From alien to native Asteraceae: how effects of climate, functional traits, and biotic interactions on population growth change with residence time

Dissertation to obtain the doctoral degree of Agricultural Sciences (Dr. sc. agr.)

Faculty of Agricultural Sciences

University of Hohenheim

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2023

Oral examination on 9th October 2023

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Summary

The aim of this thesis is to investigate interactions of alien species with the novel abiotic and biotic environment in their introduced range over eco-evolutionary timescales, since the introduction of alien species and their subsequent invasion pose a major threat to native biodiversity. Given the globally increasing costs of impacts and management of invasive plants, it is thus of utmost importance to gain a better understanding of limits to population growth and spread of invasive plants.

Abiotic constraints due to climatic mismatches between the area of origin and the introduced area as well as biotic resistance of native communities in the introduction area present natural barriers to invasion success. On the one hand, alien plants respond to environmental selection for instance via rapid evolution of functional traits and thereby adapt to novel abiotic conditions. Additionally, invasion success of alien plants may also be related to their competitive superiority over native plants. On the other hand, native community species are expected to adapt to the presence of the invader by gaining eco-evolutionary experience and build-up biotic resistance over time. However, most studies put only little focus on how mechanisms of adaptation to the abiotic environment and biotic resistance that determine invasion success change over residence time of alien plants (i.e., the time since introduction into a new area).

For my thesis, I conducted common garden experiments based on an alien-native species continuum to cover a broad range of residence times in Germany (7 to 12,000 years before present). Particularly, I followed the population growth of 47 annual Asteraceae (including neophytes, archaeophytes, and natives) over two years and measured their performance in intra- and interspecific plant-plant interactions to answer the following questions: 1) How are effects of climatic distances between the area of origin and the introduced area as well as functional traits on population dynamics of alien plants determined by residence time? 2) How is biotic resistance of native communities towards alien plants related to residence time? 3) How are competitive outcomes between single alien and native species shaped by residence time and serve as a predictor of range sizes?

To answer the first question, I followed population growth and demographic rates of the Asteraceae target species in monoculture mesocosms. Furthermore, I calculated climatic distances between the area of origin and the introduced area and measured functional traits that represent key axes of plant ecological strategies (i.e., seed mass, maximum height, and specific leaf area). Firstly, I tested whether negative effects of climatic distances on population growth weaken with residence time. Secondly, I investigated trait-demography relationships and tested if functional traits converge towards values that increase population growth under local climatic conditions. I found strong effects of functional traits, especially seed mass, and no effects climatic distances on population growth. Specifically, a strong negative relationship between seed mass and population growth resulted in directional selection and led to a convergence of seed mass to low values with increasing residence time.

For the second question, I measured population growth and demographic rates of the target species in community mesocosms with a Central European grassland community. I tested if the competitive effects of the community on the target species increase with residence time, respectively their co-existence time with the native community (an indication for a build-up of biotic resistance). To further disentangle if an increase in competitive effects related to a gain in eco-evolutionary experience of the native community or to inherent competitive abilities of the targets, I used a second community as control. This community consisted of species native to North American grasslands and never co-existed with and are thus naïve to the target species. To investigate how the role of functional traits for invasion success changes depending on the presence/absence of interspecific competition, I compared trait-demography relationships in both community types with monocultures. I found that both community types exert similar competitive effects on the Asteraceae targets and thus no evidence for a build-up of competition-induced biotic resistance over time. Instead, invasion success was determined by a strong seed-mass-mediated trade-off between population growth in low-competition monocultures vs. high-competition of native communities.

Answering the third question included a pairwise competition experiment with five native Asteraceae target species, each of which interacted with 47 alien and native neighbour (Asteraceae) species. I tested if the response of native targets (in terms of biomass and seed production) to competition with alien and native neighbours depends on residence time. Furthermore, I tested if competitive effects differ between invasion status groups and explain species' range sizes in Germany. I generally did not find a higher tolerance of native target individuals to competition of neighbouring alien and native targets with increasing residence time. Both established neophytes and natives showed a similarly high interspecific competitive ability and species' range sizes were not influenced by per-capita competitive effects.

The detected trait-demography relationships and related directional selection as a mechanism of adaptation to novel abiotic conditions improve the understanding of constraints on population growth and spread of invaders. The lack of interspecific competitive superiority as a determinant of range sizes might indicate that other mechanisms are more important for invasion success. The functional trade-off between population growth in low vs. high competition reveals that invaders that are likely to escape this trade-off should be of highest management concern. By the combination of experimental macroecology with approaches of functional and community ecology used in my study, I strongly advanced the understanding of mechanisms of limits to population growth and spread of alien plants and provide a fundamental basis for future research in invasion ecology.

Zusammenfassung

Ziel dieser Doktorarbeit sind Untersuchungen zu Interaktionen nicht-einheimischer Pflanzenarten mit neuen abiotischen und biotischen Umweltbedingungen in ihrem Einführungsgebiet über ökologisch-evolutionäre Zeiträume hinweg vor dem Hintergrund, dass die Einführung gebietsfremder Arten und ihre darauffolgende Invasion in hohem Maße zum Verlust einheimischer Biodiversität beitragen. Auf globaler Ebene sind die Kosten negativer Auswirkungen und Managementkosten insbesondere für invasive Pflanzen stark steigend. Aus diesem Grund ist es von äußerster Wichtigkeit, ein besseres Verständnis über Einschränkungen von Populationswachstum und Verbreitung invasiver Pflanzen zu erlangen.

Klimatische Unterschiede zwischen Herkunfts- und Einführungsgebiet stellen zusammen mit der biotischen Resistenz einheimischer Artgemeinschaften im Einführungsgebiet natürliche Hindernisse für den Invasionserfolg dar. Als Antwort auf die Selektion durch neue abiotische Umweltbedingungen sind einerseits rasche evolutionäre Anpassungen nicht-einheimischer Pflanzen zu erwarten, z.B. bei funktionellen Merkmalen. Zusätzlich kann die überlegene Konkurrenzfähigkeit gebietsfremder Pflanzen gegenüber einheimischen Pflanzen zu einem Invasionserfolg führen. Anderseits ist auch eine Anpassung einheimischer Artgemeinschaften an die Anwesenheit nicht-einheimischer Pflanzen zu erwarten. Der Gewinn ökologisch-evolutionärer Erfahrungen führt hierbei zu einem Aufbau biotischer Resistenz über die Zeit. Jedoch haben solche Mechanismen der Anpassung an neue abiotische Umweltbedingungen und der biotischen Resistenz, die den Invasionserfolg beeinflussen, bisher wenig Aufmerksamkeit bekommen, insbesondere in Bezug auf die Abhängigkeit dieser Mechanismen von der Residenzzeit nicht-einheimischer Pflanzen (Zeit seit der Einführung in ein neues Gebiet).

Im Rahmen meiner Doktorarbeit habe ich verschiedene Gartenexperimente durchgeführt, basierend auf einem Kontinuum von gebietsfremden zu einheimischen Arten, um einen möglichst weiten Bereich von Residenzzeiten in Deutschland abzudecken (von 7 bis 12.000 Jahren vor heute). Ausgehend davon habe ich das Populationswachstum von insgesamt 47 Arten der Asteraceae Familie (Neophyten, Archäophyten und Einheimische) über zwei Jahre hinweg verfolgt und deren Wachstums- und Reproduktionsleistung in intra- und interspezifischen Pflanzeninteraktionen gemessen, um folgende Forschungsfragen zu beantworten: 1) Wie wirken sich klimatische Unterschiede zwischen Herkunfts- und Einführungsgebiet ebenso wie funktionelle Merkmale in Abhängigkeit von der Residenzzeit auf das Populationswachstum gebietsfremder Pflanzen aus? 2) Wie wird der Zusammenhang

zwischen biotischer Resistenz einheimischer Artgemeinschaften gegenüber gebietsfremden Pflanzen durch deren Residenzzeit bestimmt? 3) Wie werden Konkurrenz-Effekte zwischen einzelnen gebietsfremden und einheimischen Pflanzen durch die Residenzzeit beeinflusst und dienen sie der Vorhersage von deren Verbreitungsgebietsgröße?

Für die erste Frage habe ich das Populationswachstum der Zielarten in Mesokosmos-Monokulturen verfolgt. Ich habe die klimatischen Unterschiede zwischen Ursprungs- und Einführungsgebiet berechnet und funktionelle Merkmale gemessen (Samenmasse, Maximal-Höhe und spezifische Blattfläche), welche Hauptachsen der ökologischen Strategien von Pflanzen widerspiegeln. Erstens habe ich getestet, ob sich der Effekt der klimatischen Unterschiede auf das Populationswachstum mit zunehmender Residenzzeit abschwächt. Zweitens habe ich die Zusammenhänge zwischen funktionellen Merkmalen und Populationswachstum untersucht und getestet, ob die funktionellen Merkmale über die Zeit zu Werten konvergieren, die zu einem erhöhten Populationswachstum unter lokalen klimatischen Bedingungen führen. Ich konnte starke Effekte der funktionellen Merkmale, insbesondere Samenmasse, aber keine Effekte von klimatischen Unterschieden auf das Populationswachstum feststellen. Ein stark negativer Zusammenhang zwischen Samenmasse und Populationswachstum führte zu einer gerichteten Selektion und mit zunehmender Residenzzeit konvergierte die Samenmasse hin zu kleinen Werten.

Für die zweite Frage habe ich das Populationswachstum der Zielarten in Mesokosmos-Gemeinschaften mit einer in Zentraleuropa heimischen Graslandgemeinschaft gemessen. Ich habe getestet, ob sich die Konkurrenz-Effekte auf die Zielarten mit deren Residenzzeit, respektive Ko-Existenzzeit mit der einheimischen Graslandgemeinschaft, verstärken. Um herauszufinden, ob eine mögliche Zunahme von Konkurrenz-Effekten auf den Gewinn ökologisch-evolutionärer Erfahrung der einheimischen Artgemeinschaft oder auf inhärente Konkurrenzeigenschaften der Zielarten zurückzuführen ist, habe ich eine zweite Artgemeinschaft als Kontrolle verwendet. Diese setzt sich aus Arten zusammen, die im nordamerikanischen Grasland heimisch sind und mit den Zielarten nicht koexistiert haben, also naiv gegenüber diesen sind. Ich habe die Beziehungen zwischen funktionellen Merkmalen und Populationswachstum der Zielarten in beiden Artgemeinschafts-Typen mit denen in Monokultur verglichen, um die Rolle funktioneller Merkmale für den Invasionserfolg bei An-/Abwesenheit von interspezifischer Konkurrenz zu untersuchen. Beide Artgemeinschafts-Typen haben sehr ähnliche Konkurrenz-Effekte auf die Zielarten ausgeübt, sodass es keine direkten Hinweise für einen Aufbau von biotischer Resistenz über die Zeit gegeben hat. Vielmehr wurde der Invasionserfolg durch einen Kompromiss

zwischen Populationswachstum in geringer Konkurrenz (Monokulturen) und Populationswachstum in starker Konkurrenz (einheimische Artgemeinschaften) bestimmt, der durch die Samenmasse getrieben wurde.

