

RESEARCH PAPER

WILEY

Global Ecology
and Biogeography

A Journal of
Macroecology

Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia

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Funding information

German Research Foundation, Grant/Award
Number: SH 924/1-1

Abstract

Aim: Invasions are dynamic processes. Invasive spread causes the geographical range size of alien species to increase with residence time. However, with time native competitors and antagonists can adapt to invaders. This build-up of biotic resistance may eventually limit the invader's performance and reduce its range size. Using a species-for-time approach, we test (a) whether native communities more strongly reduce the fitness of immigrants with longer residence times, and (b) whether the range size of immigrant species shows a unimodal response to residence time.

Location: Germany.

Time period: 18,000 years BP to present.

Major taxa studied: 352 plant species in the Asteraceae family.

Methods: For plant species with a wide range of minimum residence times in Germany (6–18,000 years), we combined a common garden experiment with historical and macroecological analyses. In a multi-species experiment, we quantified the effect of native communities on fitness components of 30 annual Asteraceae. For these and other species, we then analysed how current range size depends on minimum residence time and other covariates.

Results: Native communities reduced survival, reproductive output and fitness of Asteraceae. This fitness reduction was stronger for immigrant species with long residence times. We found a unimodal relationship between range size and residence time of Asteraceae in Germany, when including natives that immigrated after the last glaciation.

Main conclusions: Biotic resistance may limit the performance and geographical ranges of immigrant species over long time-scales. The initial advantages invaders have over natives thus may not persist over millennia, supporting the concept of an alien–native species continuum defined by gradual changes in eco-evolutionary processes. While our analysis controlled for major ecological, evolutionary and biogeographical factors, it is conceivable that the detected patterns are influenced by additional differences between natives and aliens. Experimental macroecology has great potential to disentangle these processes and predict long-term invasion dynamics.

KEYWORDS

alien–native species continuum, Asteraceae, biotic resistance, competitive ability, introduction bias, long-term dynamics, multi-species experiment, plant invasion, range size, residence time

1 | INTRODUCTION

Biological invasions by alien species result in a broad range of impacts on native species, communities and ecosystems and can thereby pose major threats to biodiversity (Blackburn et al., 2014; Lambertini et al., 2011; Vilà et al., 2011). Moreover, environmental change, altered human activities and new socio-political conflicts are likely to further increase invasion risk (Ricciardi et al., 2017). Yet, it is increasingly debated whether invasive species fundamentally differ from natives and whether the distinction between alien and native origin is thus valuable (Davis & Chew, 2017; Davis et al., 2011; Hulme, Pyšek, & Duncan, 2011; Lambertini et al., 2011; Richardson & Ricciardi, 2013; Russell & Blackburn, 2017; Thompson & Davis, 2011; Valéry, Fritz, & Lefeuvre, 2013; van Kleunen, Dawson, & Dostal, 2011). However, ecological arguments for distinguishing among alien and native species include the fact that alien species do not constitute a random sample of all species from across the globe. Notably, factors that influence human-mediated introductions across biogeographical barriers differ from those determining natural dispersal, thus creating an introduction bias (Buckley & Catford, 2016). For instance, recently introduced neophytes may be more competitive (Gioria & Osborne, 2014; Golivets, Wallin, & Gurevitch, 2018; Vilà & Weiner, 2004) and better adapted to disturbance or high nutrient availability (Buckley & Catford, 2016; Moles et al., 2012; Seabloom et al., 2015) than native species. Beyond that, however, the lack of evolutionary history in the new region distinguishes alien species from natives (Buckley & Catford, 2016): when competition for limiting resources exerts selection pressure, co-existing native species may have developed niche differentiation or reached a balance in competitive abilities through adaptive evolution (Thorpe, Aschehoug, Atwater, & Callaway, 2011). Conversely, alien species have advantages in their new biotic environment if they possess “novel weapons” to which native species are not adapted (Callaway & Aschehoug, 2000) or if they are released from natural enemies (Keane & Crawley, 2002).

Many of the ecological and evolutionary processes that cause differences between alien and native species are likely to change with time since introduction of a species to a new area, that is with the alien's residence time (Saul & Jeschke, 2015; Strayer, Eviner, Jeschke, & Pace, 2006). The distinct stages of transport, introduction, establishment and spread describe the process of a biological invasion (Blackburn et al., 2011). Alien species in the final stage are termed invasive, meaning that they reproduce in large numbers and spread over wide areas (Richardson et al., 2000). Residence time, along with propagule pressure, is probably the most consistent factor that explains invasiveness (Richardson & Pyšek, 2006). This is not surprising given that range expansion should cause range size to increase with residence time. Accordingly, Pyšek et al. (2015) found that residence time was strongly associated with establishment success of Central European plants in North America, and similarly Ahern, Landis, Reznicek, and Schemske (2010) found that residence time explained c. 40% of the variation in range size of alien plants in Michigan and California. A positive relationship between range size

and residence time was also found for neophytes on oceanic islands (Azores, New Zealand, Hawaii) and in several European countries (Czech Republic, Ireland, Great Britain, Germany) (Pyšek & Jarošík, 2005; Williamson et al., 2009).

Eventually, however, there will be limits to the population growth and range size of invaders. Indeed, the longer a species resides in a given biogeographical area, the less novel it is to native species. The accumulating evolutionary experience of native communities may limit invader performance (Hawkes, 2007; Saul & Jeschke, 2015). Furthermore, limits may arise due to ecological or evolutionary constraints in the invader itself (Lankau, Nuzzo, Spyreas, & Davis, 2009). The frequently invoked invader superiority (Lowry et al., 2013) thus needs to be investigated over longer time-scales to determine if it is a temporary phenomenon. In this respect, evolution of interspecific interactions may play a role in the invasion process (Carroll, 2007) as rapid evolutionary change can occur on time-scales of decades to centuries (Hairston, Ellner, Geber, Yoshida, & Fox, 2005). As a result of evolutionary responses, biotic resistance from native communities may increase over time. Indeed, a recent meta-analysis of 53 studies found that “experienced” populations of native plants (pre-exposed to plant invaders) tolerate competition from invaders better than “naïve” populations (Oduor, 2013). Furthermore, another meta-analysis showed that the initial benefits of enemy release in alien plants (lower herbivory or pathogen attack compared to congeners in the introduced range and conspecifics in the native range) disappeared 50–200 years after introduction (Hawkes, 2007). Such pathogen accumulation in alien species can result both from increasing abundance of pre-adapted pathogens in response to more abundant and widespread invaders or from the evolutionary adaptation of native pathogens to invaders (Flory & Clay, 2013). In summary, the advantages, dominance and impacts of invasive species may be transitory due to negative ecological and evolutionary feedbacks. So far, however, it has not been tested whether biotic resistance of native communities to immigrant species increases with residence time, and thereby reduces fitness of the invader. A lower average fitness of invaders should reduce their intrinsic population growth rate and increase the probability of population extinction. A build-up of biotic resistance across large geographical extents should thus reduce the range size of invaders (Schurr et al., 2012). The combination of range expansion and increasing biotic resistance may then result in a unimodal relationship between range size and residence time.

To investigate such potential limits to long-term dynamics of plant invasions, we here employ a species-for-time approach, comparing many species with a wide range of residence times. Specifically, for Asteraceae species with residence times in Germany ranging from 6 to 18,000 years, we combine an experimental test of biotic interactions with native communities, a historical reconstruction of residence times and a macroecological analysis of the factors influencing range size. Our study serves to test two hypotheses: (a) a build-up of biotic resistance causes native communities to more strongly reduce the fitness of immigrants with longer residence times, and (b) the joint effects of range expansion and a build-up of biotic resistance cause a unimodal relationship between the range size and residence

time of immigrant species. We also consider the alternative hypothesis that interspecific differences in fitness and range size may result from a temporally varying introduction bias, meaning that species characteristics depend on time and mode of introduction. In particular, we examine whether species that immigrated a long time ago are per se less competitive and thus have smaller range sizes than more recent immigrants.

