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Inter- and intraspecific selection in alien plants: How population growth, functional traits and climate responses change with residence time

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Abstract

Aim: When alien species are introduced to new ranges, climate or trait mismatches may initially constrain their population growth. However, inter- and intraspecific selection in the new environment should cause population growth rates to increase with residence time. Using a species-for-time approach, we test whether with increasing residence time (a) negative effects of climatic mismatches between the species' new and native range on population growth weaken, and (b) functional traits converge towards values that maximize population growth in the new range.

Location: Germany.

Time period: 12,000 years BP to present.

Major taxa studied: Forty-six plant species of the Asteraceae family.

Methods: We set up a common-garden mesocosm-experiment using annual plant species with a wide range of residence times (7–12,000 years) and followed their population dynamics over 2 years. We calculated climatic distance between the common garden and the species' native range. We also measured key functional traits of each species to analyse trait-demography relationships and test trait convergence with increasing residence time.

Results: We found no support for the hypothesis that negative effects of climatic mismatches on population growth weaken with residence time. However, seed mass had a clear negative effect on population growth. As expected under such strong directional selection between or within species, increasing residence time led seed mass to converge to low values that increase population growth. Accordingly, population growth tended to increase with residence time.

Main conclusions: We identify trait but not climatic mismatches as important constraints on population growth of invaders. Understanding how inter- and intraspecific selection shapes functional traits of alien species should improve the predictability of future invasions and help understanding of limits to the population growth and spread of invaders already present. In a broader context, this study contributes to the conceptual integration of invasion biology with community, functional and population ecology.

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KEYWORDS

Asteraceae, biological invasions, climatic dissimilarity, intrinsic population growth rate, long-term dynamics, multi-species experiment, plant functional traits, residence time, species-level selection, trait–demography relationships

1 | INTRODUCTION

When alien plant species are introduced into a new range, they often experience unfavourable climatic or other environmental conditions compared to those in their native range. For successful establishment under these conditions, they must reach a positive population growth rate (Bock et al., 2015). However, Allee effects due to low conspecific density (Taylor & Hastings, 2005) and a loss of genetic variation during the introduction process (Lee, 2002) can decrease their establishment likelihood. Therefore, initially, alien plants often lack the potential to respond to environmental selection and adapt to their new range (Braasch et al., 2019; Pironon et al., 2015). With increasing residence time (defined as the time since introduction of an alien species into a new range), the probability of establishing self-sustaining populations (e.g., Schmidt et al., 2017), abundance (e.g., Hamilton et al., 2005), and range size (e.g., Pyšek et al., 2015) are expected to increase. Yet it has only rarely been studied how the demographic performance of alien species changes with increasing residence time in the new range. To quantify the relevance of ecological and evolutionary processes for invasion success, investigations of population dynamics in the new range are nevertheless key (Gurevitch et al., 2011; Sakai et al., 2001).

Adaptation of alien plants to their new environment has mostly been tested in common garden experiments along environmental gradients within the new range (Colautti & Barrett, 2013; Maron et al., 2004, 2007; Moran et al., 2017). In these studies, for a given site, populations originating from conditions more similar to a specific common garden performed better (e.g., increased plant size, growth, fecundity and survival) than populations from more different conditions, which was interpreted as a sign of rapid evolutionary adaptation (Colautti & Barrett, 2013). However, studies that link demographic performance of alien plants in their new range to climatic differences from the native range remain scarce (but see Braasch et al., 2019; Sotka et al., 2018). Instead, the role of climatic mismatches for rapid adaptation of alien plants has been studied in terms of climatic niche shifts (the ability to occur and persist in a climatically distinct niche space after the introduction into a new range) estimated from species distributions (Broennimann et al., 2012; Guisan et al., 2014). To date, there is no consensus on whether climatic niche shifts in invasive plants are rare (Petitpierre et al., 2012) or common (Atwater et al., 2018) and whether climatic niche shifts in general are related to residence time (see Li et al., 2014 for alien reptiles and amphibians) or not (see Petitpierre et al., 2012 for alien plants). This highlights the urgent need to study adaptation processes in alien species over longer time-scales, considering population dynamics rather than performance proxies. Hence, in this study, we do not aim

to quantify the magnitude of climatic niche shifts of alien species. Instead, in the first part of our study, we investigate the effect of climatic mismatches between the new and native range on actually measured population dynamics and test if this effect depends on the time since introduction of the alien species.

There has recently been revived interest in how demographic performance depends on the interaction between functional traits and environmental conditions (Salguero-Gómez et al., 2018). In the new environment, introduced alien plants are subject to selection both within (Colautti et al., 2017; Keller & Taylor, 2008; Lambrinos, 2004) and between species (Vellend, 2016). Within-species selection may either lead to extinction from the new range or cause adaptation to the new environment (Colautti et al., 2017; Keller & Taylor, 2008; Lambrinos, 2004; Saul & Jeschke, 2015). Hence, species with long residence times are expected to have trait values that increase fitness and population growth in the new environment. Between-species selection will also favour species with trait values conferring high population growth rates at the expense of other species with suboptimal trait values (Vellend, 2016). Hence, in the second part of this study, we will also investigate which traits increase population growth, and test how they are related to residence time. Intra- or interspecific selection on traits of alien species may be imposed by climate in the new range, but it may also result from other environmental factors that change as a consequence of range expansions (Burton et al., 2010). For instance, invasion into low-competition habitats favours life histories with high investment into reproduction and dispersal but poor competitive ability (Burton et al., 2010).

The parallel effects of intra- and interspecific selection should cause distinctive patterns in multi-species comparative studies: first, population growth in the new range should show negative effects of climatic mismatches, which corresponds to a unimodal relationship to climatic distance (calculated as climatic conditions in the new range minus conditions in the native range, Figure 1a). Population growth should be optimal when new and native climates match perfectly (so that climatic distance is zero) and it should decline as climatic distance becomes either positive or negative (Figure 1a). However, intra- and interspecific selection should cause this negative effect of climatic mismatches to weaken as residence time increases (Figure 1a). Second, intra- and interspecific selection should cause functional traits to converge towards values that maximize population growth rate in the new environment (Shipley et al., 2006). Traits with a monotonic effect on population growth (Figure 1b) are subject to directional selection on trait values. The longer the period over which selection acts, the stronger its effects should be. In a comparative study, one thus expects a monotonic relationship between