Für die dritte Frage habe ich ein Konkurrenz-Experiment durchgeführt, bei dem paarweise fünf einheimische Asteraceae-Zielarten mit 47 nicht-einheimischen und einheimischen Nachbararten (Asteraceae) interagiert haben. Ich habe untersucht, ob die Reaktion von Wachstums- und Reproduktionsleistung der einheimischen Zielarten auf die Konkurrenz der Nachbararten von der Residenzzeit abhängt. Ich habe getestet, ob sich die Konkurrenz-Effekte zwischen den Invasions-Statusgruppen unterscheiden und diese die Verbreitungsgebietsgröße in Deutschland erklären können. Eine höhere Toleranz der einheimischen Zielarten gegenüber der Konkurrenz mit den nicht-einheimischen und einheimischen Nachbararten mit zunehmender Residenzzeit konnte im Allgemeinen nicht festgestellt werden. Etablierte Neophyten und einheimische Arten haben eine ähnliche interspezifische Konkurrenzfähigkeit aufgezeigt und die Verbreitungsgebietsgröße der Arten wurde nicht durch die Pro-Kopf-Konkurrenz-Effekte beeinflusst.

Die erkannten Zusammenhänge zwischen funktionellen Merkmalen und Populationswachstum und die daraus resultierende gerichtete Selektion als Anpassungsmechanismus an neue abiotische Umweltbedingungen, tragen zu größerem Verständnis über Einschränkungen von Populationswachstum und Verbreitung invasiver Pflanzen bei. Überlegene interspezifische Konkurrenz konnte nicht als Einflussgröße auf die Verbreitungsgebietsgröße festgestellt werden, sodass für den Invasionserfolg wahrscheinlich andere Mechanismen eine größere Rolle spielen. Der funktionell bedingte Kompromiss zwischen Populationswachstum in geringer Konkurrenz und Populationswachstum in starker Konkurrenz deutet darauf hin, dass Invasoren, die diesen funktionell bedingten Kompromiss überwinden können, von höchstem Belang für das Management sein sollten. Durch die Kombination aus experimenteller Makro-Ökologie mit Ansätzen aus der funktionalen Ökologie und der Ökologie von Artgemeinschaften in dieser Doktorarbeit, konnte ich in erheblichem Maße zu einem verbesserten Verständnis über die Mechanismen beitragen, die eine Einschränkung von Populationswachstum und Verbreitung invasiver Pflanzen bestimmen, und darüber hinaus eine wesentliche Grundlage für zukünftige Studien auf dem Gebiet der Invasionsökologie liefern.

Acknowledgements

I want to thank numerous people who helped and supported me – without them, I never would have finished this thesis. First of all, a big THANK YOU to my supervisor Christine Sheppard who kept motivating me over such a long timescale. Thank you very much for your endless patience and feedback, which was always helpful and constructive, for being attentive to details and for being positive, whenever things seemed hopeless (at least to me). Hereby, I developed to become a better scientist. A big thank you also goes out to my co-supervisor Frank Schurr for "doubling the size of the experiment" and always being supportive and having a sympathetic ear, and for giving me the opportunity to gain experience in teaching and various other branches of academia.

I also want to thank the group of Landscape Ecology and Vegetation Science in Hohenheim for providing a highly comfortable and inspiring working atmosphere, especially because of my office mates Jinlei, Nick, Dominique, Viki, and Nataša – you made me laugh countless times and kept up the good mood. I am also very grateful to Betty, Carsten, and Huw who helped me setting up the experiments and solving the many practical and technical issues an experimental plant ecologist has to face. Additional thanks to Stephanie, Felix, Hannah, Nick, and Huw (once again) for field and lab assistance.

I especially thank Vicky Temperton who inspired me to study interactions between native plants and an invasive plant for my Master's thesis – the cornerstone of my interest in invasion ecology. I also thank Jonathan T. Bauer for helping to select the North American community species and ship the seeds – a foundation of my second chapter.

A big thank to my friends who went with me through my emotional ups and downs. Magnus Müller for inviting me over for a "Kölsche Ovend" when distraction was necessary and Claudia Harhammer for going to the movies on Monday evenings. This helped me to keep a clear head.

Finally, I would like to thank my family for their unconditional support, for always believing in me and for making it possible to study and follow my interest in this one particular topic for such a long time. A very special thank you to Julia Jungbluth – without her emotional support, I never would have managed the final phase of completing my thesis.

This project received funding by the German Research Foundation assigned to Christine Sheppard.

General Introduction

Biological invasions present a crucial part of global environmental change as they pose a great threat to biodiversity (Lambertini *et al.* 2011) and even drive native species to extinction (Bellard *et al.* 2016; Blackburn *et al.* 2019). Negative impacts of invasions encompass various mechanisms, for instance competition, predation or herbivory, and parasitism that affect native species and communities and disrupt the structure and functioning of whole ecosystems (Mack *et al.* 2000). Particularly, invasive alien plants (see definition in Box 1) reduce abundance and diversity of native plants (Richardson *et al.* 2000a; Vilà *et al.* 2011). All of these impacts can lead to significant changes of ecosystem services from which humans directly and indirectly benefit (Vilà & Hulme 2017; Kumar Rai & Singh 2019). The invasion process, until an alien species ultimately becomes invasive, follows the key stages of transport, introduction, establishment, and spread (Blackburn et al. 2011).

Box 1: Definition of invasive alien plants

The term invasive plants refers to alien plants that establish self-sustaining populations and thus become naturalized, thereby producing very large numbers of reproductive offspring which makes them capable of spreading over a considerable area (Richardson *et al.* 2000b). Alien plants that successfully reproduce become naturalized but not necessarily invasive via high reproductive output and fast spread over a large area (Pyšek & Richardson 2006). From a Central European perspective, alien plants (i.e., plant taxa whose presence is due to intentional or accidental human transport/introduction to a new area) are differentiated according to their introduction history: neophytes that were introduced after the discovery of America in 1492 A.D. and archaeophytes that were introduced before 1492 A.D. (Pyšek *et al.* 2004b). Among neophytes, it is further distinguished between established and casual neophytes, whereby the latter do not have established self-sustaining populations and rely on repeated introductions for persistence (Richardson *et al.* 2000b). In contrast to alien plants, native plants are defined as “plant taxa that have arrived at a place without intentional or unintentional human intervention from an area in which they are native or that originated there naturally” (Pyšek *et al.* 2004a).

Over the last century, the human-mediated translocation of species from their native origin to different parts across the globe (and the associated naturalization of these species in their new range) has drastically increased for the vast majority of taxa including vascular plants; yet, a saturation in the accumulation of alien species (that may become invasive) is not expected (Seebens *et al.* 2017). Specifically, the number of established alien species per continent is predicted to increase from the year 2005 to 2050 by 36% on average with a particularly strong increase for Europe of more than 2,000 alien species until 2050 (plus 64% with reference to 2005) (Seebens *et al.* 2021). In this context, key drivers of plant invasions are intensification of global trade and transport (Hulme 2009), introduction for ornamental purposes and domestic gardens (van Kleunen *et al.* 2018), land-use change (Pauchard & Alaback 2004), and access to new source pools (Seebens *et al.* 2018). Furthermore, the risk of naturalization of alien plants that have already been introduced, for instance ornamental plants in gardens, is expected to increase as a result of climate change (Dullinger *et al.* 2017). The current naturalization of alien plants has already led to a loss of floristic uniqueness globally and, considering the projected future trends, floristic homogenization is likely to continue and even accelerate with largely unknown ecological, evolutionary, and socioeconomic consequences (Yang *et al.* 2021).

On a global scale, the economic costs of invasive alien species have been estimated to accumulate to at least US$1.3 trillion for the period between 1970 and 2017, whereby the average annual costs increased gradually (Diagne *et al.* 2021). In this context, damage of invasions reached more than 10-fold higher costs compared to expenses for their management. Regarding taxonomic groups, plants rank the third-highest economic impact (after vertebrates and invertebrates) with US$8.9 billion between 1970 and 2017 (Diagne *et al.* 2021). However, Novoa *et al.* (2021) stress that the global costs of plant invasions are strongly underestimated; yet, more accurate estimations are urgently needed to improve the prioritization of invasive species management in order to reduce their ecological and socio-economic impacts (Novoa *et al.* 2021). From the total accumulated costs of US$140.2 billion related to biological invasions in Europe between 1960 and 2020, agriculture was the most impacted sector with US$36.0 billion that equals to 26% of total costs (Haubrock *et al.* 2021). Furthermore, the Asteraceae species *Ambrosia artemisiifolia* was detected as the second-highest cost-contributor, thereby impacting most countries in Europe (Haubrock *et al.* 2021). Additionally, it presents a serious health risk as its pollen can cause allergic asthma (Buters *et al.* 2015). These examples clearly highlight the severity of economic losses associated with invasive alien species and the extent to which humans are directly affected.

Ecological impacts of invasive alien plants are manifold and include disruptions of whole ecosystem processes via alterations of fire regimes (Brooks *et al.* 2004) and increased nutrient inputs through nitrogen fixation (Vilà *et al.* 2011). Furthermore, invader impacts are also related to changes of interactions between native species. For instance, invasive plants can reduce abundances of native specialized pollinators by outcompeting their host plants (Vanbergen *et al.* 2018) and a stronger attraction of native generalist pollinators to invasive plants may lead to fitness disadvantages of native plants due to lower flower visitation in habitats with high invader abundances (Dietzsch *et al.* 2011). The highest levels of invasion by neophytes in Europe were found for agricultural (segetal) and ruderal habitats that are characterized by frequent disturbances and nutrient inputs (Chytrý *et al.* 2009). In contrast, natural and semi-natural European grasslands have relatively low levels of neophyte invasions, with two Asteraceae species, *Erigeron annuus* and *E. canadensis*, among the three most abundant invaders (Axmanová *et al.* 2021). However, such semi-natural grasslands but also ruderal habitats play a key role in supporting insect functional diversity and are therefore of high conservation concern (Eyre *et al.* 2003; Bonari *et al.* 2017; Kalarus *et al.* 2019). Almost 40% of the total land area in Europe is used for agriculture (Eurostat, www.ec.europa.eu; last access in 2022), covering semi-natural grasslands and ruderal habitats. Particularly, in Germany, grasslands, including semi-natural grasslands, also harbour approximately 40% of endangered native plant species and are thus of additional conservation value (Bundesamt für Naturschutz 2017). Furthermore, semi-natural and managed grasslands, where extensive grazing provides the highest benefits for biodiversity conservation (Tälle *et al.* 2016), are getting invaded by the Asteraceae species *Senecio inaequidens* that is toxic to humans and livestock (Scherber *et al.* 2003; Lachmuth *et al.* 2011; Delory *et al.* 2019). Hence, ecological research of plant invasions in Europe should focus on semi-natural grasslands and ruderal habitats to further support management and conservation strategies.