2 | METHODS

2.1 | Study system

As a study system of phylogenetically related plant species that are functionally similar and share similar habitat requirements, we chose herbaceous Asteraceae in Germany. Asteraceae are one of the most species-rich plant families in Europe and globally (Funk et al., 2005) and comprise a large number of established alien species (Hanspach, Kühn, Pyšek, Boos, & Klotz, 2008). Starting from all the Asteraceae occurring in Germany according to local floras and databases, we compiled data on a set of 451 Asteraceae species, for which information on residence times, range size and phylogenetic relationships was available. This species set was then filtered to exclude species of specialized habitats, which are unlikely to occur in open vegetation where the majority of Asteraceae are found. Specifically, we used the BioFlor database (Kühn, Durka, & Klotz, 2004, www.biolflor.de) and the German flora Rothmaler (Jäger, 2016) to exclude all species restricted to saline or tidal habitats, bogs, forests and alpine habitats. We excluded species indicating cold temperatures (with Ellenberg indicator values for temperature of $T = 1$ or $T = 2$, Ellenberg & Leuschner, 2010) that may have persisted in Germany through the last glaciation. The final species set of open-vegetation Asteraceae included 352 species: 94 neophytes (recent invaders introduced after year 1492), 40 archaeophytes (alien species that were introduced to Europe since the Neolithic, i.e., since c. 7,500 years ago) and 218 native species (that immigrated after the last glacial maximum).

Because exact dates of introduction are often unknown, minimum residence time (MRT), estimated as time since the first recorded occurrence, was used as a proxy (Rejmánek, 2000). We extracted MRTs (relating to a species' first record in Germany) of neophytes and archaeophytes from plant checklists, the floristic and archaeobotanical literature, herbaria records and 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.biolflor.de; Naturkundemuseum Stuttgart, www.florabw.recorder-d.de). Given that we excluded native species with a high affinity to cold climates, it is very likely that the remaining native species immigrated between the last glacial maximum (18,000 years ago, Clark et al., 2009) and the end of the last glacial period (10,000 years ago). However, as the year of immigration is unknown, we used randomly selected MRT values (between 10,000–18,000 years) for native species, repeating the random assignment of MRT values 1,000 times to use in

the analyses described below. For the common garden experiment, we used a subset of 30 annual Asteraceae species consisting of 11 neophyte, 12 archaeophyte and 7 native species covering the full range of minimum residence times (Supporting Information Table S1). This subset was selected from the 79 annual species by choosing only species occurring in ruderal or segetal (growing among crops) habitats as these are the habitats most commonly occupied by annual species. We aimed for an even spread across invasion status and minimum residence time, but excluded the two black-listed annual neophyte Asteraceae species (Nehring, Kowarik, Rabitsch, & Essl, 2013). We standardized taxonomic names following The Plant List (Kalwij, 2012, www.theplantlist.org) and determined phylogenetic relationships using the Daphne phylogeny (Durka & Michalski, 2012; Supporting Information Figure S1).

2.2 | Common garden experiment

We carried out a common garden experiment to investigate biotic interactions of a native community with immigrant plant species of varying residence times. The experiment consisted of two treatments in which the focal species was either grown in a native community or in isolation. For each of the 30 focal species and two treatments, we established five replicates (reduced to two to four replicates for seven of the species due to a lack of germinated seedlings, Supporting Information Table S1), resulting in 262 pots in total.

The common garden was located at the agricultural field station of the University of Hohenheim in Stuttgart, Germany (400 m a.s.l.; mean annual temperature 8.5 °C; annual precipitation 685 mm). We used pots of 15 L volume (32 cm diameter, 25 cm height), filled with a mixture of 50% sand and 50% sterilized compost. In half of the pots, we established the community treatment by sowing a typical Central European meadow mixture composed of regional genotypes of 30% herbs and 70% grasses (certified regional mixture "Fettwiese (2)", Rieger-Hoffmann GmbH, Blaufen-Raboldshausen, Germany; Supporting Information Table S2). In May 2015, this seed mixture was sown at the recommended sowing density of 3 g/m² and covered with a thin layer of sand. The other half of the pots was subject to the control treatment (growing the focal species in isolation), and hence only covered with a thin layer of sand.

Seeds of the focal species were obtained from botanical gardens in Germany and commercial seed suppliers (Supporting Information Table S1). Although regionally sourced seeds are preferable whenever possible, the specific populations used are here not as crucial given that we are interested in interspecific variation and only consider relative performance measures (and thus remove e.g., any effect of adaptation to local climate, see below). Nevertheless, we note that performance may also depend on seed source. Natives more frequently were obtained from botanical gardens and neophytes from commercial sources. Visual inspection of the data suggests that there are low and high performing individuals from all seed sources. A control analysis adding seed source (botanical garden vs. commercial) as a covariate did not change the direction of the results reported below, but reduced effect sizes.

In May 2015, we sowed the seeds in a greenhouse into seed trays that were filled with the soil mixture also used for the experimental pots. 2 weeks after sowing, when most seedlings had germinated, we moved the trays to the common garden to acclimatize seedlings to outside conditions. 3 to 4 weeks after sowing we then re-potted the seedlings into small individual pots. Between 5 to 6 weeks after sowing (late June 2015), we planted four seedlings of a single focal species into each experimental pot. Throughout the experiment we recorded premature plant mortality. We harvested the plants when they had completed their life cycle, starting from 7 weeks after the beginning of the experiment (mid-August 2015) continuously until mid-October 2015 (after 16 weeks). Aboveground biomass was dried at 70 °C for 3 days before weighing. To assess reproductive output, we counted the number of capitula (flower heads) of each individual.

Data were analysed in R 3.3.2 (R Core Team, 2016). For each species and treatment, we considered three performance measures: the number of surviving individuals, the reproductive output as quantified by the number of capitula and as a fitness proxy for annual plant species, the product of survival and reproductive output for each individual. Effects of biotic interactions with the native community were quantified as the ratio between performance in the community and performance in isolation. These relative performance measures have a value of 1 if the focal species shows equal survival, reproductive output or fitness in both treatments. Specifically, to calculate relative survival, the proportion of survivors in each pot in the community treatment was divided by the species' mean proportion of survivors per pot in isolation. Relative reproduction and fitness were calculated by dividing reproduction or fitness of each individual in the community treatment by the species' mean reproduction or fitness in isolation. To address our first hypothesis of whether native communities more strongly reduce the fitness of the focal immigrant species with longer residence times, we regressed each of these response variables against log-transformed MRT. Relative survival in the community was $\log(x + 0.1)$ -transformed and relative reproduction and relative fitness were $\log(x + 0.01)$ -transformed to ensure normality and variance homogeneity of residuals. Response variables were scaled to compare the strength of residence time effects among performance measures. We employed a Bayesian approach to analyse relative survival, reproduction and fitness, using Markov chain Monte Carlo methods in the MCMCglmm package (Hadfield, 2010). We included the phylogenetic correlation structure, species and pot (the latter for relative reproduction and relative fitness only) as random effects in our models. For the variance components of each random effect, we used non-informative priors that correspond to an inverse-Gamma distribution with shape and scale parameters equal to 0.01. We ran the models for 1,000,000 iterations, using a burn-in phase of 1,000 and thinning interval of 500. For each measure of relative performance, we ran 1,000 models using the 1,000 datasets generated with randomly assigned MRT values for the native species. To evaluate the effect of including native species in our immigrant species set and for comparison with previous studies, we repeated the analysis excluding native species and we also compared our results to

an analysis using invasion status (neophyte, archaeophyte or native) as an explanatory variable instead of MRT. Furthermore, in consideration of the alternative hypothesis on whether there are a priori differences in competitive ability due to an introduction bias, we examined growth rate in isolation as a proxy for competitiveness in benign environments (Grime, 1974, 1977; Lambers & Poorter, 1992). When competing for limiting resources, plants with high growth rates benefit from being able to rapidly occupy a large space (Lambers & Poorter, 1992). Hence, we tested whether (log-transformed) aboveground biomass in isolation differs among invasion statuses or whether it depends on MRT of the focal species.