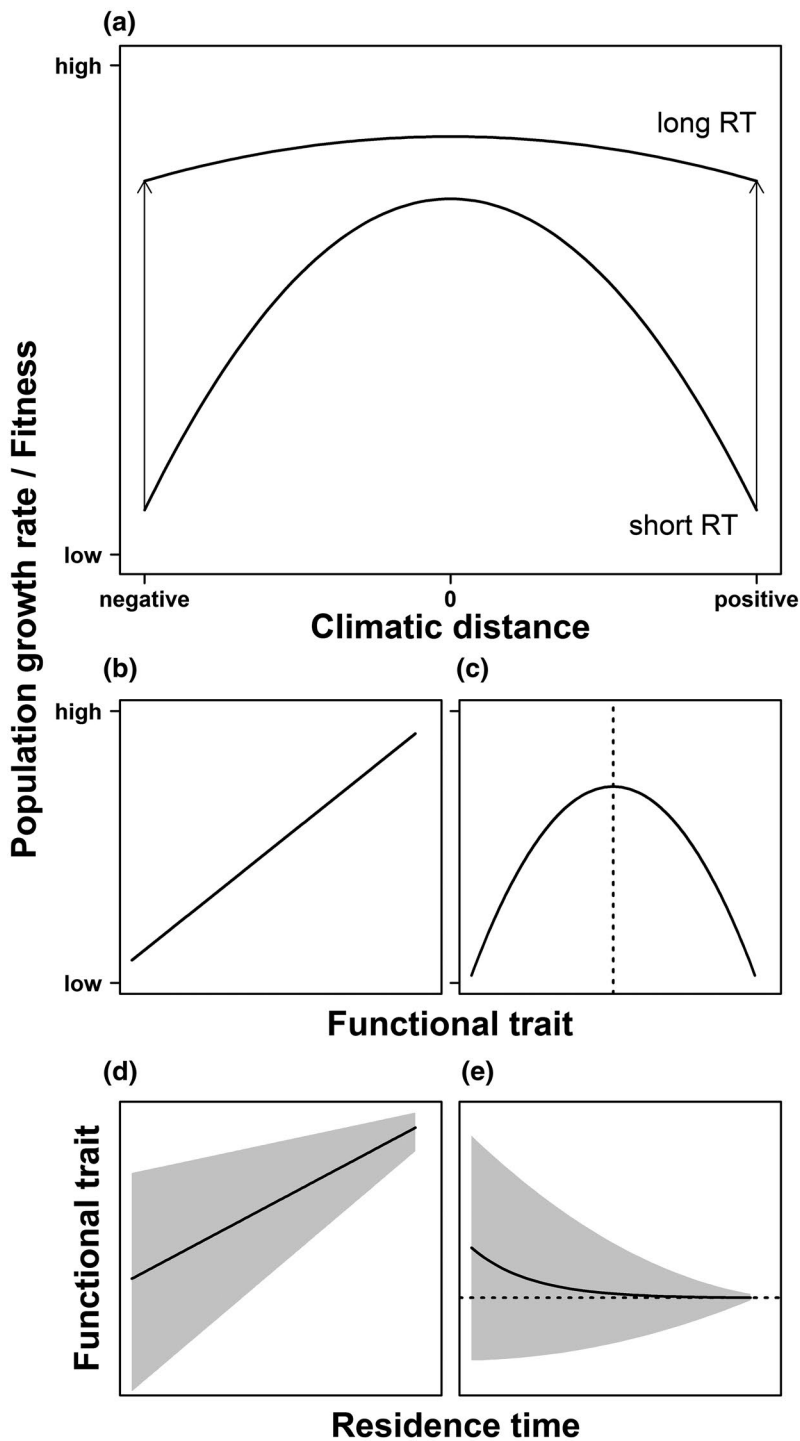


FIGURE 1 Inter- and intraspecific selection on alien plants in their new range should shape the relationships between population growth, climatic distance, functional traits and residence time. (a) Unimodal effects of climatic distance between the new and native range (corresponding to negative effects of climatic mismatches, whereby positive distances indicate a warmer and negative distance a colder climate in the new range) on population growth rate weakened (arrows) with residence time (RT) of alien species in their new range. (b) A linear relationship between a functional trait and population growth rate implies directional selection, whereas (c) a unimodal relationship, where a particular trait value (vertical dotted line) maximizes population growth rate, leads to stabilizing selection. (d) In the case of directional selection, the trait shows a continuous response to residence time and under (e) stabilizing selection, the trait converges on the value that maximizes population growth rate (horizontal dotted line). In both cases, between-species variance in the traits (shaded area) should decrease with residence time

residence time and interspecific trait means (Figure 1d). Whether this residence-time-trait relationship is positive or negative depends on whether the trait-population-growth relationship is positive or negative, respectively. In contrast, traits with a unimodal effect on population growth (Figure 1c) are subject to stabilizing selection. As residence time increases, interspecific means of these traits should converge towards the intermediate trait value that maximizes population growth (Figure 1e). Under both directional and stabilizing selection, interspecific trait variance should decrease with residence time (Figure 1d and e).

To test these predictions, we set up a common garden experiment based on a species-for-time approach. For this, we chose 46 annual Asteraceae species that form an alien-native continuum covering minimum residence times in Germany from 7 to 12,000 years. Under near-natural conditions, we followed the population dynamics of each species over 2 years. This enabled us to study the relationships between population growth rate, climatic distance between the new and native range, functional traits, and residence time in the new range. Specifically, we here test whether (a) negative effects of climatic mismatches on population growth rate weakened with

residence time in the new range (Figure 1a), and (b) with increasing residence time, functional traits converge towards values that maximize population growth in the new range (Figure 1b–e).

2 | MATERIALS AND METHODS

2.1 | Alien–native species continuum

Our experimental approach takes advantage of the long and well-documented immigration and introduction history of Asteraceae in Central Europe. This plant family is one of the most species-rich in Europe, including a high number of established alien species in Germany (Hanspach et al., 2008). We chose 46 annual Asteraceae species along an alien–native continuum (Figure 2) from recently introduced neophytes, over archaeophytes, to natives that immigrated after the Last Glacial Maximum between approx. 10,000–12,000 years before present (see Sheppard & Schurr, 2019). This represents the widest possible continuous gradient of residence times in Germany. Among the neophytes, we further distinguished between casual and established neophytes. Casual neophytes do not have established self-sustaining populations and rely on repeated introductions for persistence (Richardson, Pyšek, et al., 2000). From a total of 92 annual species of Asteraceae occurring in Germany, we chose the 46 study species so that they are functionally similar and share similar habitat requirements (ruderal and segetal habitats), only excluding species from differing habitats and those that were not common enough to obtain a sufficient amount of seed material. We determined the species-specific minimum residence time (MRT) (*sensu* Rejmánek, 2000) as the time span between the first record of a species in the wild and the start of the experiment (2016). First records were compiled from the floristic and archaeobotanical

literature as well as from online databases (Sheppard & Schurr, 2019; latest access to online databases in 2017). We collected seeds from wild populations in Baden-Württemberg, the state in which the common garden is located. For each population, seeds from c. 10 mother-plants were sampled in 2015 and mixed before sowing. These seed collections were complemented by seeds from botanical gardens across Germany to ideally include three populations per species, totalling 115 populations (see Supporting Information Table S1).