The focus of research on determining invasion success or susceptibility of native communities towards invasions has led to various hypotheses to explain the so-called “paradox of invasion” (Sax & Brown 2000). This paradox is related to the question, why alien species that are expected to be poorly adapted to local conditions in their new range, are able to establish there and in some instances even outcompete locally adapted native species (Sax & Brown 2000). Particularly, differences in climatic conditions between the area of origin and the new range can impair invasion success (Donaldson *et al.* 2014), for instance due to a lack of adaptation potential related to low genetic variation of initially small populations (Dlugosch *et al.* 2015) or the introduction of maladapted genotypes (Braasch *et al.* 2019). Conversely, the success of invasive species has been proposed to be the result of a benefit from a release from natural enemies (Keane & Crawley 2002). As a consequence, invasive species may invest less into defence mechanisms and evolve an increased competitive ability (Blossey & Nötzold 1995). Furthermore, invasive species can also possess “novel weapons”, for instance phytotoxic compounds that are released into the soil (i.e., allelopathy), to which native species are not adapted (Callaway & Aschehoug 2000). The invasibility of a community is related to its biotic resistance (i.e., interactions between native and alien species that hinder establishment and spread of alien species; see Maron & Vilà 2001) that can be mediated by competition, parasitism, and predation/herbivory (Levine *et al.* 2004; Alpert 2006). Specifically, biotic resistance can cause invaders to completely fail to establish, or more commonly found, lead to a decrease of invasion success (Levine *et al.* 2004). However, the conflicting results on the general applicability of all these hypotheses suggest that invasion success is likely to be context-dependent and a better integration of knowledge from the fields of invasion, community, and functional ecology are postulated to improve the mechanistic understanding of plant invasions (Catford *et al.* 2009; Enders *et al.* 2020).

Another topic of particular interest in invasion ecology is related to the question whether successful invasive species functionally differ from native species (Thompson *et al.* 1995; van Kleunen *et al.* 2011; Leffler *et al.* 2014; Mathakutha *et al.* 2019) and if so, whether this results in competitive advantage of invasive species over native species (Daehler 2003; Leishman *et al.* 2007; Tabassum & Leishman 2016; Ni *et al.* 2018). Research based on trait-based approaches revealed specific functional characteristics of successful invasive plants, for instance, higher relative growth rates, higher specific leaf area, greater maximum height, smaller seed mass, and greater phenotypic plasticity compared to native plants that may lead to higher competitive ability (van Kleunen *et al.* 2010; Ordonez 2014; Ruprecht *et al.* 2014; te Beest *et al.* 2015). However, in a multi-species experiment with 48 pairs of native and alien plants, Zhang & van Kleunen (2019) found that common alien (invasive) plants had a higher competitive ability than rare native plants but not than common native plants. Additionally, characteristics of native communities were found to be more important than intrinsic characteristics of invasive species in determining invader abundance in experimental grasslands (see Catford *et al.* 2019). Thus, it remains unclear, under which conditions particular functional traits lead to invasion success and if their role depends on interactions with native species.

A further fundamental determinant of invasion success is related to eco-evolutionary changes during the invasion process (Lankau *et al.* 2009; Eppinga & Molofsky 2013; Saul & Jeschke 2015). Since ecological and evolutionary processes can occur on similar timescales (Schoener 2011), ecological changes can lead to rapid evolution that in turn affects ecological processes (i.e., reciprocal interactions between ecological and evolutionary processes; Brunner *et al.* 2019). Specifically, after the introduction into a new area, alien plants are exposed to selection by novel abiotic and biotic conditions (Theoharides & Dukes 2007; Moran & Alexander 2014). This leads to responses in the invading alien species for instance via phenotypic plasticity or evolutionary adaptation (Strayer *et al.* 2006). The invading species itself might also act as a selection agent, leading to changes of the invaded community (Leger & Espeland 2010) or single native species (Carroll 2007). This, in turn, can affect the invader and may create co-evolution of alien and native species (Yoshida *et al.* 2007; Leger & Espeland 2010). Hence, these eco-evolutionary dynamics between native and alien species suggest that invasion success may depend on residence time (i.e., the time since introduction into a new area; *sensu* Rejmánek 2000). Specifically, as residence time increases, eco-evolutionary changes of the invader itself may constrain population growth and spread; or native species gain eco-evolutionary experience to the presence of an invader, leading to a decrease in its novelty and an increase in biotic resistance of native species (Hawkes 2007; Lankau *et al.* 2009; Saul & Jeschke 2015). Indeed, Huang *et al.* (2018) tested the competitive tolerance of a native species from populations of increased length in co-existence with an invasive species (ranging from complete absence of the invader to 60 years of co-existence). They showed that native species populations with longer co-existence times were able to tolerate the novel weapons (i.e., allelopathic effects) of an invader more than populations that never interacted with the invader. In contrast, Lyytinen & Lindström (2019) compared seedling performance of a native species from sites with approximately 40 years of experienced invasion to uninvaded sites and did not find that the tolerance of the native species to allelochemicals of an invader depends on co-occurrence history. However, so far, most studies neglected temporal dynamics (but see Corli & Sheppard 2019; Sheppard & Schurr 2019) and either focused on analyzing differences between alien and native species (Godoy *et al.* 2009; Ordonez & Olff 2013) or between the area of origin and the introduced area to determine invader performance (Callaway *et al.* 2008; Yang *et al.* 2013). Thus, the question remains, how to study eco-evolutionary processes involved in invasion success over sufficiently long timescales?

In my doctoral thesis, I combined approaches of functional and community ecology with an approach based on experimental macroecology to study long-term population dynamics of 47 annual Asteraceae species. I performed common garden experiments based on an alien-native species continuum including neophytes, archaeophytes, and natives to cover a wide range of residence times in Germany. In macroecological studies on patterns of plant invasions, residence time presents a strong predictor of abundance of alien plants at regional and continental scale in Australia (Hamilton *et al.* 2005), range sizes of alien plants introduced to Czech Republic, Azores, New Zealand, and Hawaii (Pyšek & Jarošík 2005) as well as range sizes of alien and native Asteraceae species in Germany

(Sheppard & Schurr 2019). For my thesis, I made use of the long and well-documented introduction history of annual Asteraceae in Germany. Specifically, I used multiple species each of which represents a specific point in time along a residence time axis, ranging from few decades (represented by recently introduced neophytes) to the time of the last glacial maximum (represented by re-immigrated native species), to study temporal dynamics. Particularly, the residence time of each species serves a measure of length of co-evolutionary history both with the abiotic and biotic environment in their introduced area. Based on this species-for-time approach, I conducted common garden experiments to investigate i) how effects of climatic distances between the area of origin and the introduced area as well as functional traits on population dynamics of alien plants are determined by residence time (Chapter 1), ii) how biotic resistance of native communities towards alien plants is related to residence time (i.e., length of co-existence time) and functional traits (Chapter 2), and iii) how competitive outcomes between single alien and native species are shaped by residence time and if they serve as a predictor of range sizes (Chapter 3). This doctoral thesis is part of a project that was founded by the German Research Foundation (SH 924/1-1) and includes three manuscripts (represented by each chapter) either published in or submitted to peer-reviewed ecological journals. My authorship and the contribution to each manuscript are indicated. Please note that I adapted the format and layout of each manuscript to reach a uniform type face.

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Chapter 1

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

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*This chapter refers to a manuscript published in *Global Ecology and Biogeography*:

Brendel, M.R., Schurr, F.M. & Sheppard, C.S. (2021). Inter- and intraspecific selection in alien plants: how population growth, functional traits and climate responses change with residence time. *Global Ecology and Biogeography 30(2)*, 429-442. (https://doi.org/10.1111/geb.13228)

Publisher: John Wiley & Sons Ltd (https://onlinelibrary.wiley.com/)

Format and layout were adapted as a matter of consistency.

Abstract

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). We set up a common-garden mesocosm-experiment using annual 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. 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. 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 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.

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 (Pironon *et al.* 2015; Braasch *et al.* 2019). 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 (Sakai *et al.* 2001; Gurevitch *et al.* 2011).

Adaptation of alien plants to their new environment was mostly tested in common garden experiments along environmental gradients within the new range (Maron *et al.* 2004, 2007; Colautti & Barrett 2013; 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 Sotka *et al.* 2018; Braasch *et al.* 2019). Instead, the role of climatic mismatches for rapid adaptation of alien plants was 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 of studying adaptation processes in alien species over longer timescales, 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 (Lambrinos 2004; Keller & Taylor 2008; Colautti *et al.* 2017) and between species (Vellend 2016). Within-species selection may either lead to extinction from the new range or cause adaptation to the new environment (Lambrinos 2004; Keller & Taylor 2008; Saul & Jeschke 2015; Colautti *et al.* 2017). 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, Fig. 1.1a). 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 (Fig. 1.1a). However, intra- and interspecific selection should cause this negative effect of climatic mismatches to weaken as residence time increases (Fig. 1.1a). Secondly, 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 (Fig. 1.1b) 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 residence time and interspecific trait means (Fig. 1.1d). 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 (Fig. 1.1c) 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 (Fig. 1.1e). Under both directional and stabilizing selection, interspecific trait variance should decrease with residence time (Fig. 1.1d 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 two 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 weaken with residence time in the new range (Fig. 1.1a), and (b) with increasing residence time, functional traits converge towards values that maximize population growth in the new range (Fig. 1.1b-e).

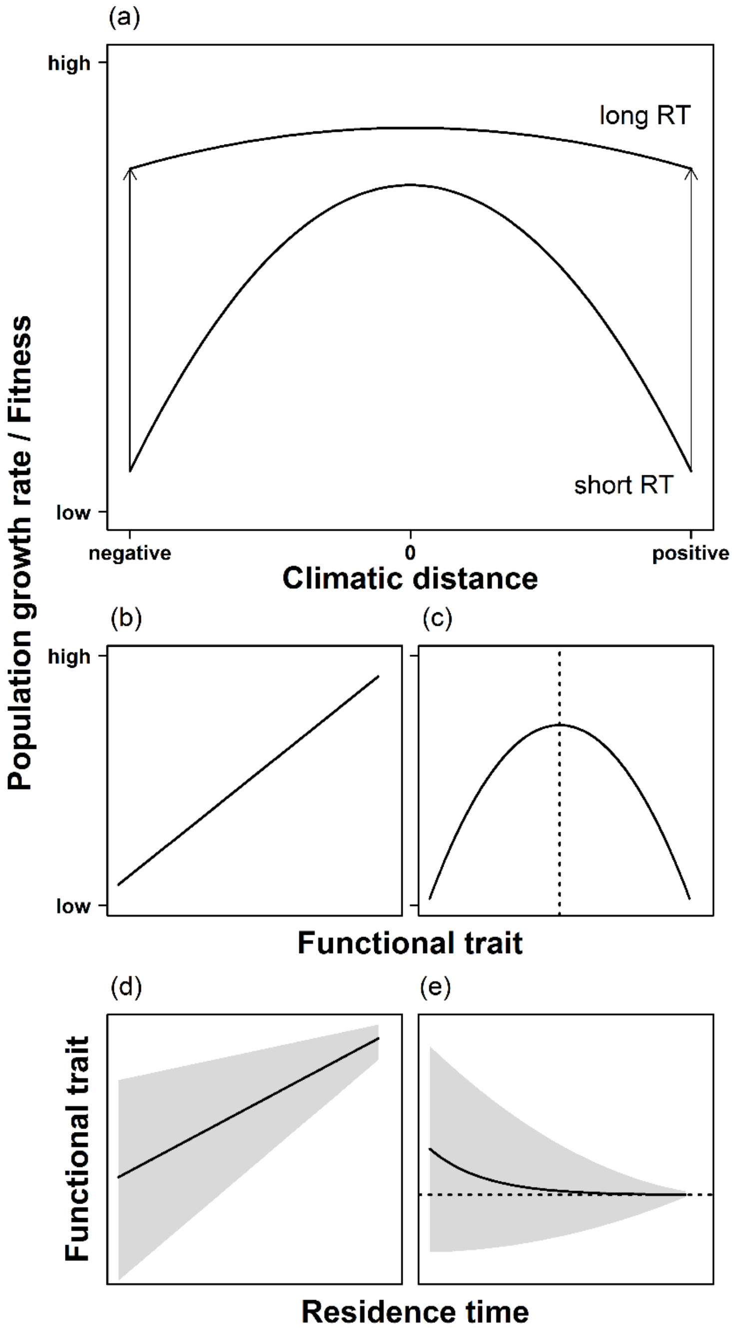

Figure 1.1: Inter- and intraspecific selection on alien plants in their new range should shape the relationships between population growth, climatic distance, functional traits, and residence time. (a) Unimodal effects of climatic distance between the new and native range (corresponding to negative effects of climatic mismatches, whereby e.g., positive distances indicate a warmer and negative distances a colder climate in the new range) on population growth rate weaken (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.