2.3 | Range size analysis

To address the hypothesis of a unimodal relationship between the range size of immigrant plant species in Germany and residence time, we analysed the effect of minimum residence time on range size in Germany across the full set of 352 study species. Data on range size in Germany were obtained from the database of FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. (www.deutschlandflora.de), documenting species' occurrence per grid cell of 10×6 arc minutes (c. $11 \text{ km} \times 11 \text{ km}$) divided into four quadrants. We then calculated the response variable range size in Germany as the proportion of occupied cells and applied a logit-transformation (Warton & Hui, 2010). Data were analysed using phylogenetic generalized least squares (PGLS) regression to account for phylogenetic non-independence (function `gls` in `nlme` package, Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016) with Pagel's λ correlation structure (Pagel, 1999) estimated by maximum likelihood. To test whether the relationship between range size and minimum residence time is unimodal, we compared a model with a linear effect of log-transformed MRT to one with linear and quadratic effects of $\log(\text{MRT})$ using likelihood ratio tests. To account for the increasing uncertainty of the MRT estimates with residence time, MRT was log-transformed and 1,000 models were run using the 1,000 datasets generated with randomly assigned MRT for the native species. To create a confidence envelope around the unimodal relationship, we generated 10 bootstrap resamples of residuals for each of the 1,000 models. This yielded 10,000 bootstrap range sizes for each MRT value from which the 95% confidence interval was calculated. Furthermore, we calculated the position of the peak in the unimodal relationship (i.e., maximum range size) and its 95% confidence interval using the 1,000 models. To check whether a quadratic regression reasonably approximates the relationship between range size and residence time, we also analysed the data using a generalized additive model (GAM; R package `mgcv`, Wood, 2011), estimating the optimal amount of smoothing by cross-validation and using a cubic regression spline.

In a series of supplementary analyses, we controlled for several other factors that may affect range size. We repeated the analysis excluding casual neophytes (i.e., neophytes that have not established self-sustaining populations and rely on repeated introductions for persistence, Richardson et al., 2000) to reduce uncertainty

in minimum residence time and range size data associated with these species. Casual status was determined from the German flora Rothmaler (Jäger, 2016) and the online database of the Bundesamt für Naturschutz (www.floraweb.de). We also checked red list status for all species (Ludwig & Schnittler, 1996) to control for a potential bias in the analysis by including red-listed archaeophytes and native species. Thus, we repeated the analysis after restricting the species set to non-red-listed species (i.e., not classified as critically endangered, endangered or vulnerable). Moreover, we conducted further analyses of the full dataset that included an additional covariate. As range size in Germany may depend on how widespread and generalist a species is across its global range, we compiled data on global range size and habitat breadth. Global range data were extracted from the Global Biodiversity Information Facility (GBIF, www.gbif.org). Duplicates and erroneous occurrence records in the ocean were removed. Combining the GBIF data with the German data from the FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. database, we calculated the global range size as the number of occupied 2.5 arc minutes grid cells. We also used the global occurrence data to determine habitat breadth of each focal species by counting the number of World Wildlife Fund (WWF) terrestrial ecoregions of the world (Olson et al., 2001) in which each species occurs. Furthermore, to assess how well climatic conditions in Germany match median conditions within the global range of a species, we used Worldclim data (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005, www.worldclim.org). Specifically, we determined the global median for annual mean temperature and annual precipitation at the occurrences of each species, and calculated the distance to the median of these climatic variables in Germany (i.e., temperature and precipitation distance). We also determined the global climatic amplitude of each species by calculating the range of the central 95% (2.5–97.5% quantile) of annual mean temperature and annual precipitation at the occurrences of each species (i.e., temperature and precipitation amplitude). Furthermore, to account for the fact that not all of Germany may be climatically suitable for our species, we estimated the potential range in Germany. Using global occurrence data (given that native and invaded ranges are not clearly distinguishable across the globe, especially for archaeophytes) and six bioclimatic variables from Worldclim (Hijmans et al., 2005), we calculated Mahalanobis distances (Farber & Kadmon, 2003) from the climatic optimum to each grid cell in Germany. We chose the bioclimatic variables mean diurnal range, maximum temperature of warmest month, minimum temperature of coldest month, precipitation of wettest month, precipitation seasonality and precipitation of warmest quarter because of their ecological relevance for plant growth and their low multicollinearity (Sheppard, 2013). The potential range in Germany was calculated as the proportion of cells with a Mahalanobis distance less than 4 (Farber & Kadmon, 2003; using a more conservative threshold of 2.5 as in Wilson et al., 2007 did not change the results qualitatively). To ensure that results are not caused by climatic range limits, a supplementary analysis examined how log(MRT) affects range filling, that is, the proportion of suitable habitat in Germany occupied. Furthermore, we considered edaphic

affinity as a further covariate: we compiled Ellenberg indicator values for soil fertility, which classify the affinity of plant species to soil nitrogen on an ordinal scale (Ellenberg & Leuschner, 2010). Adding these values as a covariate in the analysis enabled us to control for neophytes being potentially pre-adapted to fertile conditions (Seabloom et al., 2015). Finally, differences in plant functional strategies may affect range size. Thus, we categorized all species according to Grime's CSR (Grime, 1974, 1977) using information from Hunt et al. (2004) and the BiolFlor database (Kühn et al., 2004). We then used quantitative C- and R-coordinates according to Hunt et al. (2004) as covariates in the analysis. In these series of supplementary analyses most explanatory variables (except potential range in Germany, Ellenberg indicator values and Grime's CSR coordinates) were log-transformed (adding 0.1 in the case of temperature distance due to some zero values); and the explanatory and response variables were scaled to enable comparison of effect strength among alternative models. Finally, to evaluate the effect of including native species in our immigrant species set and for comparison with previous studies, we also compared our results to an analysis excluding natives and we tested for differences in range size according to invasion status (casual neophyte, established neophyte, archaeophyte or native).

Potential differences in responses to native communities need not be caused by co-evolution after introduction. Instead, they might result from an introduction bias that causes species introduced at different times to differ in competitive ability. To examine this alternative hypothesis, we assessed whether the unimodal relationship remained when including the C-coordinate of Grime's CSR scheme, thus accounting for potential differences in competitive ability. Additionally, we tested whether species characteristics depend on introduction history by relating CSR coordinates to MRT or invasion status. Specifically, we used a linear model of log(MRT) or invasion status on logit-transformed coordinates (for the full species set and the subset used in the common garden experiment), adding the smallest non-zero proportion to both the numerator and denominator of the logit-function (Warton & Hui, 2010).