2.2 | Experimental design

In March 2016, we set up a common garden experiment on a field site at the University of Hohenheim, Germany (Versuchsstation Heidfeldhof: 48°43'02.1" N, 9°11'03.1" E, 400 m a.s.l.; annual precipitation: 698 mm; mean annual temperature: 8.8 °C). We established monocultures of each species in mesocosms (265 mesocosms with seeds sown to follow population dynamics plus 92 mesocosms with transplanted seedlings for functional trait measurements). Mesocosms consisted of 50-L pots (0.159 m² soil surface area, 50 cm upper diameter, 38 cm lower diameter, 40 cm height) and were randomly placed in five spatial blocks. We filled the pots with local soil of sandy-loamy texture (70% sand, 14% clay and 16% silt) and a nutrient content of 1.81 mg/L NO³⁻, 0.015 mg/L NH⁴⁺, 21.36 mg/L P; and a pH of 7.88. Before filling the pots, we added a layer of expanding clay to improve drainage. The mesocosms were watered daily throughout the growing season with an automatic drip-irrigation system and received a maximum of 2 L/day during the warmest period (June to August). They were weeded before sowing and regularly throughout the experiment. We established usually six mesocosms (ranging between two and eight) per study species (for the number of replicates at population- and species-level see

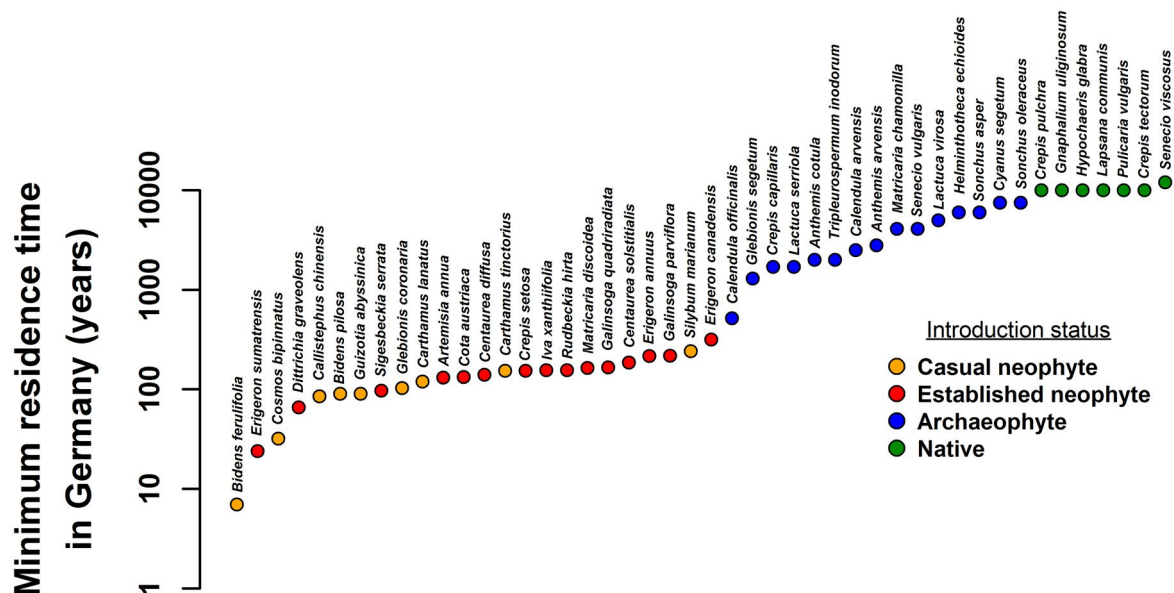


FIGURE 2 The alien–native continuum of 46 Asteraceae species varying in their minimum residence time and introduction status in Germany [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Comparison of models for effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{\max}), minimum residence time (MRT), and T_{\max} amplitude on finite rate of increase (λ_0)

Climatic distance	MRT	ΔT_{\max} -MRT interaction	DIC	Δ DIC	Mean R^2 (95% credible interval)		Mean phylogenetic signal (95% credible interval)
					Marginal	Conditional	Pagel's lambda
No	Yes	No	925.48	0.00	.12 (< .01, .26)	.68 (.55, .81)	.51 (.24, .72)
Yes (apex = 0)	Yes	Yes	925.65	0.17	.21 (.05, .39)	.70 (.57, .82)	.50 (.20, .74)
Yes (apex = 0)	Yes	No	926.04	0.56	.16 (.02, .32)	.69 (.56, .82)	.49 (.11, .73)
Yes (apex = 0)	No	No	926.45	0.97	.11 (< .01, .24)	.68 (.54, .81)	.48 (.0006, .69)
No	No	No	926.51	1.03	.03 (< .01, .10)	.67 (.53, .80)	.52 (.12, .74)
Yes (flexible apex)	Yes	No	926.56	1.08	.22 (.05, .40)	.68 (.55, .81)	.42 (.001, .67)
Yes (flexible apex)	Yes	Yes	926.73	1.25	.26 (.09, .46)	.70 (.56, .82)	.44 (.001, .67)
Yes (flexible apex)	No	No	927.12	1.64	.17 (.03, .36)	.67 (.52, .81)	.40 (.0004, .68)

Note: We compared eight models (using the deviance information criterion, DIC): with or without linear effects of ΔT_{\max} (quadratic relationships with apex either fixed at $\Delta T_{\max} = 0$ K or flexible), with or without interactions between the ΔT_{\max} terms and MRT, and with or without MRT. The analyses included 39 species, 101 populations and 230 mesocosms. Models are shown in order of their DIC ranking. Effect sizes are shown in Supporting Information Figure S4; corresponding analyses for the other demographic performance measures are given in Supporting Information Table S2 and Figures S5–S13.

Supporting Information Table S1). In each mesocosm, 20 seeds from a given source population were sown in late June 2016. Thus, the initial populations size S_0 in each mesocosm amounted to 20 seeds. The seeds were covered with a thin layer of sand. Before the first seed set of the study species in 2016, each mesocosm was surrounded by open-top organza fabric (Supporting Information Figure S1) that prevented seed immigration and emigration, while allowing light and pollinators to enter.

2.3 | Measures of demography and population dynamics

By the end of each of the two growing seasons, we counted the total number of capitula and recorded the presence/absence of mature seeds in each mesocosm. We additionally sampled ideally 10 intact capitula per mesocosm and calculated the average seed number per capitulum (at population-level) by dividing average seed mass per capitulum by the average mass of an individual seed (see 'Functional trait measurements' below). The product of capitula number and average seed number per capitulum is the estimated seed number per mesocosm at the end of each year (S_1 and S_2 , respectively).

To quantify population dynamics, we calculated the growth of the seed population from 1 year to the next as $\lambda_t = S_{t+1}/S_t$ (following Venable & Brown, 1988). Since each population was initiated at low density ($S_0 = 20$ seeds per mesocosm), the population growth rate in the first year, λ_0 , approximates the finite rate of increase. While our approach did not consider failed invasions in the new range (on which information is usually lacking), it is important to note that the speed of invasions and hence the success of a species invading a

competition-poor environment depends not only on whether populations can grow ($\lambda_0 > 1$) but also on the magnitude of the population growth rate. In the studied annual plants, variation in λ_0 may arise from variation in establishment (the seed-plant transition) or from variation in fecundity (the plant-seed transition). We thus used the number of established plants per mesocosm at the end of the first year (N_1) to decompose λ_0 into establishment ($E_0 = N_1/S_0$) and per-plant fecundity ($F_0 = S_1/N_1$) in the first year. In total, we thus obtained four measures of population dynamics and demographic performance for each mesocosm: λ_0 , λ_1 , E_0 and F_0 . We only calculated λ_0 for species that produced seeds at the end of the first year in at least one mesocosm and that thus successfully completed their life cycle. For these species, we considered all populations and mesocosms (see Table 1 for the resulting sample sizes). We thereby avoided assigning $\lambda_0 = 0$ to species that did not set seed in the first year due to the relatively short first growing season (Supporting Information Figure S2) or because they are facultative annuals.