Materials and Methods

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 (Fig. 1.2) from recently introduced neophytes, over archaeophytes, to natives that immigrated after the last glacial maximum between approx. 10,000 – 12,000 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 *et al.* 2000b).

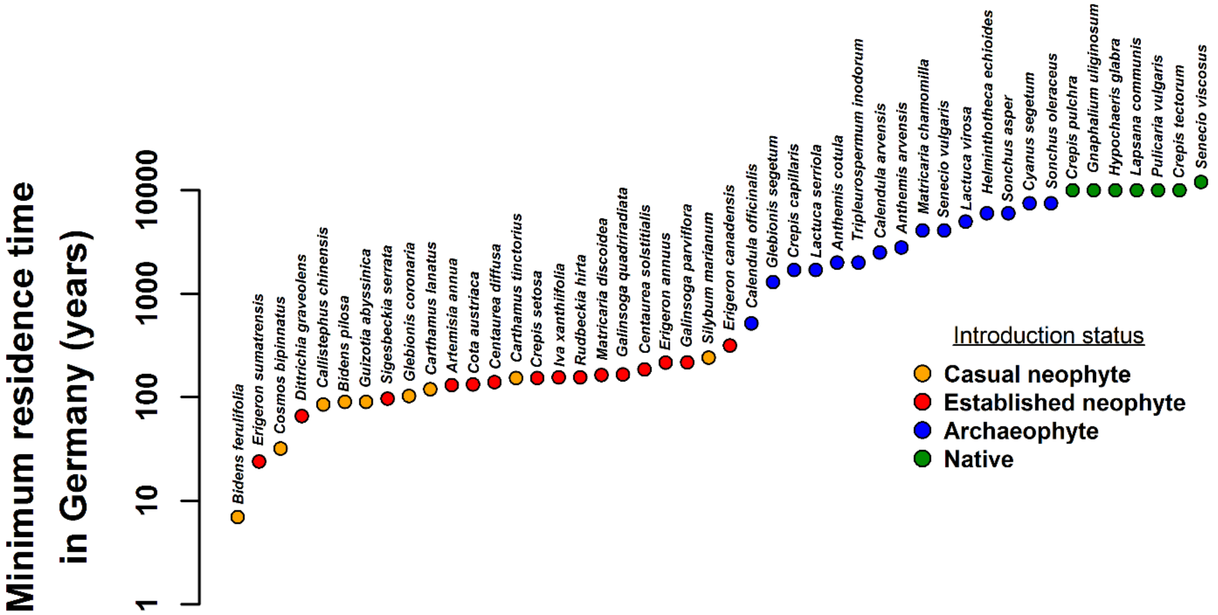

Figure 1.2: The alien-native continuum of 46 Asteraceae species varying in their minimum residence time and introduction status in Germany.

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 ca. 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 Chapter 1, Table S1).

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-litre pots (0.159 m^2 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 NO^{3-}, 0.015 mg/l NH^{4+}, 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 6 mesocosms (ranging between 2 and 8) per study species (for the number of replicates at population- and species-level see Supporting Information Chapter 1, 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 Chapter 1, Fig. S1) that prevented seed immigration and emigration, while allowing light and pollinators to enter.

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 one 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 1.1 for the resulting sample sizes). We thereby avoided assigning $\lambda_0 = 0$ to species which did not set seed in the first year due to the relatively short first growing season (Supporting Information Chapter 1, Fig. S2) or because they are facultative annuals.

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 (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 Chapter 1, Fig. 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 which 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. On the other hand, 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 Chapter 1, Table S1) and the FlorKart, 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 Chapter 1, Fig. S3a). For the native range of 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), which covers the Mediterranean basin and the Fertile Crescent (Supporting Information Chapter 1, Fig. 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; daily maximum and minimum temperatures) placed at 10 cm belowground 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 Chapter 1, Fig. 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.

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 (amongst 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 for the demographic performance and possibly for 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 Chapter 1, Appendix S1, for further details).

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

(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 & 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.

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 (Fig. 1.1a), we fitted a model that included MRT, the quadratic effect of ∆T, and their interaction as fixed effects. This model assumes that ∆T effects have an apex (maximum or minimum) at ∆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 ∆T = 0 K by including additionally a linear effect of ∆T and its interaction with MRT. This allows the apex to be at a non-zero value of ∆T. For each of these two models we fitted a simplified version by dropping the interaction between MRT and ∆T 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 ∆T 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 ∆T – an interaction between ∆T and amplitude. We included the ∆T-amplitude interaction to account for the fact that – for a given ∆T – 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.

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.

Results

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 minimum residence time (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 ($\Delta DIC < 2$; Table 1.1). While the model representing this hypothesis ranked second-best ($\Delta DIC = 0.17$; marginal $R^2 = 0.21$; Table 1.1), 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 (Fig. 1.3b).

Table 1.1: 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). 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 Chapter 1, Fig. S4; corresponding analyses for the other demographic performance measures are given in Supporting Information Chapter 1, Table S2 and Fig. S5-13.

					Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**
Climatic distance	**MRT**	**ΔT_{max}-MRT interaction**	**DIC**	**ΔDIC**	**marginal**	**conditional**	**Pagel's lambda**
no	yes	no	925.48	0.00	0.12 (< 0.01, 0.26)	0.68 (0.55, 0.81)	0.51 (0.24, 0.72)
yes (apex = 0)	yes	yes	925.65	0.17	0.21 (0.05, 0.39)	0.70 (0.57, 0.82)	0.50 (0.20, 0.74)
yes (apex = 0)	yes	no	926.04	0.56	0.16 (0.02, 0.32)	0.69 (0.56, 0.82)	0.49 (0.11, 0.73)
yes (apex = 0)	no	no	926.45	0.97	0.11 (< 0.01, 0.24)	0.68 (0.54, 0.81)	0.48 (0.0006, 0.69)
no	no	no	926.51	1.03	0.03 (< 0.01, 0.10)	0.67 (0.53, 0.80)	0.52 (0.12, 0.74)
yes (flexible apex)	yes	no	926.56	1.08	0.22 (0.05, 0.40)	0.68 (0.55, 0.81)	0.42 (0.001, 0.67)
yes (flexible apex)	yes	yes	926.73	1.25	0.26 (0.09, 0.46)	0.70 (0.56, 0.82)	0.44 (0.001, 0.67)
yes (flexible apex)	no	no	927.12	1.64	0.17 (0.03, 0.36)	0.67 (0.52, 0.81)	0.40 (0.0004, 0.68)

In general, models in which the apex (maximum or minimum) was fixed at a ΔT_{max} = 0 K performed somewhat better than their counterparts with flexible apex (Table 1.1). 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 Fig. 1.3b, with marginal R^2 = 0.16; alternative models in Supporting Information Chapter 1, Fig. S4 and S9). The overall best model for λ_0 however only included MRT and had a marginal R^2 of 0.12 (Table 1.1). 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; Fig. 1.3a).

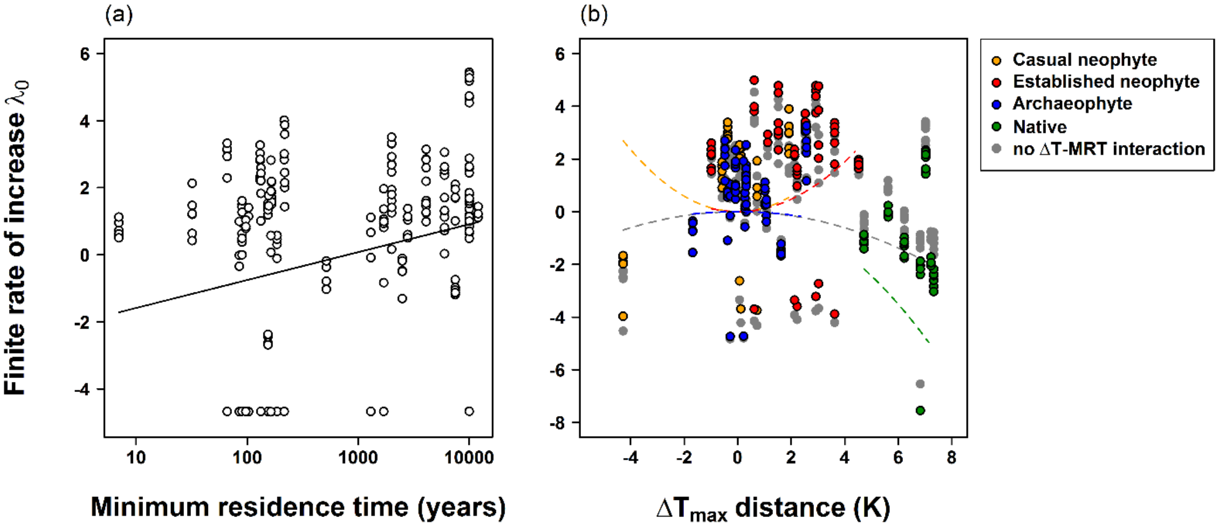

Figure 1.3: (a) Effects of minimum residence time (MRT) and (b) climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}) on finite rate of increase (λ_0). Note that the y-axis depicts partial residuals 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 ofΔT_{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).

Analyses of the other demographic performance measures yielded similar results as for λ_0 with all alternative models having DIC differences < 2 (Supporting Information Chapter 1, Table S2, Fig. S5-S8, Fig. 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 Chapter 1, Table S2, Fig. 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 = 0.18; Supporting Information Chapter 1, Fig. S13b).

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 1.2). In particular, λ_0 clearly decreased with seed mass (partial marginal $R^2 = 0.17$; Fig. 1.4a, Table 1.2) and showed a weak unimodal response to maximum plant height (partial marginal $R^2 = 0.03$; Fig. 1.4b, Table 1.2). 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 (Fig. 1.4). 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 Chapter 1, Table S3 and Fig. S14). Population growth rate in the second year (λ_1) did not show clear responses to any functional trait (Supporting Information Chapter 1, Table S3 and Fig. S14g-i).