3 | RESULTS

3.1 | Common garden experiment

The native community generally reduced the survival of the focal immigrant Asteraceae species. Only two of the 30 species (the neophytes *Cota austriaca* and *Centaurea benedicta*) had overall higher survival in the native community than in the control treatment. This negative effect of the native community on survival became stronger as minimum residence time of the focal species increased (posterior mean MRT effect across 1,000 models -0.22 , with 95% credible interval $-0.50, 0.06$; Figure 1a). **Phylogenetic signal was estimated to be weak with mean Pagel's $\lambda = .12$ (95% credible interval $.002, .39$).**

Reproductive output was also generally lower in the presence of the native community. Five of the 30 focal species in the experiment did not reproduce in the community treatment even though they

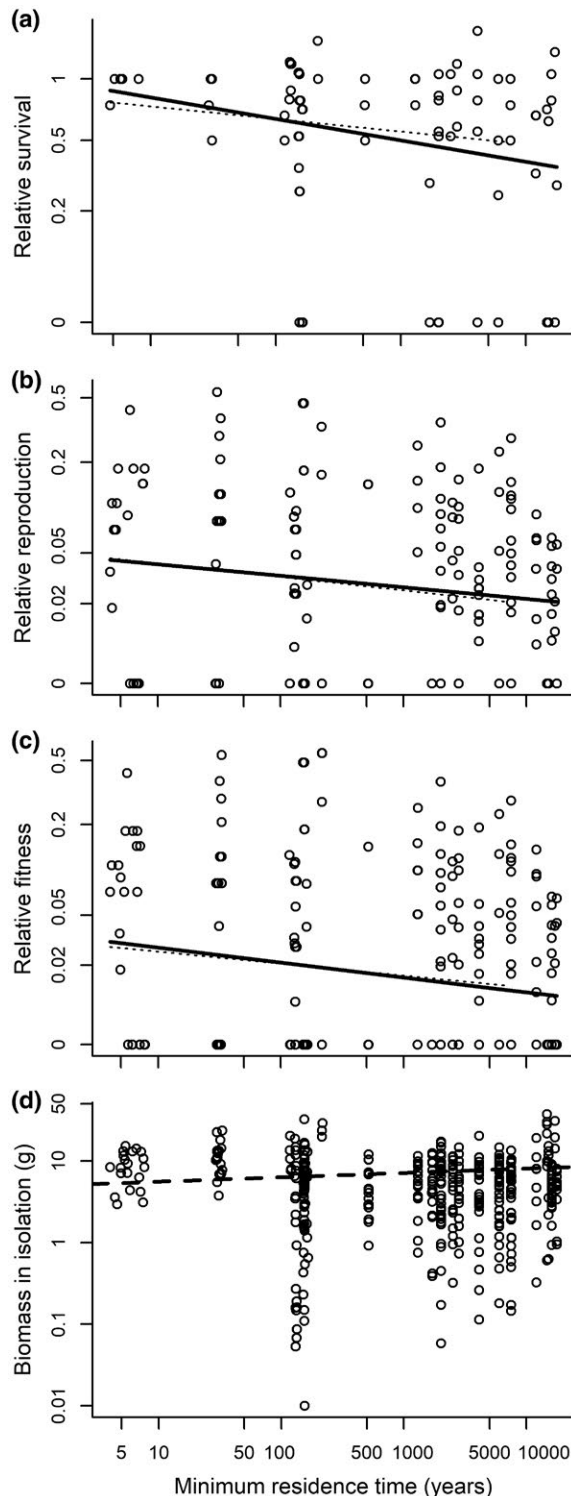


FIGURE 1 Results of the multi-species common garden experiment, showing the effect of minimum residence time (MRT, axis shown on a logarithmic scale) of the 30 focal immigrant Asteraceae species on (a–c) the relative performance in the community (all axes on log-scale): (a) the relative survival (measured as the ratio between the proportion of surviving individuals per pot in the community and the mean proportion in isolation, $N = 131$), (b) the relative reproductive output (measured as the log ratio between an individual's number of capitula in the community and the mean number in isolation, $N = 294$) and (c) the relative fitness (measured as the log ratio of the fitness, i.e., the product of an individual's survival and reproductive output, in the community versus mean fitness in isolation, $N = 509$). (d) Relationship between MRT and a proxy for competitive ability (aboveground biomass of focal individuals in isolation, $N = 425$). Solid (and dashed) lines show the mean prediction over 1,000 models (using datasets with randomly assigned MRT values between 10,000 and 18,000 years for native species) of the MCMCglmm regression models, dotted lines the prediction for a model without natives for comparison (only in a–c). Original data are plotted using one randomly chosen set of MRT values for native species and are jittered for better visibility

The presence of the native community also reduced the fitness proxy (the product of survival and reproductive output) for all focal species. The native community reduced individual fitness more strongly for species with increasing minimum residence times (posterior mean MRT effect -0.18 , with 95% credible interval -0.40 , 0.04 ; Figure 1c). Phylogenetic signal was estimated to be $\lambda = .15$ (95% credible interval $.002$, $.43$). In summary, the strength of the reduction in performance in the presence of the native community for immigrant species with longer residence times was strongest for survival, followed by fitness and reproductive output. In the control analysis excluding natives, model predictions remain similar, but the effect is weaker for survival (Figure 1). Furthermore, the models including the effect of $\log(\text{MRT})$ on relative performance reported here were slightly better compared to models that replaced $\log(\text{MRT})$ with invasion status [slightly lower deviance information criterion (DIC); Supporting Information Figure S2].

Regarding the alternative hypothesis, we found no indications of a priori differences in competitive ability: growth in isolation (as a widely used proxy for competitive ability in benign environments) was not significantly affected by $\log(\text{MRT})$ (posterior mean MRT effect across 1,000 models -0.06 , with 95% credible interval -0.23 , 0.35 for $N = 425$ individuals; Figure 1d). Accordingly, the focal species included in the experiment showed no relationship between the C-coordinate of the CSR-strategy scheme and $\log(\text{MRT})$ or invasion status (Figure 2).

3.2 | Range size analysis

We found a unimodal relationship between range size in Germany and MRT of the full set of 352 immigrant Asteraceae species [likelihood ratio test for the quadratic effect of $\log(\text{MRT})$, $\chi^2_{1 \text{ df}} = 32.42$, $p < .001$; Figure 3a]. Phylogenetic signal in this PGLS regression was estimated to be $\lambda = .34$ (95% confidence interval $.16$, $.52$). Removing casual neophytes or red list species from the analysis did

reproduced in isolation (the neophyte *Crepis setosa*, the archaeophytes *Crepis capillaris* and *Helminthotheca echioides*, and the natives *Crepis pulchra* and *Senecio viscosus*). The MRT of the focal species had a negative effect on the relative reproduction in the community, so that the native community tended to reduce the number of capitula per individual more strongly for species with increasing MRT (posterior mean MRT effect across 1,000 models -0.15 , with 95% credible interval -0.40 , 0.11 ; Figure 1b). Phylogenetic signal was estimated to be $\lambda = .13$ (95% credible interval $.002$, $.37$).