2.4 | Climatic distance

We measured climatic distance as ΔT , the local temperature extremes in the common garden (i.e., new range) minus the median temperature extremes in the study species' native range (at species-level). The median temperature in the native range estimates the typical conditions in which a population occurred before being introduced. Long-term within-species selection should cause a species to have optimal demographic performance under these typical conditions. We note, however, that other factors, such as biotic interactions, dispersal limitation and time-delayed extinction might

cause a mismatch between median conditions in the native range and the conditions for which demographic performance is optimal (J. Pagel et al., 2020). Here, we focus on the maximum temperature of the warmest month, T_{\max} (bio5 variable, WorldClim dataset; Hijmans et al., 2005), for the experimental period in 2016 and additionally considered the minimum temperature of the coldest month, T_{\min} (bio6 variable), for 2017 (whereas the length of the experimental period in 2016—see Supporting Information Figure S2—excluded climatic variables related to winter or average annual temperatures of that year). These temperature extremes impose strong limitations to plant performance in various ecosystems and across different plant types (Berry & Björkman, 1980). To ensure that these temperature variables are likely to affect demographic performance, we controlled other abiotic factors such as water availability and soil conditions in our experiment: since we watered the pots, they were not water-limited (and any precipitation variables would thus not provide any information on the actual amount of water the plants received), and since we used a fairly nutrient-rich soil, nutrients were likely not limiting (at least in the first year). Moreover, the study populations were grown in isolation, thus excluding interactions with other plant species.

To calculate climatic distances, the climatic changes that our study species experienced in the past 12,000 years can be decomposed into a spatial and a temporal component. The study species differ in the spatial component of climatic change they experienced when being introduced to Germany from their origin. Moreover, the species differ in residence time and thus in the time for which selection imposed by the spatial component could act. Moreover, the temporal component of climate change should not affect our results, assuming that climatic changes since the last glaciation had a similar magnitude in Germany and in the native ranges of our study species (in particular, temperate and Mediterranean, see below; Annan & Hargreaves, 2013). Thus, to quantify the spatial component, we compiled data on the global distribution of the 46 Asteraceae species from the Global Biodiversity Information Facility database (GBIF, www.gbif.org, removing duplicates and erroneous occurrence records in the ocean; for species-specific references see Supporting Information Table S1) and the FlorKart (Floristische Kartierung Deutschlands, Bundesamt für Naturschutz BfN) and NetPhyD (Netzwerk Phytodiversität Deutschlands e.V.) database (www.deutschlandflora.de) (Sheppard & Schurr, 2019). To quantify climatic conditions in the native range, we defined broad-scale native ranges of the study species according to their introduction history (natives, archaeophytes, neophytes), whereby native species originate from temperate Europe, archaeophytes from the Mediterranean and Fertile Crescent, and neophytes from their respective native ranges. Therefore, we first restricted the global distribution of natives and archaeophytes to their native ranges that fall within a spatial extent of latitudes between 30° N and 60° N and longitudes between 10° W and 55° E. We then used the Köppen-Geiger climate classification (Kottek et al., 2006) to further delineate likely native ranges. We used the classification 'Cfb' (warm temperate, fully humid, warm summer) for the native range of natives, which covers temperate

Central Europe (Supporting Information Figure S3a). For archaeophytes, we used the classifications 'Csa' (warm temperate, summer dry, hot summer), 'Csb' (warm temperate, summer dry, warm summer) and 'Csc' (warm temperate, summer dry, cool summer) for the native range of archaeophytes, which covers the Mediterranean basin and the Fertile Crescent (Supporting Information Figure S3b). For casual and established neophytes, we assigned native ranges using information from the US National Plant Germplasm System (<https://npgsweb.ars-grin.gov>), the Plants database of the United States Department of Agriculture Natural Resources Conservation Service (<https://plants.sc.egov.usda.gov>), the Euro + Med PlantBase database (<https://ww2.bgbm.org/EuroPlusMed/query.asp>), CABI's Invasive Species Compendium (<https://www.cabi.org/isc>) and Kew Garden's Plants of the World Online (<https://plantsoftheworldonline.org/>). Generally, native ranges were determined at country level. However, for larger countries (i.e., United States, Canada, Russian Federation) as well as continental countries with oceanic islands native ranges were determined at state levels.

Using the occurrence data within the defined native ranges, we calculated the median and amplitude (the range between the 2.5 and the 97.5% quantile) for T_{\max} and T_{\min} across each of the 2.5 arc minutes resolution grid cells (resolution of the climatic data) where a species was present. For local T_{\max} and T_{\min} , we used daily maxima and minima of each year (measured at 2 m above the ground) from a weather station close to the field site (48°42'40.212" N, 9°11'45.384" E, 389 m a.s.l.), provided by the state institution on agro-meteorology (Agrarmeteorologie Baden-Württemberg, www.wetter-bw.de). Based on these, we calculated monthly averages to identify the corresponding WorldClim variables. To account for microclimatic modifications in the mesocosms, we compared measurements of data-loggers (Tinytag TGP-4500 by Gemini Data Loggers; daily maximum and minimum temperatures) placed at 10 cm below ground in an additional mesocosm and in the surrounding field. From the data-logger measurements, we calculated T_{\max} and T_{\min} for the same months obtained from weather station data (see Supporting Information Figure S2) and added the average difference between mesocosm and field temperatures to the weather station variables.

The signed temperature differences, ΔT_{\max} and ΔT_{\min} , were then calculated by subtracting the temperature median of each species' native distribution from the local temperature value (corrected for the mesocosm effect). To test the climatic response of λ_1 , we calculated the arithmetic mean of ΔT_{\max} in 2016 and 2017.

2.5 | Functional trait measurements

We measured seed mass, maximum height, and specific leaf area (SLA), which represent three key axes of plant ecological strategies (Westoby, 1998). SLA and maximum height should affect population growth rates in high resource, low competition environments (such as we simulate in our experiment): high SLA is related to rapid individual growth, which in turn leads to high population growth rates (Westoby, 1998); whereas high maximum size implies higher

investment into growth rather than reproduction, which in turn leads to lower population growth rates (Pianka, 1970). Furthermore, seed mass is central to the acclimatization of plants to their environment (Fernández-Pascual et al., 2019). Also, Pérez-Ramos et al. (2020) found that SLA and plant height play an important role in responses of growth and fecundity of annual plants (among them *Anthemis arvensis*, which was also included in our study) to experimentally increased temperatures. Given that seed mass, plant height, and SLA are related to fecundity, the size to reach maturity, and relative growth rate, respectively, these functional traits should also play an important role in the demographic performance and possibly in the climatic adaptation of the annual plants in our study system.

We determined the average seed mass at population-level before the start of the experiment. To measure maximum height and SLA (at population-level), we established additional monoculture mesocosms with transplanted seedlings. Trait measurements followed the standard protocols of Pérez-Harguindeguy et al. (2013) (see Supporting Information Appendix S1 for further details).