Table 1.2: 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. 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 Chapter 1, Table S3 and Fig. S14.

		Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**
Functional trait	**Mean effect size (95% credible interval)**	**marginal**	**conditional**	**Pagel's lambda**
log(seed mass)	**-0.47 (-0.85, -0.10)**	0.17_{par}	-	-
log(seed mass)^2	0.06 (-0.07, 0.17)			
log(max. height)	**13.10 (2.24, 23.57)**	0.03_{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	-	0.25 (0.07, 0.42)	0.67 (0.54, 0.79)	0.45 (0.09, 0.70)

Relationships between functional traits and residence time

As expected under directional selection, the mean and the standard deviation (SD) of seed mass significantly decreased with MRT (Fig. 1.4c; MRT-effect on mean: $t_1 = -15.6$, $P < 0.001$; MRT-effect on SD: $t_1 = -3.0$, $P = 0.004$). Species with a high MRT thus have small values of seed mass that increase λ_0 (Fig. 1.4a). Results for maximum plant height are less conclusive: mean height also changed with MRT (t_1 =

-3.6, $P < 0.001$), but the MRT effect on height SD was only weakly negative ($t_1 = -0.3$, $P = 0.741$). The central 95% of the plant height distribution predicted for a maximum MRT of 12,000 years comprise the plant height value that maximizes λ_0 (Fig. 1.4d). Control analyses of the relationships between functional traits and MRT for only wild populations yielded similar results (see Supporting Information Chapter 1, Appendix S2 and Fig. S15).

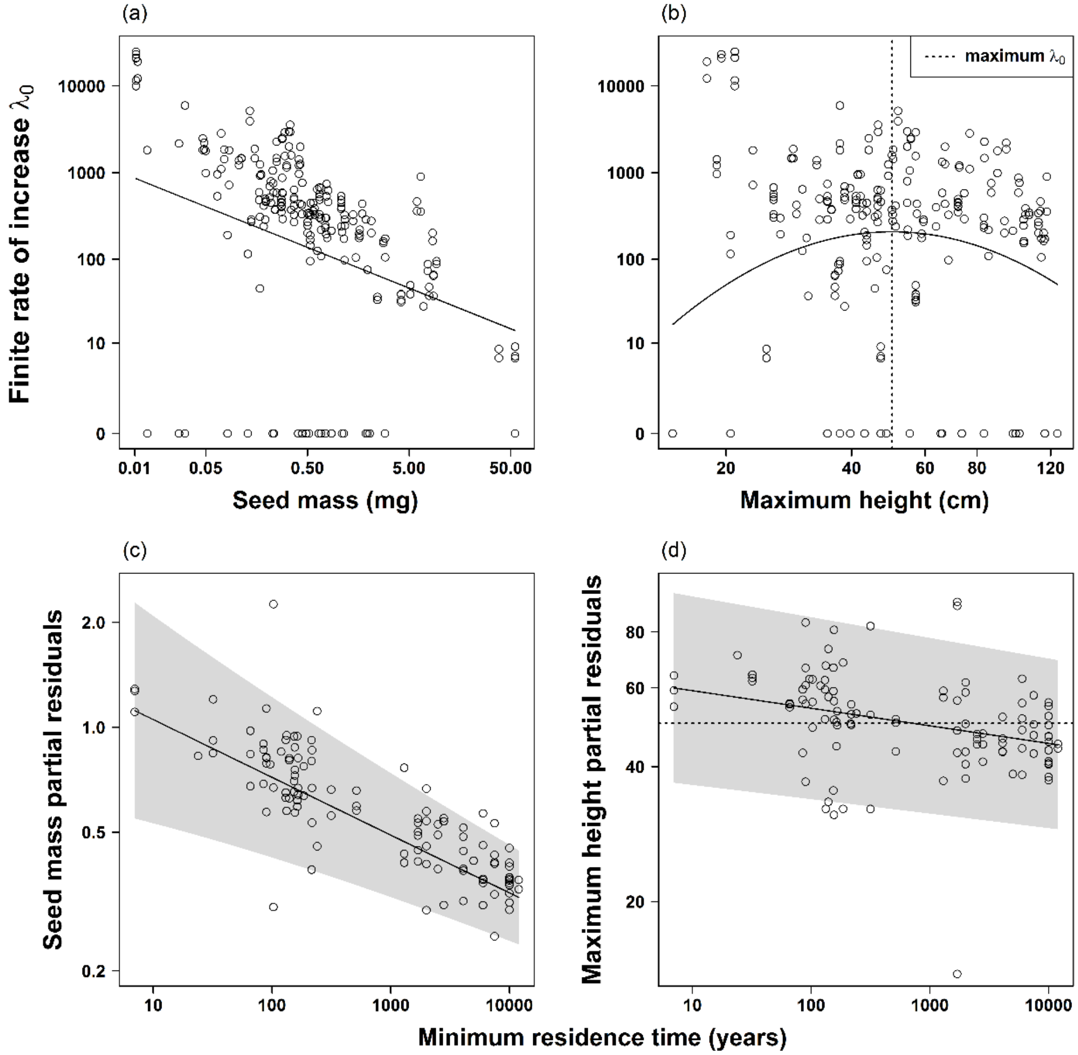

Figure 1.4: (a and b) Relationships between functional traits and finite rate of increase (λ_0). Predictions (solid lines) are based on the full model and show significant trait effects (with 95% credible intervals not overlapping zero) with the other explanatory variables set to their mean value (see Table 1.2). 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 (d) represents the value of plant height that maximizes λ_0. All axes are shown on log-scales.

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 minimum residence time (MRT; Fig. 1.3b). In support of our second hypothesis, seed mass – which has a strong negative effect on λ_0 (Fig. 1.4a) – converges towards low values as MRT increases (Fig. 1.4c). For plant height – which has a weak unimodal effect on λ_0 (Fig. 1.4b) – the effect of MRT was less clear (Fig. 1.4d). Directional inter- and intraspecific selection on seed mass may thus explain why λ_0 tended to increase with MRT (Fig. 1.3a).

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 (Ne) of *Centaurea solistitialis* (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 timespan 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 which 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, 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 *et al.* 2000a). 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).

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 (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 dispersing 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). On the other hand, 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 which 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).

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 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 & 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 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- vs. 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.

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 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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Chapter 2

Alien plant fitness is limited by functional trade-offs rather than a long-term increase in competitive effects of native communities *

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*This chapter refers to a manuscript submitted to *Ecology and Evolution*.

Format and layout were adapted as a matter of consistency.

During the examination process, a different version of the manuscript was published in *Ecology and Evolution*:

Brendel, M.R., Schurr, F.M. & Sheppard, C.S. (2023). Alien plant fitness is limited by functional trade-offs rather than a long-term increase in competitive effects of native communities. *Ecology and Evolution 13(9)*, e10468 (1-16). (https://doi.org/10.1002/ece3.10468)

Publisher: John Wiley & Sons Ltd (https://onlinelibrary.wiley.com/)

Abstract

Alien plants experience novel abiotic conditions and interactions with native communities in the introduced area. Intra- and interspecific selection on functional traits in the new environment may lead to increased population growth with time since introduction (residence time). However, selection regimes might differ depending on the invaded habitat. Additionally, in high-competition habitats, a build-up of biotic resistance of native species due to accumulation of eco-evolutionary experience to aliens over time may limit invasion success. We tested if the effect of functional traits and the population dynamics of aliens depends on interspecific competition with native communities. We conducted a multi-species experiment with 40 annual Asteraceae that differ in residence time in Germany. We followed their population growth in monocultures and in interspecific competition with an experienced native community (varying co-existence times between focals and community). To test the robustness of our findings, we used a naïve community that never co-existed with the focals. We found that high seed mass decreased population growth in monocultures but tended to increase population growth under intense interspecific competition. We found no evidence for a build-up of competition-mediated biotic resistance by the experienced community over time. Instead, population growth of the focal species was similarly inhibited by the experienced and naïve community. By comparing the effect of experienced and naïve communities on population dynamics over two years across a large set of species with a high variation in functional traits and residence time, this study advances the understanding of the long-term dynamics of plant invasions. In our study system, population growth of alien species was not limited by an increase of competitive effects by native communities (one aspect of biotic resistance) over time. Instead, invasion success of alien plants may be limited because initial spread in low-competition habitats requires different traits than establishment in high-competition habitats.

Introduction

The success of alien species is commonly studied in terms of their invasiveness and community invasibility (Alpert *et al.* 2000; Milbau *et al.* 2003). However, the success of aliens may depend on the environmental conditions in the new range. Moreover, community invasibility may depend on the time native species had to gain eco-evolutionary experience of the invader. Thus, the combined effects of the new biotic and abiotic environment directly affect fitness and consequently impose selection on alien species. This selection can operate both between species (causing extinction of poorly adapted species and persistence of better adapted ones; Vellend 2016) or it can operate within species (causing better adapted genotypes to increase in frequency). For instance, due to poor adaptation to the abiotic environment, alien fitness may initially be constrained in the new area (Colautti *et al.* 2010; Brendel *et al.* 2021). Alien fitness may then potentially increase with residence time due to the joint effect of intra- and interspecific selection exerted by the new abiotic environment (Brendel *et al.* 2021). However, how a gain in eco-evolutionary experience of native species affects alien fitness, has only rarely been tested.

Higher fitness may result from functional trait values that better reflect adaptations to the new environment. Functional traits are defined as morphological, physiological or phenological characteristics of an organism which impact fitness indirectly via their effects on demography (Violle *et al.* 2007). Functional traits that increase invasiveness are for instance low seed mass (that is related to a high reproductive output and dispersal rate), high specific leaf area (SLA, related to fast growth) and increased height (van Kleunen *et al.* 2010; Conti *et al.* 2018; Catford *et al.* 2019). The latter might evolve as a result of enemy release and a higher investment in competition than defence (evolution of increased competitive ability; Blossey & Nötzold 1995). However, the role of functional traits that favour invasiveness might change depending on the habitat type being invaded (Alpert *et al.* 2000; Müller-Schärer & Steinger 2004; Dietz & Edwards 2006). Indeed, in various habitats alien plants may experience differential selection regimes on functional traits related to population growth, dispersal, and competitive ability that in turn determine invasion success in the new area (Dietz & Edwards 2006; Theoharides & Dukes 2007; Richardson & Pyšek 2012). In particular, ruderal habitats with low interspecific competition select for species and genotypes with low individual seed mass and high reproductive capacity (Grime 2001) that increase their abundance more rapidly than others (Dietz & Edwards 2006). Seed mass shows an inverse relationship with per capita fecundity (Moles *et al.* 2004) and leads to increased fecundity of small-seeded species (Henery & Westoby 2001). In low-density monocultures, alien annual plants with low seed mass showed the highest intrinsic population growth rate (Brendel *et al.* 2021). Accordingly, as expected from intra- and interspecific selection, with increasing residence time seed mass converged towards low values (Brendel *et al.* 2021). On the other hand, in semi-natural habitats (i.e., remnants of habitats created by extensive, traditional farming, or restored natural vegetation for instance on land abandoned from agriculture; Pigott & Walters 1954) with high interspecific competition, selection might favour traits related to enhanced competitive ability (Dietz & Edwards 2006), such as increased height (Westoby 1998) and high seed mass (Moles & Westoby 2004). Under strong interspecific competition, a high investment in reproduction is disadvantageous (Lachmuth *et al.* 2011). Thus, it seems reasonable to expect that a trait-mediated trade-off between rapid population growth in low-competition habitats and high competitive ability in competitive habitats limits alien plant invasions. Indeed, such trade-offs strongly contribute to species co-existence in native communities (Maron *et al.* 2021). However, direct links between functional traits of alien plants and intrinsic population growth rates (i.e., population fitness, as opposed to individual demographic rates or performance proxies) in different environments are so far lacking, although being vital for robust predictions of population dynamics (Laughlin *et al.* 2020).