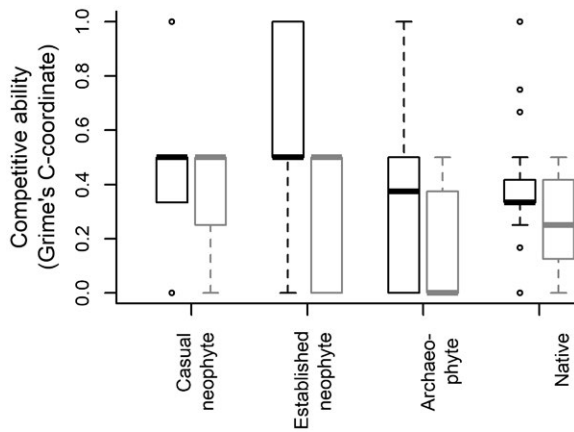


FIGURE 2 Boxplots showing differences in competitive ability (C-coordinate of Grime's CSR strategy scheme) between plant species of different invasion status. Black boxes represent all 335 Asteraceae species, whereas grey boxes represent the species used in the common garden experiment (28 species for which CSR information is available)

not qualitatively change the shape of the relationship (Figure 3a, Supporting Information Figure S3 and Table 1). However, when removing natives from our species set, we obtained a positive rather than unimodal relationship between range size and residence time (Table 1, Figure 3a). For the full range of immigrant species, we also found a highly significant quadratic effect of $\log(\text{MRT})$ when controlling for global range size, number of ecoregions, temperature and

precipitation distance, temperature and precipitation amplitude, potential range in Germany, Ellenberg indicator values for soil fertility or plant functional strategies after Grime's CSR (Table 1). In particular, the unimodal relationship also remained when accounting for differences in competitive ability by including the C-coordinate. The C-coordinate had no significant effect or a weak negative effect on range size, depending on whether the R-coordinate was also included or not (Supporting Information Figure S4). For all other analyses including these various covariates, the effect of the covariate was highly significant (Supporting Information Figure S4, Table 1). In these alternative analyses, range size was estimated to peak at MRTs between 1,998 and 4,129 years (Table 1). For all analyses, the 95% confidence intervals of this optimal residence time fell well within the range of MRTs considered (Table 1). Hence, the quadratic effect of $\log(\text{MRT})$ describes a unimodal rather than an asymptotic response of range size to MRT.

Furthermore, using GAM as an alternative modelling approach also showed a unimodal relationship with a peak in range sizes at intermediate MRT values (Supporting Information Figure S5). Replacing range size with range filling as the response variable showed a unimodal relationship between the percentage of suitable range occupied and residence time (Table 1, Supporting Information Figure S6). Investigating if range size depended on categorical invasion status as explanatory variable instead of continuous minimum residence time also showed a highly significant effect ($\chi^2_{3\text{df}} = 88.19$, $p < .001$; with $\lambda = 0.27\%$ and 95% confidence interval 0.11, 0.44; Figure 3b). The Akaike's information criterion (AIC) of this model was

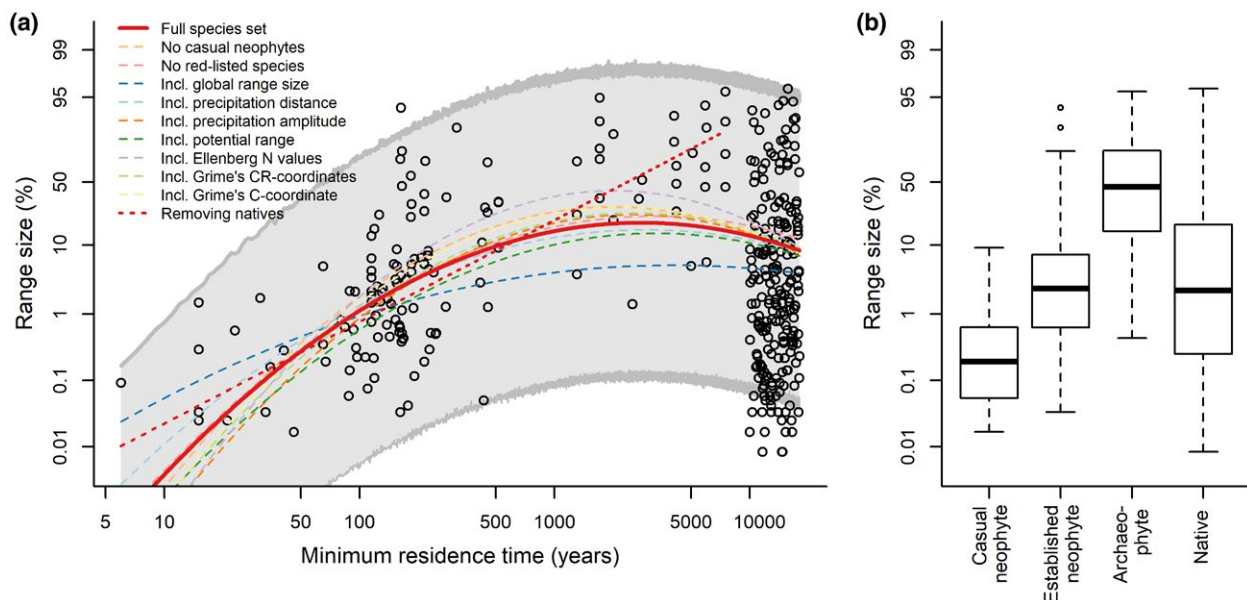


FIGURE 3 (a) Relationship between range size and minimum residence time (MRT) for 352 immigrant Asteraceae species. Range size (% of Germany occupied by a species) was logit-transformed and MRT log-transformed, with both axes shown on a logarithmic scale. The solid red line shows the mean prediction over 1,000 models (using datasets with randomly assigned MRT values between 10,000 and 18,000 years for native species), the grey polygon and lines show the 95% confidence interval. Dashed lines show the mean predictions of alternative models (Table 1), with covariates fixed at their mean, with the red dotted line showing the linear prediction for a model without natives. Original data are plotted using one randomly chosen set of MRT values for native species. (b) Boxplot showing the relationship between range size and invasion status (27 casual neophytes, 67 established neophytes, 40 archaeophytes and 218 natives) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results of alternative phylogenetic generalized least squares (PGLS) models for the relationship between range size in Germany and minimum residence time (MRT). Standardized regression coefficients for the quadratic effect of $\log(\text{MRT})$ with 95% confidence intervals in parentheses over 1,000 models (using datasets with randomly assigned MRT values for native species) are indicated. For all models, significance of the quadratic effect of $\log(\text{MRT})$ was tested using likelihood ratio tests. If applicable, effect sizes (regression coefficients) of the covariates are reported and their significance according to likelihood ratio tests. χ^2 is indicated, with p -values: n.s., not significant; * $p < .05$; ** $p < .01$; *** $p < .001$. Peak MRT (where range size is maximized) with 95% confidence interval, sample sizes in the respective analysis and estimated phylogenetic signal (with 95% confidence intervals in parentheses) are shown. For related covariates using the same sample sizes, only the model with lowest Akaike's information criterion (AIC) is reported. All reported values are averaged across 1,000 replicate models using randomly assigned MRT values for native species