2.6 | Statistical analyses

Data were analysed in R 3.5.1 (R Core Team, 2018). We used Bayesian generalized linear mixed models fitted with Markov chain Monte Carlo methods (MCMCglmm package; Hadfield, 2010). All Bayesian models accounted for phylogenetic non-independence among the study species using Pagel's lambda (M. Pagel, 1999) and included experimental block and population nested in species as random effects. Information on phylogenetic relatedness was extracted from the Daphne Phylogeny (Durka & Michalski, 2012) using the R packages picante (Kembel et al., 2010) and phytools (Revell, 2012). For the demographic performance measures λ_0 , λ_1 and F_0 , we used a Gaussian model with non-informative priors for the variance components of each random effect, corresponding to an inverse-Gamma distribution (shape and scale parameters equal to 0.01). To normalize residuals, we followed the recommendation by Sokal and Rohlf (2012) and $\log(x + 1)$ -transformed λ_0 , λ_1 and F_0 . To analyse E_0 , we used a binomial model (contrasting success = N_1 and failure = $S_0 - N_1$) with an inverse-Wishart prior for the variance components of each random effect (shape and scale parameters equal to 0.001). For fixed effects, the default was used, which is a normal distribution with a mean of zero and a very large variance (10^{10} ; Hadfield, 2010). We ran the models for 1,000,000 iterations, using a burn-in phase of 250,000 and a thinning interval of 500.

2.6.1 | Effects of climatic distance and residence time on demographic performance

To represent our first hypothesis that unimodal effects of climatic distance between the new and native range (i.e., negative effects of climatic mismatches) on population growth rate weaken with MRT (Figure 1a), we fitted a model that included MRT, the quadratic effect of ΔT and their interaction as fixed effects. This model assumes

that ΔT effects have an apex (maximum or minimum) at $\Delta T = 0$ K. We note that climatic effects may not just depend on the absolute difference, but for instance on whether climate is warmer (positive distance) versus colder (negative distance) in the new range. Thus, we here consider signed climatic distances to evaluate effects of climatic mismatches on population growth. In an alternative model, we however relaxed the strict assumption of an apex at $\Delta T = 0$ K by including additionally a linear effect of ΔT and its interaction with MRT. This allows the apex to be at a non-zero value of ΔT . For each of these two models we fitted a simplified version by dropping the interaction between MRT and ΔT terms to test whether climatic distance effects vary with MRT. We further simplified these models by additionally dropping the main effect of MRT. Finally, we also fitted a model containing only MRT and a null model without MRT and ΔT effects. These eight alternative models were then compared using the deviance information criterion (DIC). In all models, we additionally included a main effect of temperature amplitude of the study species' native range distribution and—in all models including ΔT —an interaction between ΔT and amplitude. We included the ΔT -amplitude interaction to account for the fact that—for a given ΔT —a species with a broad amplitude is expected to perform better than a species with a narrow amplitude. This holds both if all individuals of a species have the same niche or if there is intraspecific niche differentiation. In the latter case, a broad amplitude increases the likelihood that at least one introduced genotype is suited to conditions in the new range (Bock et al., 2015). Before entering the models, MRT was log-transformed, scaled and centred, and temperature amplitude was scaled and centred. To ensure that $\Delta T = 0$ represents perfect climatic similarity, ΔT was scaled but not centred.

We analysed the effect of ΔT_{\max} and amplitude also on each of the other demographic performance measures and ran separate models to test the effects of ΔT_{\min} (and amplitude) on λ_1 . To test which temperature extremes better explain the second-year demographic performance measure, we compared the ΔT_{\max} and ΔT_{\min} models via DIC.

2.6.2 | Relationships between traits, demographic performance and residence time

Testing the second hypothesis involved two steps. In the first step, we identified functional trait values that maximize population growth and fitness. To this end, we ran a Bayesian model for each demographic performance measure, using the aforementioned structure for random effects and data transformations for response variables. To test for both directional and stabilizing selection, the full models included the linear and quadratic term of all three log-transformed traits as fixed effects. We considered trait effects to be significant, if the 95% credible intervals (CI) of their estimated effects did not overlap zero. For traits with significant effects, we calculated the partial marginal R^2 as the difference between the marginal R^2 of the full model and the model without the linear and quadratic effects of the trait of interest.

In the second step, we examined whether for maximum MRT (12,000 years) the functional traits converge towards values that increase population growth rate and fitness. To quantify the effect of MRT on the mean and standard deviation (SD) of functional trait values, we used generalized additive models for location scale and shape (gamlss package; Stasinopoulos & Rigby, 2009) and accounted for random effects of species in these models. Both MRT and traits were log-transformed and MRT was additionally scaled and centred. To ensure that significant results were robust, we conducted an additional control analysis including only wild populations, since seeds from botanical gardens were not grown under entirely natural conditions.

3 | RESULTS

3.1 | Effects of climatic distance and residence time on demographic performance

We found no support for the hypothesis that unimodal effects of climatic distance (corresponding to negative effects of climatic mismatches) on the finite rate of increase (λ_0) weaken with MRT of alien species in their new range: all eight alternative models relating λ_0 to distance in maximum temperature of the warmest month (ΔT_{\max}) and/or MRT had similar performance ($\Delta\text{DIC} < 2$; Table 1). While the model representing this hypothesis ranked second-best ($\Delta\text{DIC} = 0.17$; marginal $R^2 = .21$; Table 1), the interaction between ΔT_{\max} and MRT was not significant (posterior mean = -0.77 , 95% credible interval = -1.92 , 0.44) and the posterior mean estimate of the interaction deviated

from the expectation, suggesting that unimodal effects of ΔT_{\max} strengthen (rather than weaken) with increasing MRT (Figure 3b). In general, models in which the apex (maximum or minimum) was fixed at a $\Delta T_{\max} = 0$ K performed somewhat better than their counterparts with a flexible apex (Table 1). The models without the interaction of ΔT_{\max} -MRT predicted a (non-significant) optimum at or near (for flexible apex models) zero (third-best ranked model shown in Figure 3b, with marginal $R^2 = .16$; alternative models in Supporting Information Figures S4 and S9). The overall best model for λ_0 however only included MRT and had a marginal R^2 of $.12$ (Table 1). This best model described a near-significant positive effect of MRT on λ_0 (posterior mean = 0.74 , 95% credible interval = 0.04 , 1.49 ; Figure 3a).

Analyses of the other demographic performance measures yielded similar results as for λ_0 with all alternative models having DIC differences < 2 (Supporting Information Table S2, Figures S5–S8, S10 and S11). Population growth rate in the second year (λ_1) tended to be better explained by distance in minimum winter temperature (ΔT_{\min}) than by ΔT_{\max} (Supporting Information Table S2, Figures S12 and S13). The best model for λ_1 included a non-significant unimodal effect of ΔT_{\min} with optimum at 0 K (marginal $R^2 = .18$; Supporting Information Figure S13b).

