different local populations also germinated at similar rates (see Figure S5).

Germination timing The mean time to germination was 12.33 days. Overall, all species germinated slower at the lowest temperature, but germinated at similar, faster speeds at the three higher temperatures, showing that temperature response is non-linear (see Figures 2,S3; Table S3). Overall, stratification and seed origin had no noticeable effect; however, PLALAN did show faster germination in response to med-low temperature × stratification interaction (see Figure S5). Additionally, all species showed a significant positive interaction effect of origin, stratification and the higher temperature (95% CrI: 1.05–2.9 days). Populations showed fairly homogeneous responses, though temperature × stratification interactions did show some inter-population variability (see Figure S5).

Growth rate The mean growth rate was 1.2 mm/day. Overall, growth rate was the most sensitive to treatments, though it was still unaffected by stratification length or population origin (see Figures 2, S4; Table S4). Growth rate decreased at warmer temperatures for all species, but especially DACGLO. This decrease got progressively bigger for each higher temperature; this is in contrast to germination timing, where the decrease with temperature was more constant (see comparison in absolute change displayed in Table 1). However, this decreased growth rate at high temperatures was not uniform across all treatments: for one of the higher temperatures (temp2) seeds stratified for 60 days and originating in North America (the invasive range) grew 0.74mm faster per day (95% CrI: 0.22–1.27) than those stratifed for 30 days from Europe (see 'origin × strat × temp2' in Table S4).

Table 1: Average predictive comparisons provide an additional interpretation of the results. They show, on average, how much change in the dependent variable results from a one unit change in the predictor variable. Note that all changes, whether positive or negative, are reported as positive. The table shows that higher temperatures had indistinguishable effects on germination timing, but sequentially bigger effects on growth rate.

variable	germination rate (fraction)	germination date (days)	growth rate (mm/day)
stratification	0.44 ± 0.02	9.6 ± 0.52	0.42 ± 0.02
temperature 1	0.39 ± 0.03	10.2 ± 0.34	0.29 ± 0.03
temperature 2	0.39 ± 0.03	10.2 ± 0.35	0.79 ± 0.03
temperature 3	0.38 ± 0.03	10.3 ± 0.34	0.91 ± 0.03

4 Discussion

This study leveraged the power of a multi-species growth chamber experiments of native and introduced populations to investigate the importance of rapid evolution for invasive success. Across seven highly invasive plant species, we found only isolated support for the prevalence of post-introduction rapid evolution of key invasion traits of germination rate, timing, and growth rate. Instead, our results support the theory that these traits do not need to evolve for these species to invade: weediness, wide environmental tolerance, plasticity, or generalist traits in the source populations likely provide sufficient capacity to exploit novel environments (Baker, 1965). Rapid evolution may provide a helping hand, but contrary to the many claims about the essentiality of rapid evolution in invasive species, it but may not be the dominant mechanism for invasion success, at least for these traits and these species.

These findings are especially pronounced in germination rate, where all species germinated well and with scant sensitivity to climatic conditions, suggesting that the source populations of invading species provided invaders with the capacity to germinate in any environment, without the need to evolve. Some have suggested that while initially species may not need to evolve, they may once achieving a foot-hold (Lamarque et al., 2015). However, many of the study species (e.g., *Dactylis glomerata*) have occupied their invasive range for centuries, yet still show little sign of an evolving germination response.