Model	Mean effect of $\log(\text{MRT})^2$ (95% confidence interval)	Mean χ^2 for the effect of $\log(\text{MRT})^2$	Mean effect of the covariate (95% confidence interval)	Mean χ^2 for the effect of the covariate	Mean peak MRT (95% confidence interval)	Sample size	Mean phylogenetic signal (95% confidence interval)
Full species set	-2.83 (-3.09, -2.57)	32.42***	-	-	2,799 (2,520–3,154)	352	.34 (.16, .52)
Casual neophytes removed	-3.33 (-3.74, -2.94)	29.12***	-	-	1,998 (1,855–2,182)	325	.32 (.13, .52)
Red-listed species removed	-2.68 (-2.92, -2.42)	28.18***	-	-	3,261 (2,875–3,760)	303	.36 (.18, .54)
With covariate log global range size ^a	-1.29 (-1.43, -1.14)	18.98***	0.90 (0.90, 0.91)	486.9***	4,129 (3,563–4,928)	341	.31 (.04, .58)
With covariate log precipita- tion distance ^b	-2.33 (-2.65, -2.02)	19.23***	-0.39 (-0.39, -0.40)	79.22***	2,949 (2,569–3,462)	341	.24 (.09, .38)
With covariate log precipita- tion amplitude ^c	-3.49 (-3.84, -3.14)	35.27***	0.18 (0.17, 0.19)	15.52***	2,529 (2,313–2,806)	341	.32 (.13, .52)
With covariate potential range	-2.86 (-3.13, -2.58)	31.33***	0.54 (0.53, 0.54)	115.4***	3,327 (3,000–3,775)	333	.20 (.00, .40)
With covariate Ellenberg indicator values for soil fertility	-4.30 (-5.06, -3.57)	16.63*** ^d	0.30 (0.28, 0.32)	17.85*** ^d	2,011 (1896–2,161)	184	0
With covariates plant functional strategy after Grime's CSR	-3.22 (-3.66, -2.79)	25.79***	0.09 (0.08, 0.11) (C-coordinate) 0.23 (0.21, 0.25) (R-coordinate)	1.28 n.s. (C-coordinate) 8.32** (R-coordinate)	2,583 (2,298–2,968)	335	.29 (.13, .46)

(Continues)

TABLE 1 (Continued)

Model	Mean effect of log(MRT) ² (95% confidence interval)	Mean χ^2 for the effect of log(MRT) ²	Mean effect of the covariate (95% confidence interval)	Mean χ^2 for the effect of the covariate	Mean peak MRT (95% confidence interval)	Sample size	Mean phylogenetic signal (95% confidence interval)
As above, but including only the C-coordinate	-3.51 (-3.96, -3.09)	30.27***	-0.10 (-0.11, -0.09)	3.91*	2,148 (1,981–2,361)	335	.34 (.16, .52)
Natives removed: linear effect of log(MRT) ^e	log(MRT): 0.82 (0.70, 0.95)	0.36 n.s.	-	-	-	134	.44 (.05, .83)
Range filling (%) as response variable	-3.60 (-3.92, -3.24)	33.28***	-	-	2,741 (2,505–3,054)	333	.25 (.06, .44)

^aThis model is better than a model including log number of ecoregions ($\Delta AIC = 273.6$). ^bThis model is better than a model including log temperature distance ($\Delta AIC = 26.0$). ^cThis model is better than a model including log temperature amplitude ($\Delta AIC = 6.2$). ^dResults of F-test (linear model as λ estimated to be 0). ^eFor a model fitted separately for neophytes and archaeophytes, the regression coefficient of the linear effect of log (MRT) for neophytes is 0.52 (0.36, 0.69) and for archaeophytes 0.37 (0.04, 0.69).

lower compared to the quadratic model with a $\Delta AIC = 41.4$. Finally, we investigated CSR-strategies across the full species set to test if there are a priori differences in species characteristics. This indicated that there are differences between the various plant groups, with neophytes being more competitive (Figure 2, while natives tend to be more stress-tolerant and archaeophytes more ruderal, Supporting Information Figure S7). Invasion status explains more variation in these differences than residence time (lower AIC).

4 | DISCUSSION

The multi-species common garden experiment supported our first hypothesis that native communities more strongly reduce the fitness of immigrants with longer residence times. The macroecological analysis also supported the second hypothesis of a unimodal relationship between range size and residence time (when including natives that immigrated after the last glaciation). Hence, as we discuss below, biotic resistance by native communities may contribute to limiting performance and range size of immigrant plant species over long time-scales. On the other hand, we found no clear support for the alternative hypothesis that a temporally varying introduction bias caused a priori differences in competitive ability for the species included in the experiment. Nevertheless, it is likely that varying species characteristics associated with an introduction bias contribute to the unimodal relationship between range size and residence time (Figure 4).

4.1 | The unimodal relationship between range size and residence time

No study has previously tested for a unimodal relationship between range size and residence time. This is understandable given that the effects of residence time were previously not studied over the wide range of residence times that we investigated here. Previous studies demonstrated a linear relationship between range size of neophytes and residence time (Ahern et al., 2010; Pyšek & Jarošík, 2005; Williamson et al., 2009), with Williamson et al. (2009) and Gassó, Pyšek, Vilà, and Williamson (2010) estimating that it takes neophytes in Europe on average around 150 years before spread levels off. Moreover, common aliens (as a group including both neophytes and archaeophytes) have been shown to reach similar range sizes as common native species (Stohlgren et al., 2011). However, Pyšek and Jarošík (2005) still found a positive effect of MRT on the range size of archaeophytes in the Czech Republic and Great Britain, even though this positive effect was weaker than for neophytes. This is in line with what we found in an analysis of range size excluding natives (Figure 3). Going a step further, Williamson et al. (2009) compared range sizes of natives, archaeophytes, and casual or established neophytes in four European countries. For Germany (as well as for Britain and the Czech Republic) they found that range size increased from casual species over established neophytes, to native species and finally to archaeophytes, also similar to what we found here for

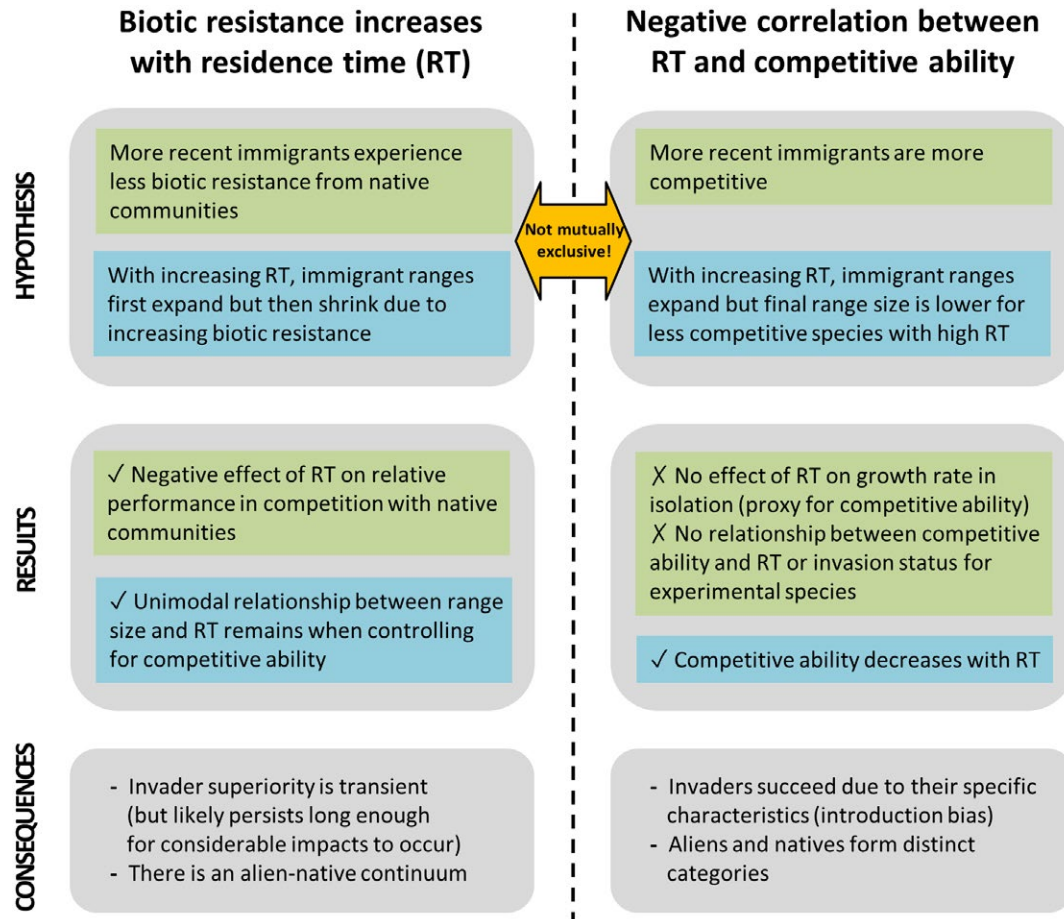


FIGURE 4 Two alternative hypotheses for relationships between performance of immigrant plant species and residence time. The figure summarizes evidence for (✓) and against (✗) each hypothesis and sketches implied consequences (see section on “Experimental macroecology and the alien–native species continuum: benefits and challenges” for suggestions for future research to differentiate the two hypotheses). Green boxes refer to experimental studies, blue boxes to macroecological analyses [Colour figure can be viewed at wileyonlinelibrary.com]