Invasion success may also depend more strongly on characteristics of native communities than on the traits and competitive ability of the invader (Perry *et al.* 2009; Catford *et al.* 2019). In particular, competition, parasitism, and predation/herbivory can all mediate “biotic resistance” of the native community to the invader (Levine *et al.* 2004; Alpert 2006). Biotic resistance can either completely repel invaders, or, as found to be more likely, reduce invasion success (Levine *et al.* 2004). As for competition-mediated biotic resistance, native plant species are expected to gain eco-evolutionary experience to the presence of the invader and might thus increase their competitive effects on the invader over time (Strauss *et al.* 2006; Saul *et al.* 2013). Whether a build-up in such competition-mediated biotic resistance decreases the fitness of alien species over time has rarely been tested (but see Sheppard & Schurr 2019 and Germain *et al.* 2020), although it is key to gain a more mechanistic understanding of the drivers of such a natural barrier to invasions (Gallien & Carboni 2017).

In a recent study on biotic resistance of a native community to alien plants with varying residence times, Sheppard & Schurr (2019) found that the native community supressed species of longer residence time relatively more. However, it is possible that this finding results from potentially confounding effects of species characteristics that may co-vary with time since introduction and determine invasion success in interspecific competition. Specifically, alien species with longer residence times (i.e., archaeophytes, defined as plant species that were introduced into Europe prior to A.D. 1500) and natives may per se be less competitive than species that have been introduced only recently (i.e., neophytes; Sheppard & Schurr 2019). For instance, archaeophytes are adapted to a release from competition with agricultural crops late in the growing season (Knapp & Kühn 2012), whereas neophytes are commonly thought to be highly competitive. To conclusively disentangle such an inherent competitive ability from an evolutionary build-up of biotic resistance, the following steps are required: a) population growth of alien plants needs to be investigated and linked to invader functional traits (Laughlin *et al.* 2020) in different competitive regimes (i.e., habitats of low vs. high competition; Dietz & Edwards 2006) and b) biotic resistance needs to be studied in an experienced native community whereby the length of potential co-existence time between aliens and natives varies (Sheppard & Schurr 2019) as well as c) in a naïve community that never co-existed with the introduced species (Germain *et al.* 2020). To our knowledge, these three aspects have not yet been integrated into one experiment covering a large number of species and a wide range of functional traits and residence times.

In this study, we conducted a multi-species common garden experiment with 40 Asteraceae species of varying functional traits and residence times in Germany (from recently introduced neophytes over archaeophytes to natives). We tested if the fitness of the focal species is limited by functional trade-offs between fitness under low vs. high competition intensity or by an evolutionary build-up of competition-mediated biotic resistance, whereby both processes are not necessarily mutually exclusive and may act simultaneously. To study these potential limits to invasion success, we measured population growth of the focal species over two years in a monoculture, in an experienced community (with varying potential co-existence times between focal species and the community), and a naïve community (with a co-existence time of zero). According to Dietz & Edwards (2006), functional traits should cause a trade-off between alien fitness under low vs. high competition, irrespective of co-existence time (Fig. 2.1a-c). Under low competition (monocultures), only intra- and interspecific selection imposed by the new abiotic environment plays a role, whereby species of longer residence times have either changed their trait values accordingly or only those species persisted that have beneficial trait values (Brendel *et al.* 2021; Fig. 2.1d). As a result, population growth of the focal species is expected to increase and eventually saturate (Fig. 2.1d). In contrast, under high competition, native communities may eventually pose limits to population growth of invaders if they accumulate eco-evolutionary experience. Specifically, one possible scenario is that fitness shows a unimodal response to residence time in the experienced community (Fig. 2.1d). This is expected if native biota only experience selection for increased biotic resistance once alien species become abundant by adapting to their new abiotic environment. Such local adaptation to new abiotic conditions has been shown to occur over short timescales (Colautti & Barrett 2013). In contrast, a build-up of biotic resistance as a result of changing competitive interactions between the experienced community and the alien focal species encompass highly complex reciprocal responses of co-evolving species (Thompson *et al.* 2002). If competition-mediated biotic resistance is relevant, this unimodal effect of residence time (or any alternative patterns that suggest a limit to fitness with increasing residence time) should be detected only in competition with the experienced community, whereas the fitness-residence time relationship for the naïve community should be parallel to that of the monoculture, given that the competitive effect of the community in this case should be independent of residence and co-existence time (Fig. 2.1d).

In this study, we will thus test the following hypotheses: i) Effects of functional traits on population growth of alien plants depend on competition intensity so that traits beneficial in low-competition monocultures are disadvantageous or unimportant under intense interspecific competition. ii) Under low competition, population growth of the focal species increases with residence time, whereas in the experienced community, the fitness-residence time relationship is unimodal due to a build-up of competitive effects of the native community (as one aspect of biotic resistance) over time. In contrast, in the naïve community (co-existence time of zero), the strength of competitive effects does not vary with residence time.

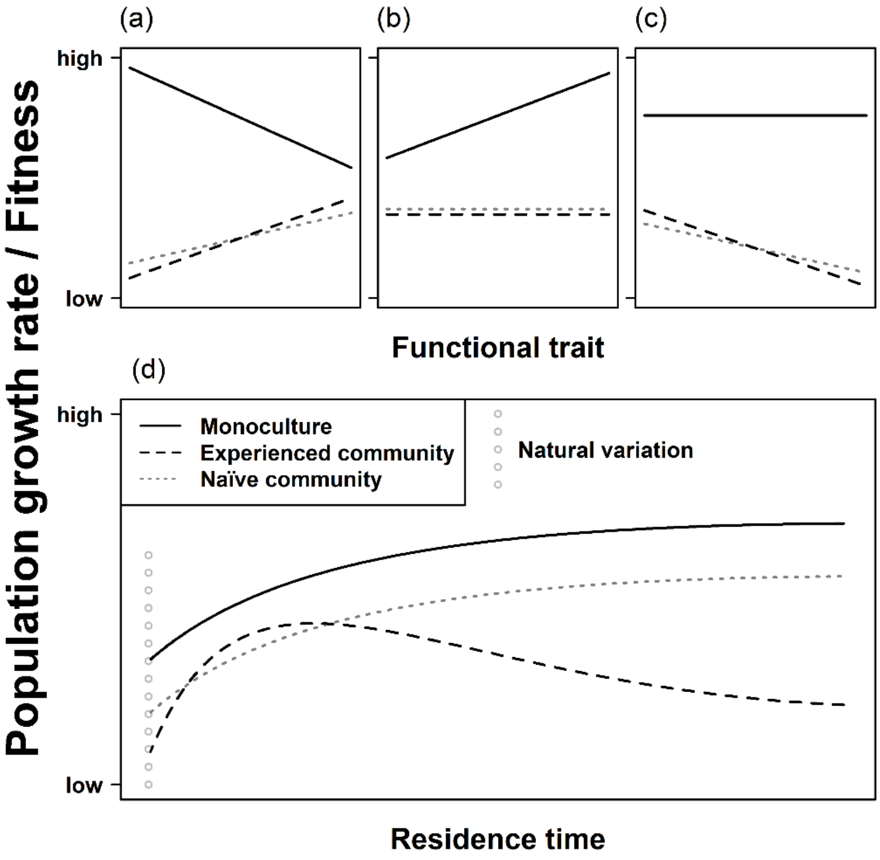

Figure 2.1: The fitness of alien plants in their new area should be determined by functional traits that are related to invasiveness and effects of competition by native communities that may depend on their eco-evolutionary experience and thus interact with residence time of the invader. Since the role of traits for fitness is likely to change depending on the habitat that is being invaded and may thus be determined by competition (e.g., low-density monoculture vs. high-density interspecific competition), relationships between functional traits and population growth can be (a) opposing for monoculture and the community, (b) present in monoculture but absent in the community and (c) absent in monoculture but present in the community. In this context, trait-fitness relationships in interspecific competition should be independent of the eco-evolutionary experience of the community and thus be similar for the experienced and naïve community. As a result of intra- and interspecific selection to the new abiotic environment, population growth asymptotically increases with residence time in monoculture (d). In contrast, in a community that shares varying length of co-existence times with the alien species (experienced community), population growth may show a unimodal response to residence time: the native community might gain eco-evolutionary experience with the alien species and increases its competitive effects over time (i.e., builds-up competition-mediated biotic resistance), thereby eventually counteracting positive effects of adaptation to the new abiotic environment. In a naïve community that does not share any co-evolutionary history with the alien species, the general negative competitive effect of the community is not expected to vary with residence time and the performance pattern of the alien species should follow that in monoculture. Note that the initial population size (i.e., the starting point of population growth in the new area before intra- and interspecific selection to the new abiotic environment leads to a potential fitness increase and competitive effects of the resident communities to a potential fitness decrease) can naturally vary (indicated by grey circles).

Materials and Methods

Alien-native species continuum

This experimental study is based on a species-for-time approach, for which we chose 40 annual Asteraceae species, including recently introduced neophytes, archaeophytes, and natives that arrived in Germany after the last glacial maximum (10,000 – 12,000 years before present; see Sheppard & Schurr 2019; Brendel *et al.* 2021; Sheppard & Brendel 2021). Neophytes represent those alien species that were introduced after the discovery of America in 1492 A.D. (usually rounded to 1500 A.D.) and archaeophytes were introduced before that date (Pyšek *et al.* 2004). The neophytes can be further divided into casual and established neophytes. In contrast to established neophytes, casual neophytes do not have self-sustaining populations and rely on repeated introductions for persistence (Richardson *et al.* 2000). We obtained the categorisation into these groups from the online database FloraWeb (Bundesamt für Naturschutz (BfN), www.floraweb.de; latest access to online database in 2016). We here do not further distinguish established and invasive neophytes, because FloraWeb does not make such a distinction as this categorisation is often subjective and there is no official black list of invasive species in Germany. The long and well-documented immigration and introduction history of the Asteraceae family in Central Europe and its high proportion among established alien species in Germany (Hanspach *et al.* 2008), allowed us to cover a wide gradient of minimum residence times (MRT) in Germany (from 32 to 12,000 years; see Supporting Information Chapter 2, Fig. S1).