Overall, germination timing and growth rate did not show signs of post-invasion evolution. However, there was some evidence that particular responses have evolved: North American (invasive) populations appear to have evolved to germinate later and grow faster under high-temperature/long stratification combinations. Taking the climate of North American populations into account (Figure 1), this growth rate evolution may be adaptive. North American populations experience climates with longer winter stratification (lower mean March temperatures) and hotter growing temperatures (higher mean May temperature). Thus, the capacity to grow faster at high temperatures after being exposed to our long stratification treatment may provide fitness advantages. Although it is possible that these differences could be residual founder effects (Shirk et al., 2014), a result of genetic drift (Eckert et al., 1996), or that germination rate is not a fitness trait, the convergence with experienced climate

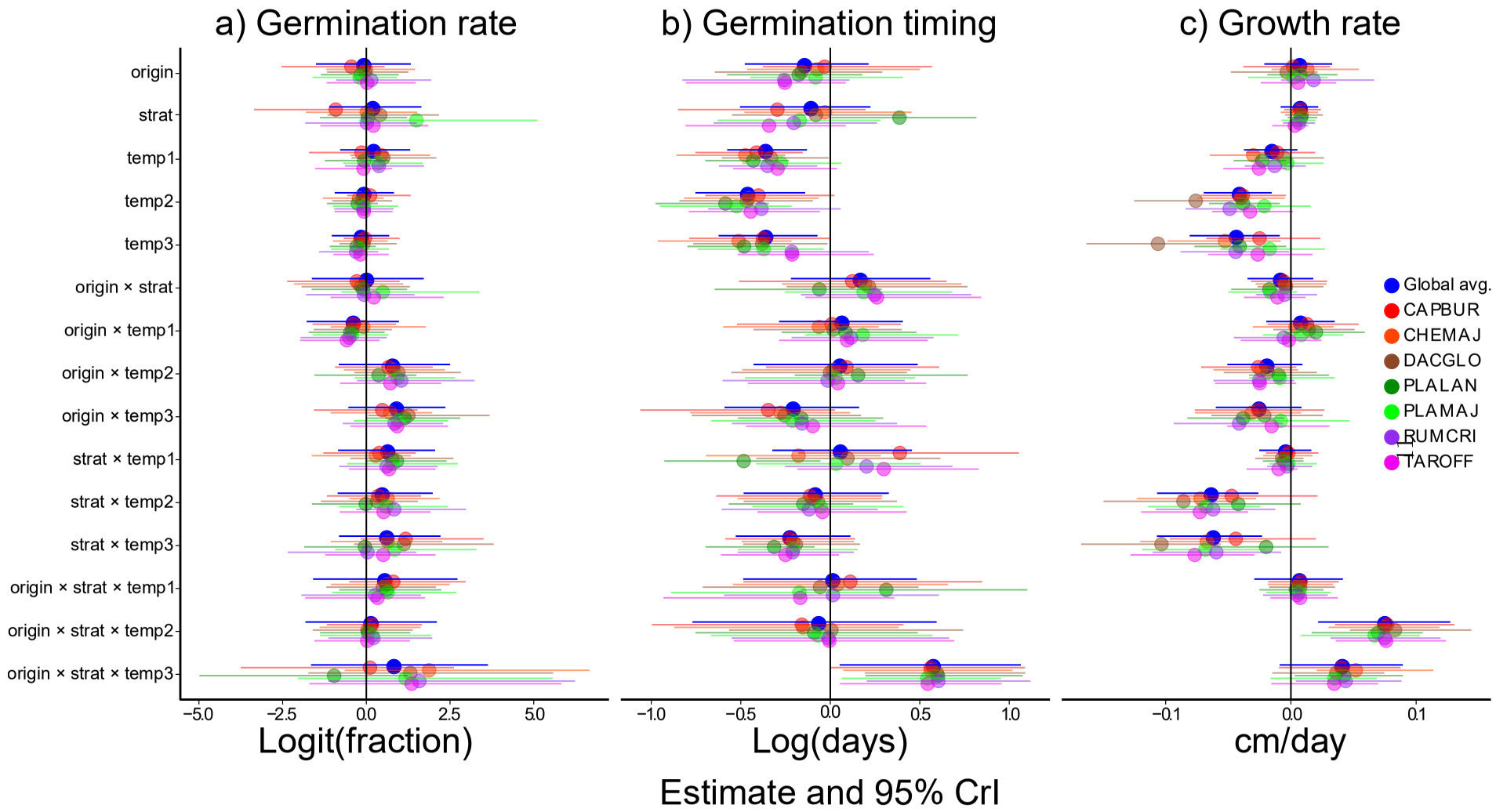

Figure 2: Multilevel model coefficients with 95% credible intervals, showing global average effects and species random effects. Intercept coefficients not shown. a) model of germination rate, b) model of germination timing and c) model of growth rate

suggests that this observed change in growth rate is a sign of adaptive evolution.