Asteraceae (Figure 3b). Beyond these findings, however, we here for the first time show a unimodal relationship between range size and residence time, which was robust irrespective of how we tested for it (Figure 3a, Supporting Information Figures S3 and S5). Range size is estimated to peak 1,800–5,000 years after arrival (Table 1). The fact that the unimodal relationship is only apparent when considering the full species set (including native immigrant species) may highlight the importance of including longer time-scales to elucidate invasion dynamics (i.e., an alien–native continuum, see below), but could also indicate that natives as a group (even if they are immigrants themselves) are not fully comparable to aliens (Hulme et al., 2011; Richardson & Ricciardi, 2013; van Kleunen et al., 2011).

The unimodal relationship between range size and residence time was not altered when we included 10 potential determinants of range size as covariates in the macroecological analysis (Table 1). Hence, these covariates explain neither the general unimodal relationship nor range size differences between aliens and natives. Still, we find that all covariates have important effects on range size. Our results support the well-known finding that global range sizes and

broad habitat or climatic tolerances contribute to invasion success (Cadotte, Murray, & Lovett-Doust, 2006; Dyer et al., 2016; Hayes & Barry, 2008; Pyšek et al., 2009, 2015). Climatic differences between Germany and a species' global range also had a negative effect on range sizes, indicating that pre-adaptation to climatic conditions may be an important determinant of invasion success (Hayes & Barry, 2008; Petitpierre et al., 2012). In line with suggestions by Wilson et al. (2007), potential range in Germany had a strongly positive effect on range size, although for most species a high percentage of Germany was estimated to be climatically suitable. In a related study, Bradley, Early, and Sorte (2015) found that invasive plant species in the USA have larger potential ranges but lower range filling than natives. Yet, in our analysis the unimodal effect of residence time became even more apparent when considering range filling instead of range size. This suggests that this unimodal relationship is not determined by potential range size. Furthermore, affinity to fertile soils increased range sizes, which may reflect superior adaptation to environmental conditions arising from human disturbances. Accounting for these differences in affinity to soil fertility resulted

in an even stronger effect of quadratic $\log(\text{MRT})$. Finally, plant species with a ruderal strategy (following Grime's CSR, Grime, 1974, 1977) had larger range sizes. Overall, although our results provided evidence that all discussed covariates are important determinants of range size, none of the covariates seems responsible for the unimodal effect of MRT on range size.

4.2 | Fitness reduction by native communities for species with longer residence times: Evidence for increasing biotic resistance?

Which mechanisms could eventually limit the range sizes of immigrant species as residence time increases? One possibility is that increasing eco-evolutionary experience (Saul & Jeschke, 2015) of native communities may over time compensate for invader superiority. In the common garden experiment, we indeed found that the longer the residence time of a species the more its survival, reproduction and fitness were reduced by the native community, which could indicate a build-up of biotic resistance of the native community. There are various ways in which native communities may exhibit biotic resistance, including competition from native plants, herbivory or attack from soil pathogens. A meta-analysis on biotic resistance showed that these various factors are unlikely to prevent the establishment of invaders, but affect their abundance (Levine, Adler, & Yelenik, 2004). Antagonistic plant-plant interactions may not only involve competition for resources but also allelopathic effects (Callaway, Ridenour, Laboski, Weir, & Vivanco, 2005). Given the potential for rapid evolutionary change (Whitney & Gabler, 2008), eco-evolutionary novelty of the invader and its interaction with the native community may well decrease over the time-scales covered in our study system. In systems such as ours that experienced recent glaciation (or other strong climatic changes), a large share of "native" species only immigrated over the last 18,000 years. This contrasts with more climatically stable regions in which native species have a much longer local co-evolutionary history, while human-mediated introductions started only a few centuries ago. The latter situation less likely represents a continuum between aliens and natives and thus may not be expected to show a unimodal relationship between range size and residence time. To gain further insight into the mechanisms of potential eco-evolutionary novelty of biotic interactions, it may be informative to investigate effects of functional traits on biotic resistance (e.g., Grutters, Roijendijk, Verberk, & Bakker, 2017) and, particularly, to look at trait differences between older and more recent immigrant species.

Experimental evidence for eco-evolutionary limits to invader performance at the intraspecific level and on even much shorter time-scales is provided by a study by Dostál, Müllerová, Pyšek, Pergl, and Klinerová (2013). They compared invasion success of *Heracleum mantegazzianum* in the Czech Republic among populations with residence times of 11–48 years. Their study showed decreasing cover of the invader with time, which may have been due to a negative plant-soil feedback resulting from the accumulation of soil pathogens. Moreover, impacts on native communities changed: initially richness and productivity of native species decreased, but they increased

again after around 30 years (Dostál et al., 2013). Such higher performance of experienced native species that had the opportunity to adapt to an invasive plant's presence has been observed in several other studies (Oduor, 2013): for example, native grasses growing for 20–30 years with *Centaurea maculosa* in North America tolerate the allelochemicals better than native grasses from uninvaded habitats (Callaway et al., 2005). These studies thus also provide evidence for a build-up of biotic resistance over shorter time-scales, although little is known about the long-term or large-scale consequences.

4.3 | Could an introduction bias result in a negative correlation between residence time and competitive ability?

An important aspect that needs to be considered when using the species-for-time approach is that certain species characteristics may covary with time of introduction and thus with residence time. Hence, the relationship between range size and residence time may be a result of a priori differences in species characteristics that depend on the time and mode of introduction (Figure 4). Particularly, because of the introduction bias (Buckley & Catford, 2016), species introduced at different times may differ in their competitive abilities. If competitive ability is negatively correlated with residence time, this could potentially explain our experimental results without any changes in biotic resistance from the native community. In addition to species-specific differences, there is also a possibility of a bias arising from the different seed source types we used, which may lead to differences in competitive ability or other performance traits.

Across the full species set, we indeed find indications that invasion status is related to CSR-strategy, with neophytes being more competitive, natives more stress-tolerant and archaeophytes more ruderal (Supporting Information Figure S7). These differences may, instead of (or in addition to) biotic resistance from the native community, contribute to the unimodal relationship between range size and residence time (Figure 4). Yet, for the subset of species used in the common garden experiment there are no significant differences among invasion statuses in the C-coordinate (neither in S- or R-) of Grime's CSR scheme (Figure 2). Also, the C-coordinate had even a weak negative effect on range size and its inclusion did not alter the unimodal relationship between range size and residence time. This suggests that the residence time effect cannot simply be explained by interspecific variation in competitive ability. In addition, residence time did not affect aboveground biomass of the focal species in isolation. Assuming that competitive ability in benign environments is dependent on rapid maximum potential relative growth rates to maximize resource capture (Grime, 1974, 1977; Lambers & Poorter, 1992), we hence expect no consistent differences in competitive ability with residence time.