The 40 focal species are functionally similar and include all annual species occurring in ruderal and segetal habitats, which are common enough to obtain a sufficient amount of seed material (and do not originate from North America, see below). For each species, the time span between the first record in the wild and the start of the experiment in 2016 defines its MRT (*sensu* Rejmánek 2000). We used the first records of each species compiled by Sheppard & Schurr (2019) from the floristic and archaeobotanical literature as well as online databases. Seeds were collected from wild populations (seeds from approx. 10 mother-plants were sampled in 2015 and mixed before sowing) in the state of Baden-Württemberg (the location of the common garden). Aiming to include three populations per species, we complemented the wild seed collections by seeds from botanical gardens across Germany. In total, 101 populations were included in this study (see Supporting Information Chapter 2, Table S1).

Experimental communities

To test if the effect of competition by experimental communities on fitness/population growth of the focal species varies with functional traits and potential co-existence time, the 40 focal species were grown in isolation as low-density monocultures and in two plant communities. The two communities served to test if trait effects are consistent across different communities, and if the length of potential co-existence time plays a role, by using an experienced and a naïve community. For the experienced community, we chose 12 perennial species (four grasses and eight forbs; Supporting Information Chapter 2, Table S2) that belong to the grassland community association of *Festuco-Brometea* and occur in mesic to dry calcareous grasslands in Central Europe (Ellenberg 2009). Furthermore, they can also be found in ruderal and segetal habitats (Ellenberg 2009) as well as on fallow land (for a case study in Germany see Klimaschewski *et al.* 2006), where the Asteraceae species occur, and are widespread across Germany (see Supporting Information Chapter 2, Table S2, for species-specific range sizes). Thus, the MRT of the 40 focal species in Germany (Supporting Information Chapter 2, Fig. S1) serves as a measure for the length of potential co-existence time between the Asteraceae and the experienced community species. To disentangle if competitive effects on fitness of the focal species are related to a build-up of biotic resistance by the experienced community with MRT or to competitive abilities of the focal species that might co-vary with MRT, we used a naïve community as control. This naïve community consists of species native to prairie grasslands of the Northeastern United States of America (Gleason & Cronquist 1991). Particularly, they belong to the plant communities of dry to mesic prairies in the natural vegetation division "Grand Prairie Division" of the state Illinois (Mohlenbrock 2002). The species have not been introduced to Germany (checked via Global Invasive Species Database: www.iucngisd.org; latest access to online database in 2016). The naïve community matches the experienced community at genus-level (nine out of twelve) and family-level (the remaining three) to keep both communities as functionally similar as possible (for detailed information on species composition of the experienced community and its congeneric/confamilial counterparts of the naïve community see Supporting Information Chapter 2, Table S2). However, the naïve community never interacted with the focal species. To keep the phylogenetic relatedness between each community and the focal species constant, the two communities did not include any additional Asteraceae species.

Experimental design

In March 2016, we set up a mesocosm-experiment at the experimental station of 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). In this experiment, populations of each of the 40 Asteraceae focal species were exposed to three competition treatments. To investigate population growth in isolation, we established monocultures of each focal species (232 mesocosms with sown seeds to follow population growth over two years plus 78 mesocosms with transplanted seedlings for functional trait measurements). To investigate effects of interspecific competition on population growth, we established mesocosms of each community type (236/234 mesocosms with seeds of the focal species sown into the experienced/naïve community). Combinations of species and competition treatment were usually replicated in 6 mesocosms, with the number of replicates ranging from 4 to 8 (the number of replicates at population- and species-level for monocultures and each community type are listed in Supporting Information Chapter 2, Table S1). Mesocosms were randomly assigned to five spatial blocks and each block contained the same number of mesocosms. The distance between mesocosms within each block was 0.5 m and the distance between blocks was 1 m. Mesocosms were placed in a parcel of 180 m^2 (60 m times 30 m) on a former meadow within a mosaic of crop fields. Before the mesocosms were arranged, the ground was covered with a weed mat to suppress growth of the surrounding vegetation. Each mesocosm consisted of a 50-litre pot (0.159 m2 soil surface area, 50 cm upper diameter, 38 cm lower diameter, and 40 cm height) filled with local soil (texture: 70% sand, 14% clay, and 16% silt; nutrient content: 1.81 mg/l NO3-, 0.015 mg/l NH4+, 21.36 mg/l P; pH-value: 7.88) on top of a layer of expanding clay to improve drainage. During the growing season, the mesocosms were watered daily with an automatic drip-irrigation system. We weeded the mesocosms before sowing and regularly throughout the experiment (once per week before and every second week after they were surrounded by an open-top organza fabric; see below).

By the end of April, we sowed a seed-mixture of the 12 perennial species of each community type into the respective mesocosms (at an overall density of 3 g/m^2). The seeds were covered with a thin layer of sand. To ensure that the total seed mass of each experienced community species was comparable to its naïve counterpart, we determined the number of sown seeds per species based on the species' per-seed mass (for seed mixtures see Supporting Information Chapter 2, Table S2, and for further compositional characteristics of each community type see Supporting Information Chapter 2, Appendix S1 and Fig. S2). In late June, when the communities were fairly well established, we added

20 seeds from a given Asteraceae population to each mesocosm (i.e., only one population of one Asteraceae species was introduced to a mesocosm). Hence, the initial population size S_0 equals 20 seeds. Before the first seeds of the study species ripened in 2016, we surrounded each mesocosm by an open-top organza fabric (see Supporting Information Chapter 2, Fig. S3, also for the aforementioned spatial arrangement of mesocosms) to prevent seed immigration and emigration, without excluding light and pollinators.

Measures of demography and population dynamics

Population growth was quantified as the change in seed number per mesocosm over time. As annuals, our focal species do not reproduce vegetatively (Hirose *et al.* 2005; plus personal observation). Thus, to follow the dynamics of each experimental Asteraceae population over two years, we estimated the seed number per mesocosm at the end of each year (S_1 and S_2, respectively) as the product of total capitula number in late October and average seed number per capitulum (from Brendel *et al.* 2021). Annual growth rates of the seed populations were quantified as $\lambda_t = S_{t+1}/S_t$, according to Venable & Brown (1988). Given that the density of the initial population was low ($S_0 = 20$ seeds per mesocosm), we used the population growth rate in the first year, $\lambda_0 = S_1/S_0$, as an estimation of the finite (density-independent) rate of increase. Together with dispersal distance, λ_0 determines the spread rate (Skellam 1951) and is thus a key driver of invasion success. Since the focal species are annual, λ_0 includes two demographic components, the transition from seed to plant (establishment) and the transition from plant to seed (fecundity) (Brendel *et al.* 2021). Consequently, the number of established focal individuals per mesocosm at the end of the first growing season (N_1) was used to break down λ_0 into establishment ($E_0 = N_1/S_0$) and fecundity ($F_0 = S_1/N_1$). For each mesocosm, we thus calculated λ_0, λ_1, E_0, and F_0 as measures of population dynamics and demographic performance. We did not calculate λ_0 for the few cases when a focal species did not produce any mature seeds in the first growing season in any mesocosm across all populations (and thus did not complete their life cycle in any mesocosm; this reduced the sample size from initially 40 species and 101 populations to 36 species and 94 populations, see Table 2.1). In this way, we avoided that $\lambda_0 = 0$ was assigned to species whose seed-set was restricted by the relatively short growing season in the first year (lasting from end of June to end of October due to logistical challenges beyond our control that delayed the experimental set-up; Supporting Information Chapter 2, Fig. S4) or because they are facultative annuals (Brendel *et al.* 2021). If only some mesocosms of a given focal species did not produce a seed-set, however, $\lambda_0 = 0$ was retained as in this case a population growth rate and fecundity of zero is likely a response to the competitive effects of the interacting community. For the analyses of E_0, we used all 40 species and 101 populations. Note that while we present data on λ_1 in the Supporting Information, we are careful not to over-interpret these findings. Given the limited size of the mesocosms, λ_1 strongly depended on population size after the first year (and thus on λ_0), obscuring effects of traits and biotic resistance.

Functional trait measurements

We measured seed mass, maximum height, and specific leaf area (SLA) as three major axes of ecological strategies in plants (Westoby 1998). For an extended set of 46 Asteraceae species (including the 40 focal species plus 6 North American neophytes), low seed mass and intermediate height maximized population growth and fecundity in monoculture mesocosms (Brendel *et al.* 2021). A high seed mass increases seedling establishment in temperate grasslands (Moles & Westoby 2004), but usually trades off with reproductive output (Moles *et al.* 2004; see Supporting Information Chapter 2, Fig. S5, for the trade-off between seed mass and seed number in our focal species). An investment in height leads to a greater light interception (Falster & Westoby 2003), and low SLA is related to a more efficient resource acquisition (Westoby 1998). Thus, we expect these three functional traits to also be relevant for population growth in interspecific competition, albeit with different optimal trait values (see Fig. 2.1a-c).

For all trait measurements (see also Brendel *et al.* 2021), we followed the standard protocols of Pérez-Harguindeguy *et al.* (2013). Before starting the experiment, we determined average seed mass at population-level (based on six times 20 seeds using a high precision balance, accuracy of 10^{-4} g). For population-level measurements of maximum height and SLA, additional monoculture mesocosms with transplanted seedlings were established (Brendel *et al.* 2021). In late June 2016, we transplanted six seedlings (previously grown in the same soil as used for the mesocosms in germination trays for six weeks in greenhouses next to the common garden facility) of each study species into two empty mesocosms. Whenever feasible, we evenly assigned the populations to the six individual plants (i.e., three populations leading to two individuals each per mesocosm). At the end of October 2016, we measured the height of 463 transplanted individuals (that survived from initially 466 individuals). During August 2016, we collected two leaves from each individual with at least four fully developed leaves (445 individuals). All leaves were scanned and their area was measured using ImageJ2 (Rueden *et al.* 2017). Afterwards, the leaves were dried (at 70°C for 72 hours) and weighed to calculate SLA

(mm^2/mg) at population-level. Due to low germination rates, we could only measure five individuals for *Cyanus segetum* per mesocosm and did not have any transplanted individuals to measure for *Crepis tectorum*. For the latter species, we thus used the individuals developed from seeds. We sampled two leaves in three random mesocosms and measured the tallest individual in each mesocosm. For four populations (of four species) used to assess demographic performance, no matching transplants were available. We thus used the corresponding species-level average of SLA and maximum height. The trait data are available from the TRY plant database (Kattge *et al.* 2020).

Statistical analyses

Data analyses were performed in R 3.5.1 (R Core Team 2018). We used phylogenetic generalized linear mixed models (GLMMs) to analyse the two measures of population growth (λ_0 and λ_1) as well as individual demographic rates in the first year (E_0 and F_0). To directly quantify competition-mediated biotic resistance, one has to compare a treatment with inter- and intraspecific competition to a control of only intraspecific competition's own species (i.e., monocultures). Hence, we quantified competition-mediated biotic resistance via two separate analyses that contrasted the experienced and naïve communities, respectively, to the control. As our analyses compare many different species (albeit of the same family, life form, and habitat), some of which are more closely related than others, we accounted for the phylogenetic relatedness among the focal species in our models. We used Pagel's lambda correlation structure (Pagel 1999) in Bayesian GLMMs fitted with Markov chain Monte Carlo methods (MCMCglmm package; Hadfield 2010). We extracted information on phylogenetic relatedness from the Daphne Phylogeny (Durka & Michalski 2012) by means of the R-packages picante (Kembel *et al.* 2010) and phytools (Revell 2012). All GLMMs furthermore included experimental block and population nested in species as random effects.