3.2 | Relationships between functional traits and population growth

The three functional traits jointly explained 25% of the variance in λ_0 (marginal R^2 of the full model, Table 2). In particular, λ_0 clearly

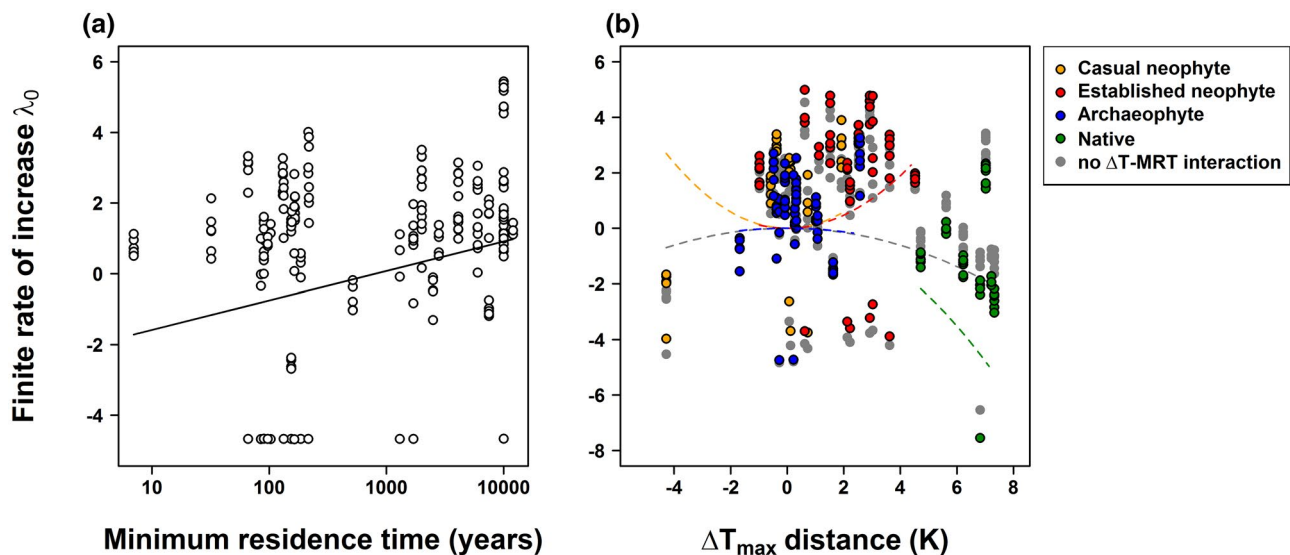


FIGURE 3 (a) Effects of minimum residence time (MRT) and (b) climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{\max}) on finite rate of increase (λ_0). Note that the y axes depict partial residuals of log-transformed λ_0 . (a) The solid line shows predictions of the model only including MRT (the best model according to the deviance information criterion, DIC). (b) Coloured lines show predictions of the model including interactions between the quadratic effect of ΔT_{\max} and MRT (the second best model based on DIC) for the median MRT of each introduction status group (casual neophyte = 90, established neophyte = 156, archaeophyte = 2,800, and native = 10,000 years). The grey line shows predictions of the corresponding model without an interaction between the quadratic effect of ΔT_{\max} and MRT (the third best model based on DIC) [Colour figure can be viewed at wileyonlinelibrary.com]

decreased with seed mass (partial marginal $R^2 = .17$; Figure 4a, Table 2) and showed a weak unimodal response to maximum plant height (partial marginal $R^2 = .03$; Figure 4b, Table 2). λ_0 is thus predicted to be highest for the smallest seed mass observed (0.01 mg) and for a plant height of 50 cm (Figure 4). The trait effects on λ_0 are mainly driven by fecundity (F_0) rather than establishment (E_0), so that the values maximizing F_0 are almost identical to those maximizing λ_0 (Supporting Information Table S3 and Figure S14). Population growth rate in the second year (λ_1) did not show clear responses to any functional trait (Supporting Information Table S3 and Figure S14g–i).

3.3 | Relationships between functional traits and residence time

As expected under directional selection, the mean and the SD of seed mass significantly decreased with MRT (Figure 4c; MRT-effect on mean: $t_1 = -15.6$, $p < .001$; MRT-effect on SD: $t_1 = -3.0$, $p = .004$). Species with a high MRT thus have small values of seed mass that increase λ_0 (Figure 4a). Results for maximum plant height are less conclusive: mean height also changed with MRT ($t_1 = -3.6$, $p < .001$), but the MRT effect on height SD was only weakly negative ($t_1 = -0.3$, $p = .741$). The central 95% of the plant height distribution predicted for a maximum MRT of 12,000 years include the plant height value that maximizes λ_0 (Figure 4d). Control analyses of the relationships between functional traits and MRT for only wild populations yielded similar results (see Supporting Information Appendix S2).

4 | DISCUSSION

In our multi-species mesocosm experiment, we found that trait but not climatic mismatches limit the population growth of introduced species. In contrast to our first hypothesis, we found that negative effects of climatic mismatches on intrinsic growth of the seed population (λ_0) tended to be stronger for species with longer MRT

(Figure 3b). In support of our second hypothesis, seed mass—which has a strong negative effect on λ_0 (Figure 4a)—converges towards low values as MRT increases (Figure 4c). For plant height—which has a weak unimodal effect on λ_0 (Figure 4b)—the effect of MRT was less clear (Figure 4d). Directional inter- and intraspecific selection on seed mass may thus explain why λ_0 tended to increase with MRT (Figure 3a).

4.1 | Relationships between climatic distance and population dynamics

Negative effects of climatic mismatches between the new range and a species' native range on demographic performance did not weaken with residence time, rejecting our first hypothesis. Since there are also no strong residence-time-independent effects of climatic distance, we found little evidence for climatic niche conservatism (Wiens & Graham, 2005). This contrasts with a strongly negative effect of climatic distance on the effective population size (N_e) of *Centaurea solstitialis* (Braasch et al., 2019). This intraspecific observational study (in which population ages ranged from 20 to 120 years) also did not find evidence that the negative effect of a climatic mismatch depends on population age. In our experimental study that used multiple species to cover a time span of MRTs from 7 to 12,000 years, the finite rate of increase tended to increase with residence time. This points to the possibility that selective forces other than climate (notably on life history traits, Burton et al., 2010) have shaped population growth of our study species.

Yet, we note that the broad approximations necessary to calculate climatic distances might have obscured climatic mismatch effects. Alternatively, other climatic variables or niche dimensions that we did not test may play an important role for adaptation in the new range. For instance, reproduction may depend not only on temperature extremes but also on duration of the growing season and day length (Colautti et al., 2009). Furthermore, biotic interactions that depend on residence time could have influenced population growth,

TABLE 2 Results of models for effects of functional traits [seed mass, maximum height and specific leaf area (SLA)] on finite rate of increase (λ_0). We tested for linear and quadratic effects of each trait in a full model

Functional trait	Mean effect size (95% credible interval)	Mean R^2 (95% credible interval)		Mean phylogenetic signal (95% credible interval)
		Marginal	Conditional	Pagel's lambda
log(seed mass)	-0.47 (-0.85, -0.10)	.17 _{par}	–	–
log(seed mass) ²	0.06 (-0.07, 0.17)			
log(max. height)	13.10 (2.24, 23.57)	.03 _{par}	–	–
log(max. height) ²	-1.67 (-3.07, -0.27)			
log(SLA)	-9.52 (-48.92, 33.52)	–	–	–
log(SLA) ²	1.51 (-4.36, 7.99)			
full model	–	.25 (.07, .42)	.67 (.54, .79)	.45 (.09, .70)

Note: Significant effect sizes (with 95% credible intervals not overlapping zero) are highlighted in bold. We calculated partial (par) marginal R^2 for significant traits as the mean marginal R^2 of the full model minus the mean marginal R^2 of the model without linear and quadratic effects of the trait of interest. Corresponding analyses for other demographic performance measures are given in Supporting Information Table S3 and Figure S14.