These results highlight the need to condition biological invasion mechanisms on specific invasion traits. We found that rapid evolution played no role in germination rate, but did play a limited role in growth rate for these species. This suggests that research and theory aimed at identifying which traits are likely to rapidly evolve to enable invasion may yield more insights than testing for an overall mechanism of invasion that is consistent across traits. We found that germination timing and growth rate traits are most likely to evolve in response to specific combinations of spring temperatures and winter length. This result suggests that considering the invasive range's interdependent *multivariate* environment may be critical for predicting how traits evolve post-introduction. Not only can these trait evolution/environment relationships be useful for understanding invasions, they can also help delineate plant capacities to adapt to the multifaceted effects of anthropogenic climate change.

Our findings preliminarily suggest that these invasive species may be able to adapt to changing climates. Because cold-stratification is a simulation of temperate winter, the evidence that species can adapt their growth rate in accordance with winter length and spring temperature suggests that they may have the capacity to adapt to changing winter lengths and spring temperatures that anthropogenic climate change is bringing (IPCC, 2015). These results also echo the importance of varying both winter length and spring temperature in order to observe responses to climate change (e.g., Bernareggi et al., 2016).

Our results come from a limited number of individuals and populations collected from the invasive range (see Figure 1; Table S1), yet our sampling sites show substantial climate variation (Figure 1), highlighting potentially important climatic differences between Europe and North America that may shape invasions. While additional sampling across the invasive range would have yielded greater geographical inference to our findings, it may also have made the complex stratification by temperature responses harder to detect—if such responses are specific to local climate regimes. Based on our findings, we suggest sampling across distinct invasive range climates could help understand which traits evolve where post-introduction. Such studies could leverage Bayesian modeling to include climate as a predictor, while controlling for other factors (as our Bayesian multilevel modeling helped control for our greater sampling effort in the native range).

Our study leveraged the capacity of growth chambers to simultaneously study how seven species respond to eight climate treatments in a precisely controlled design, however, this design does lack some of the real-world features of reciprocal common garden experiments, such as biotic interactions, which may be important for determining invasions (Blois et al., 2013; Germain et al., 2018). Nevertheless, by focusing on multivariate climate and controlling for all other factors, we were able determine that rapid evolution is largely unimportant for thriving in a range of alien climates. Furthermore, while common garden experiments are fundamentally idiosyncratic and resource-intensive, our growth chamber design and Bayesian modeling approach could be seamlessly harnessed by other research teams to test other invasive species, 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 rapid

evolution is, or is not, essential for invasion success.

As a rule, rapid evolution of germination and growth traits is not essential for invasion success. Instead, it seems likely that broad environmental tolerance is key for granting invasion success. But rapid evolution may still play a role, especially in more extreme or different environments: Linde et al. (2001) found that *Capsella bursa-pastoris* evolved to colonize high-altitude and desert environments in California. However, we found little sign of evolution in our comparisons between temperate populations of this species. Perhaps, as suggested by Baker (1965), the generalist traits contained in temperate source populations are suitable as long as the introduced environment is not too different. Our findings provide support for the speculation by van Kleunen and colleagues (2010) that future invasions can be predicted by species' characteristics, but perhaps only specific traits, such as germination rate. This finding suggests that managers can perhaps best guard against future invasions by targeting weedy species and preventing them from dispersing beyond their native ranges.

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