4.4 | Additional factors that may contribute to the relationship between range size and residence time

There are other species characteristics that potentially depend on introduction histories and may contribute to the unimodal relationship

between range size and residence time, although importantly, these cannot explain the experimental results. Species that arrived at different times may also be adapted to different environmental conditions. We accounted for major environmental covariates by including climatic distance or amplitude and soil fertility in our analyses. However, we note that Ellenberg indicator values for soil fertility were generally lower for native species compared to the other groups (with a median value of three for natives, five for casual neophytes, and six for both established neophytes and archaeophytes). Species with long residence times (i.e., before the beginnings of agriculture in Germany with the arrival of the Linearbandkeramik culture c. 7,500 years ago, Bramanti et al., 2009) may not be adapted to agriculture, which could cause them to have lower current range sizes. In support of this expectation, species with a ruderal strategy or high affinity to fertile soils had larger range sizes (especially in the case of the archaeophytes, which might explain why in this group small range sizes are rare). Furthermore, dispersal ability, human activities and with these propagule pressure may also depend on invasion status and affect range sizes. Nevertheless, while habitat association and propagule pressure may contribute to a unimodal relationship between range size and residence time, they do not explain the experimentally observed decrease in relative fitness for immigrants with longer residence times.

Finally, processes other than increasing biotic resistance might contribute to forming the patterns we observed. There are a variety of possible mechanisms potentially causing boom–bust dynamics in single species over time (Strayer et al., 2017), some of which may also apply here. For instance, antagonists from the native ranges of immigrant plant species may be gradually introduced and may limit immigrant performance (Flory & Clay, 2013). Evolutionary changes in the invader could also be relevant, as suggested by the evolution of increased competitive ability hypothesis (Blossey & Nötzold, 1995). Conversely, an interesting example of evolutionary processes limiting invader impacts is given by the invasive garlic mustard (*Alliaria petiolata*), which upon introduction to North America had a competitive advantage over native plants due to the production of an allelopathic phytotoxin (Lankau et al., 2009). However, phytotoxin production is selected against as the density of *A. petiolata* increases. Accordingly, older *A. petiolata* populations have reduced population growth and smaller impacts on native species (Lankau et al., 2009).

4.5 | Experimental macroecology and the alien–native species continuum: Benefits and challenges

Invasions are dynamic processes to which native communities respond ecologically and evolutionarily (Carroll, 2007). Yet, the frequent merging of data from various points in time along the course of an invasion makes assessment of the relevant ecological and evolutionary processes difficult (Strayer et al., 2006) and may explain some of the conflicting results on differences between native and alien species. While the availability of MRT data may have been one limiting factor explaining previous disregard of residence time, more

knowledge on the history of invasions is emerging, at least for neophytes (Seebens et al., 2017). Given the rather coarse spatial scale of such data a species-for-time approach seems appropriate. We note, however, that this approach has its limitations and is not equivalent to following a species over long time-scales. The considerable variation inherent to comparing many different species and logistic constraints make multi-species experiments challenging. Hence, they are still rarely used in ecology despite their usefulness in searching for general patterns and mechanisms (van Kleunen, Dawson, Bossdorf, & Fischer, 2014). Here, we aimed to standardize the species set by including only annual species of one family occurring in open-vegetation habitats. Moreover, given that these species do not represent independent observations, we accounted for phylogenetic relationships. With such an approach we could show that indeed, the relative strength of the ecological and evolutionary processes that determine performance and ranges of immigrant plant species are related to residence time. Hence, this suggests that there is a continuum from alien to native species, a concept that we call the alien–native species continuum. Other authors have raised the opinion that invasions should be treated as continuous phenomena rather than being divided into discrete categorical steps (Gillson, Ekblom, Willis, & Froyd, 2008; Mitchell et al., 2006) and highlighted the link to post-glacial range expansions (Gillson et al., 2008; Petit, Bialozyt, Garnier-Géré, & Hampe, 2004). For instance, the lack of natural enemies may also play a role for natural range expansions (Petit et al., 2004). This suggests that not only species introduced by humans experience a build-up of biotic resistance. While the same ecological processes apply to alien and native immigrants, the distinction among invasion status groups stresses that the initial starting point may be different, such as the characteristics of species due to an introduction bias. The difficulty in conclusively distinguishing between the two hypotheses we have raised and discussed here presents a challenge for the species-for-time approach.

Future research efforts should aim to disentangle the relative contributions of introduction bias and biotic resistance to the performance and range size of immigrant species (Figure 4). Firstly, an extended experiment could include an additional control community to which all species are naïve (i.e., with which they never interacted). Such a design would enable one to quantify the extent to which performance differences are due to species characteristics versus biotic resistance. A second experimental approach may keep the invader constant but vary the native community using a transplant experiment. Such an invader should form distinct populations that differ in their residence time in the respective native community. Moreover, there should be little gene flow between these invader populations. A possible study system would be alien food plants introduced by Polynesian voyagers during their spread across Pacific islands (Abbott & Shimazu, 1985). Finally, an alternative direct test for the evolution of biotic resistance in native species may be provided by “resurrection ecology” using dormant seeds of various ages preserved in soils or sediments (Orsini et al., 2013). These ideas for future research show that, as in the study of novel species interactions under climate change (Alexander, Diez, Hart, & Levine, 2016),

there is great potential to better understand invasion dynamics with experimental macroecology.

5 | CONCLUSIONS

Using a species-for-time approach we here for the first time show a unimodal response of range size to residence times of a wide range of immigrant plant species (although the relationship is positive for alien species only). We also demonstrate that native communities more strongly reduce fitness of immigrant species with longer residence times. This may indicate that biotic resistance contributes to the eventual decrease in range size. The initial advantages that alien species potentially have over natives thus may not persist over millennia, illustrating the usefulness of the concept of an alien–native continuum. However, while these results highlight potential limits to invader performance, they certainly do not endorse a do-nothing approach to biological invasions. In fact, range size (as a proxy for invader impact) only seems to be reduced after a long time when the invaded ecosystems may have been altered profoundly. Future research that tightly integrates macroecological analyses and multi-species experiments has the potential to disentangle the ecological and evolutionary processes underlying the relationship between performance and residence time. Such an approach will greatly benefit our understanding of complex invasion dynamics and aid in predicting long-term effects of invasions.

ACKNOWLEDGMENTS

This research was supported by the German Research Foundation DFG (grant SH 924/1-1). We thank B. Springer, T. Lukeševik, H. Cooksley and N. Sheppard for their field assistance, and J. Fix and H. Oliphant for their assistance with data compilation. Thanks to the botanical gardens of the Universities of Constance and Hohenheim in Germany for providing seed materials used in the experiment. We are grateful to C. J. B. Sorte, R. Early and J. R. U. Wilson for their helpful comments improving this manuscript.

DATA ACCESSIBILITY

The experimental data are given in the Figures and Supporting Information. Data on range size were obtained from the freely available database of FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. (www.deutschlandflora.de). Data on minimum residence times and post-processed data on covariates used in the analyses can be requested from the corresponding author, and upon completion of the German Research Foundation (DFG) -funded research project (2020) will be archived on the GFBio digital data repository.

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BIOSKETCHES

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SUPPORTING INFORMATION

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How to cite this article: Sheppard CS, Schurr FM. Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. *Global Ecol Biogeogr.* 2019;28:222–237. <https://doi.org/10.1111/geb.12844>