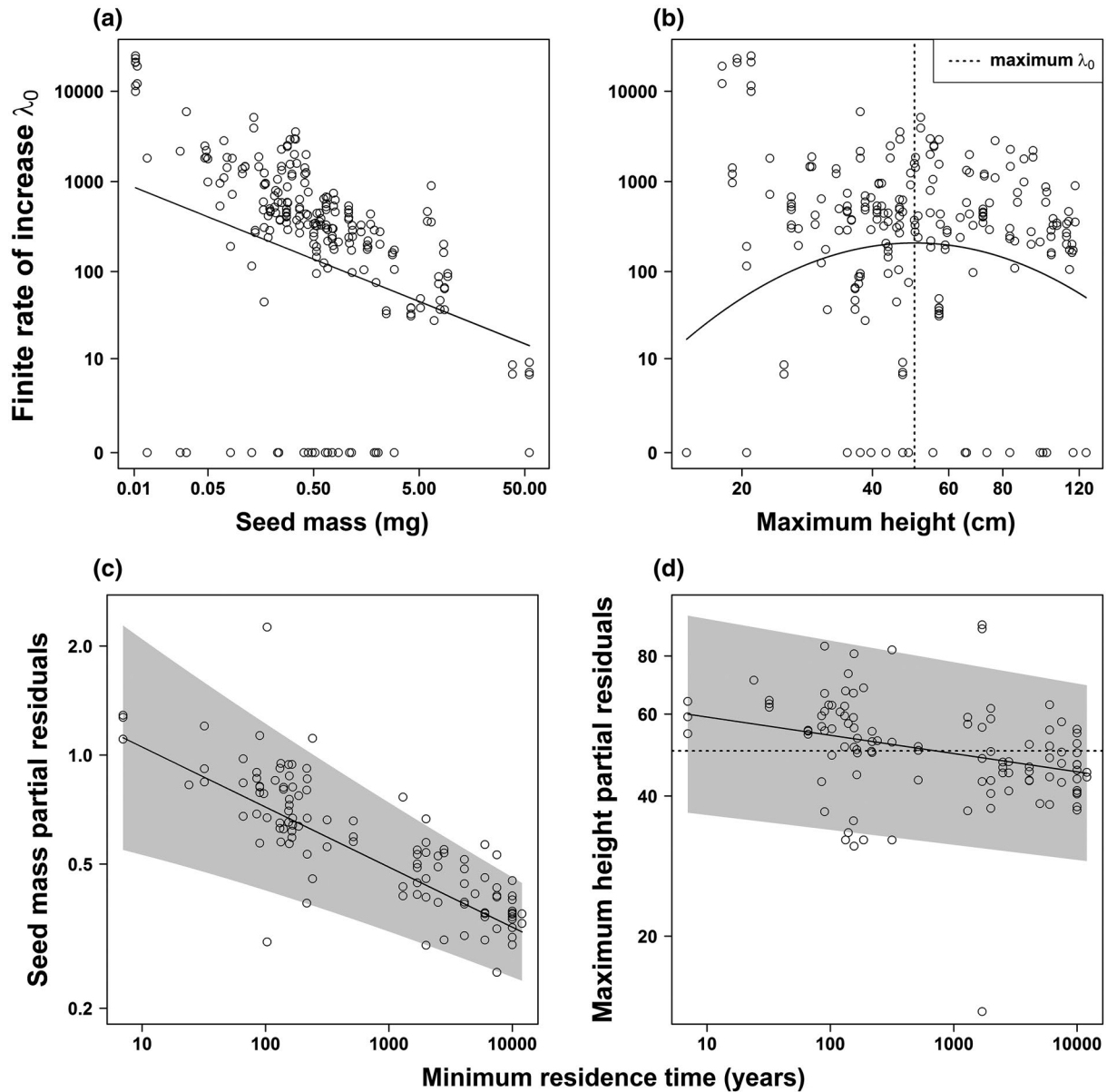


FIGURE 4 (a and b) Relationships between functional traits and finite rate of increase (λ_0). Predictions (solid lines) are based on the full model and show significant trait effects (with 95% credible intervals not overlapping zero) with the other explanatory variables set to their mean value (see Table 2). For the smallest seed mass observed (0.01 mg), λ_0 is predicted to be highest. The vertical dotted line represents the value of plant height (50 cm) that maximizes λ_0 . (c and d) Relationships between functional traits and minimum residence time (MRT). Note that y axes depict partial residuals, which were calculated by subtracting the random effects of species. The solid lines show the effect of MRT on the interspecific trait mean. The shaded areas represent the effect of MRT on the central 95% of the interspecific trait distribution. The horizontal dotted line in (d) represents the value of plant height that maximizes λ_0 . All axes are shown on log-scales

reducing the ability to detect effects of climatic mismatches. For instance, alien species often experience a reduction in abundance or even complete absence of specialist soil pathogens and herbivores in the introduced range (as predicted by the enemy release hypothesis; see Keane & Crawley, 2002) from which they can benefit. With increasing residence times, such enemies are expected to accumulate again (Mitchell et al., 2010). Conversely, lack of mutualist species (e.g., pollinators) may limit invader success initially (Richardson, Allsopp, et al., 2000). However, as our study species are annuals that have been shown to self-fertilize (Corli & Sheppard, 2019), this should be of limited importance. Finally, the climatic niche breadth

in the native range of an alien plant might reduce negative effects of climatic mismatches on introduced populations by increasing the chance of pre-adaptation (Bock et al., 2015).

4.2 | Relationships between functional traits and population dynamics

Our analyses of relationships between traits and population dynamics revealed a clear link between functional traits and the finite rate of increase (λ_0). Particularly, λ_0 strongly decreased with seed

mass in the new range. Seed mass trades off with per capita fecundity (Moles & Westoby, 2006) and leads to increased fecundity of small-seeded species (Henery & Westoby, 2001), as shown by our results (Supporting Information Table S3). However, high fecundity does not necessarily lead to high λ_0 . This is only the case if small seeds have similar establishment success as big seeds. This is in turn expected under low interspecific competition as in our experiment and in the ruderal/segetal habitats that our species (and many other aliens) invade. Additionally, low seed mass helps dispersal through space in order to colonize new suitable patches in such habitats (Westoby, 1998). Links between invasiveness and seed mass were also demonstrated in a study of alien plants introduced to Australia, where invader abundance at regional and continental scale negatively correlated with seed mass (Hamilton et al., 2005).

Maximum height is associated with greater light interception (Ordonez et al., 2010), which increases relative fitness (Falster & Westoby, 2003). Moreover, increased plant height comes at the cost of delayed maturity (Kawecki, 1993), which is especially critical for annual plants. This trade-off might explain the unimodal response of λ_0 and F_0 to maximum height in our study. With frequent disturbances common to ruderal habitats, it is crucial to complete the life cycle before the next disturbance, whereby under stressful conditions, seed production is maintained at the expense of vegetative growth (Grime, 1977). In a natural annual plant system in Australia, Lai et al. (2015) also found that alien species that coexisted well with the native species (as defined by a positive association between native and alien species richness) were of intermediate height (and possessed small seeds). They concluded that such a coexistence pattern may well be the result of environmental selection.

Low seed mass and intermediate height thus represent adaptations to the ruderal habitats invaded by the study species: independent of climatic adaptations, these are traits beneficial in environments with low interspecific competition, frequent disturbance and high nutrient availability. The remarkably strong relationships between traits and population dynamics we found in our study contribute to the emerging field of functional population ecology (Salguero-Gómez et al., 2018). Moreover, since λ_0 and dispersal distance together determine spread rate (see Skellam, 1951), our results shed further light on the role of demography as a key driver of spread in invasive plants (Coutts et al., 2011). Finally, our results can thus be used to develop optimal management strategies, which should be derived from population dynamics and their relationship with time since introduction (Yokomizo et al., 2017).

4.3 | Relationships between functional traits and residence time

With increasing residence times, seed mass converges towards values that increase λ_0 in the new range. This matches surprisingly well what is expected from selection between and/or within species (see Vellend, 2016). In a study along a 42-year chronosequence of secondary succession in a native community, Shipley et al. (2006)

observed local convergence of community-aggregated trait values. They found species' abundances to depend on how closely their functional traits match the community-aggregated ones, which could help in predicting the successful invasion of species to new environments. In our case, species with trait values that maximize λ_0 would be favoured over deviating species (as suggested by Kawecki & Ebert, 2004). Species with these optimal trait values should thus increase in abundance over time, which is in line with the finding that λ_0 increases with residence time. Clearly, these results should not be extrapolated beyond the ruderal conditions that we simulated in our experiment. However, low interspecific competition and lack of nutrient limitation are representative of the environments the study species typically invade.

The strong negative relationship detected between seed mass and λ_0 suggests directional selection, which matches the significant decrease in the mean and SD of seed mass with residence time. The unimodal response of λ_0 to maximum height implies weak stabilizing selection. Given this weak selection on plant height, it is not surprising that the relationship between plant height and residence time is less clear. Our findings are thus coherent with theoretical expectations of selection acting between or within species.

We note that the species-for-time approach limits interpretation of our results. Potentially, our findings could be confounded by temporal variation in introduction bias (e.g., a priori differences in the characteristics of our study species that depend on the time and mode of introduction), land use, and climate. However, for a similar but smaller set of Asteraceae species, Sheppard and Schurr (2019) did not find differences in competitive ability, ruderality or stress tolerance among invasion status groups. We reduced a potential introduction bias by restricting the selection of our study species to annual species of ruderal/segetal habitats and growing them in a low-competition environment. Hence, it seems plausible that selection, both within and between species (two possible mechanisms between which the species-for-time approach however does not allow us to distinguish), shaped the relationships between population growth rate, functional traits and residence time. To quantify the relative importance of within- and between-species selection (i.e., observing a trait change in a species over time and species that deviate from optimal traits going extinct or failing to establish, respectively), it would be ideal to follow multiple species over thousands of years, which is obviously impractical.

Understanding whether variation in the performance of alien plants is driven by within- or between-species selection is important for invasion management, such as deciding whether to prevent the import of genotypes or species, and whether to focus management on all species (that may evolve to become invaders) or only monitoring the species with highest population growth rates. Given the large seed mass range covered by our study species and limits to intraspecific evolution in seed mass, between-species selection is probably more likely in our case. However, we suggest two realistic follow-up experiments to further disentangle the relative importance of within- versus between-species selection for shaping the relationships between population growth, climatic mismatches,

functional traits and residence time. (a) To assess within-species selection, populations from the new and native range of multiple species should be grown in common gardens in the new range. If within-species selection was important, population growth in the new range should differ between populations from the native and new range and this difference should increase with residence time and climatic distance between the common garden and the population origin. (b) To directly test the importance of between-species selection, species with different λ_0 should be set to compete against each other in the new range.

5 | CONCLUSIONS

Our results highlight the benefit of multi-species experiments (van Kleunen et al., 2014) to detect general patterns and underlying mechanisms of long-term population dynamics of alien plants. Our species-for-time approach (systematically varying MRT along an alien–native continuum) revealed increasing population growth with residence time, whereas effects of climatic mismatches had low support. Our experimental approach allowed us to apply Vellend's (2016) concept of community ecology to long-term species-level selection in alien species assemblages. The detected trait–demography relationships and trait–residence-time relationships suggest that directional selection on seed mass was associated with a better adaptation of the species pool to novel environmental conditions, likely to ruderal habitats rather than novel climates. Our results may also apply to other annual plant species that share similar habitat requirements. They may thus improve the predictability of future invasions and help in understanding constraints on population growth and spread of invaders already present (although we note the potential importance of other factors). Finally, our study strengthens links between invasion biology and other branches of ecology and contributes to the emerging integration of functional and population ecology.

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DATA AVAILABILITY STATEMENT

The experimental data are given in the Figures and Supporting Information. Data on minimum residence time (MRT) were extracted from plant checklists, the floristic and archaeobotanical literature, herbaria records and freely available online databases [Bundesamt für Naturschutz (BfN), www.floraweb.de; FlorKart,

BfN, and NetPhyD Netzwerk Phytodiversität Deutschlands e.V., www.deutschlandflora.de; Kühn et al., 2004, www.biolflo.de; Naturkundemuseum Stuttgart, www.florabw.recorder-d.de]. Data on MRT and post-processed data on the species' global distributions (obtained from the freely available online database Global Biodiversity Information Facility, www.gbif.org) and temperature variables (obtained from the WorldClim dataset, Hijmans et al., 2005, and from Agrarmeteorologie Baden-Württemberg, www.wetter-bw.de) used in the analyses can be requested from the corresponding author and will be archived on the Dryad digital data repository (<https://doi.org/10.5061/dryad.rjdfn2z8q>).

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BIOSKETCHES

Marco R. Brendel has strong interests in invasion biology and eco-evolutionary processes of alien plants in their new range. Specifically, he is interested in how novel climatic conditions interact with biotic resistance of native species to determine constraints on population growth and spread of alien plants.

Frank M. Schurr's work focusses on how large-scale dynamics of biodiversity arise from fundamental ecological and evolutionary processes.

Christine S. Sheppard has a main research focus on plant invasions. She combines experimental approaches with macroecological analyses to investigate temporal or spatial dynamics of plant invasions, effects of climate change on invasive species, and biotic interactions among alien and native species (see <https://christinesheppard.weebly.com> for more detail).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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