To test our first hypothesis that the relationship between functional traits and performance of the focal species depends on the type of competition (Fig. 2.1a-c), we entered competition treatment (monoculture vs. experienced community), the linear and quadratic term of seed mass, maximum height, and SLA as well as the interaction between competition treatment and each functional trait as fixed-effects into the GLMMs. We ran these GLMMs for each measure of population growth and demographic rate. To further investigate if the relationship between functional traits and performance of the focal species follow the same pattern irrespective of the community type, we repeated the analyses using data from monocultures and naïve communities. In all GLMMs, functional traits were log-transformed, scaled, and centred. To ensure our results are robust, we performed control analyses for finite rate of increase (λ_0) only including wild populations since the seeds obtained from botanical gardens were not grown under entirely natural conditions.

To test our second hypothesis that the effect of competition with the community on performance of the focal species varies with MRT (Fig. 2.1d), the GLMMs included competition treatment (monoculture vs. experienced community), the linear and quadratic term of MRT, and the interaction between competition treatment and each MRT-term as fixed-effects. We ran these GLMMs for each measure of population growth and demographic rate. To distinguish between potential effects based on length of co-existence time vs. competitive abilities co-varying with MRT, we furthermore conducted control analyses comparing the monoculture to the naïve community. In all GLMMs, MRT was log-transformed, scaled, and centred. We also performed control analyses for λ_0 only including wild populations.

To analyse λ_0, λ_1, and F_0, we used Gaussian GLMMs with non-informative priors for the variance components of each random effect (corresponding to an inverse-Gamma distribution with shape and scale parameters equal to 0.01). To meet the model assumptions on residuals, we $\log(x + 1)$-transformed λ_0, λ_1, and F_0. For the analyses of E_0, we performed binomial GLMMs to contrast establishment success (N_1) and failure (S_0 - N_1). For the variance of each random effect, we used an inverse-Wishart prior (with shape and scale parameters equal to 0.001). All GLMMs ran for 1,000,000 iterations with a burn-in phase of 250,000 and a thinning interval of 500 (MCMC consistently converged). For fixed effects, we followed the default settings (Hadfield 2010) and used a normal prior with a mean of zero and a very large variance (10^{10}). We considered a model term to be significant, if its 95% credible interval (CI) did not overlap zero.

Results

Interspecific competition modifies the effect of functional traits on fitness

The relationship between seed mass and the finite rate of increase (λ_0) differed strongly between monocultures and experienced communities: λ_0 strongly decreased with seed mass in monoculture and slightly increased with seed mass in the experienced community (Fig. 2.2a and b). In monoculture,

λ_0 was predicted to be maximal for the lowest seed mass measured whereas in the experienced community, λ_0 was optimal for the highest seed mass measured (Fig. 2.2b). Very similar results were obtained when comparing monocultures and naïve communities (Fig. 2.2a and b). The contrasting effects of seed mass on λ_0 in the presence and absence of interspecific competition match our hypothesis of divergent selection on functional traits in low- vs. high-competition environments.

The relationship between maximum height and λ_0 also strongly differed between monocultures and interspecific competition (Fig. 2.2a). While maximum height had a clear unimodal effect on λ_0 in monocultures, this effect disappeared in competition with both naïve and experienced communities (Fig. 2.2c). In contrast, we did not detect clear effects of specific leaf area on λ_0 (Fig. 2.2a and d). The functional trait models explained a high proportion of variance in (log-transformed) λ_0 (Table 2.1).

Table 2.1: Properties of the models relating finite rate of increase (λ_0) to three functional traits (linear and quadratic effect of log-transformed seed mass, maximum height and specific leaf area), competition treatment, and their interaction (top row); and to minimum residence time (MRT), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction (bottom row). Corresponding analyses for other demographic performance measures are given in Supporting Information Chapter 2, Table S3 (functional traits) and Table S4 (MRT).

		Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**	
Model	**Competition treatment**	**marginal**	**conditional**	**Pagel's lambda**	**Sample size (species, populations, mesocosms)**
Functional traits	monoculture vs. experienced community	0.68 (0.61, 0.74)	0.81 (0.78, 0.84)	0.25 (0.002, 0.46)	36, 94, 436
	monoculture vs. naïve community	0.66 (0.59, 0.72)	0.82 (0.78, 0.85)	0.26 (0.002, 0.48)	36, 94, 434
Minimum residence time	monoculture vs. experienced community	0.62 (0.54, 0.69)	0.76 (0.73, 0.81)	0.23 (0.001, 0.49)	36, 94, 436
	monoculture vs. naïve community	0.60 (0.52, 0.67)	0.77 (0.72, 0.82)	0.22 (0.001, 0.51)	36, 94, 434

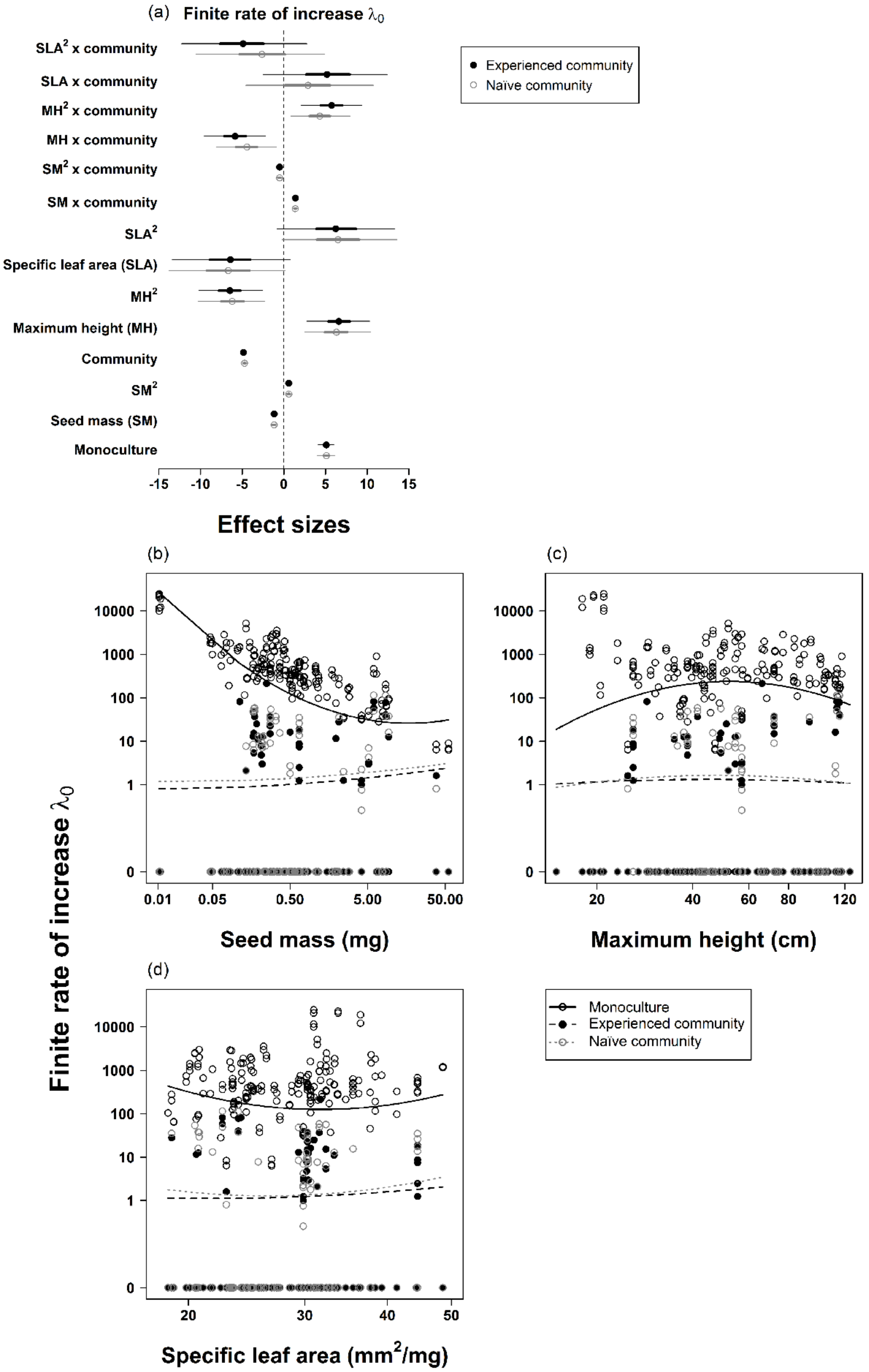

Figure 2.2: Effects of functional traits (linear and quadratic term of seed mass, maximum height, and specific leaf area), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction on the finite rate of increase (λ_0).

Figure 2.2: (Continued) (a) Effect sizes of the model contrasting monoculture vs. experienced community are shown in black and effect sizes of the model contrasting monoculture vs. naïve community are shown in grey. Note that the monoculture effect sizes refer to the intercept of the respective model and the community effect sizes refer to the contrast of monoculture vs. community. Circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals. (b-d) Relationships between functional traits and the finite rate of increase (λ_0) in monoculture and the two community types (experienced and naïve community). Predictions of the model contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). Predictions for the naïve community (based on the model contrasting monoculture vs. naïve community) are shown as grey dotted line. Both models have identical effect sizes for monoculture, thus only one prediction is shown. Predictions are based on the full model with the other explanatory variables set to their mean value (i.e. zero, since the functional traits were scaled and centred, allowing the response of λ_0 to any given trait to be interpreted independently of the other trait variables in the respective model). Note that only interactions between functional traits and competition treatment (monoculture vs. community) in (b) and (c) are significant. All axes are shown on log-scale.

The response of λ_0 to seed mass and maximum height was mostly driven by variation in fecundity (F_0). For F_0, the relationships with seed mass and maximum height differed between monoculture and interspecific competition in a similar manner as for λ_0 (Supporting Information Chapter 2, Fig. S6 and Fig. S7). In contrast, establishment (E_0) showed different and weaker responses to functional traits and competition treatments (Supporting Information Chapter 2, Fig. S6 and Fig. S7). Finally, we did not detect any clear effects of functional traits on population growth rate in the second year (λ_1) (Supporting Information Chapter 2, Fig. S6 and Fig. S7). The control analyses for λ_0 only including wild populations did not qualitatively change the results (Supporting Information Chapter 2, Table S5 and Fig. S10).

Competitive effects of native communities do not vary with residence time of the invaders

Competition by both the experienced and naïve community strongly reduced the finite rate of increase (λ_0) of the focal species (Fig. 2.3). Establishment (E_0), fecundity (F_0), and population growth in the second year (λ_1), were also significantly lower in both community types than in the monoculture (Supporting Information Chapter 2, Fig. S8 and Fig. S9). The strong competitive effects of both community types may be explained by most community species reaching high abundances (Supporting Information Chapter 2, Appendix S1 and Fig. S2). Both community types reached high total cover (Supporting Information Chapter 2, Fig. S2), which slightly differed between the experienced and naïve community in the first year (mean ± standard deviation; experienced: 86% ± 10%, naïve: 73% ± 11%) but became very similar in the second year (experienced: 99% ± 2%, naïve: 94% ± 6%).

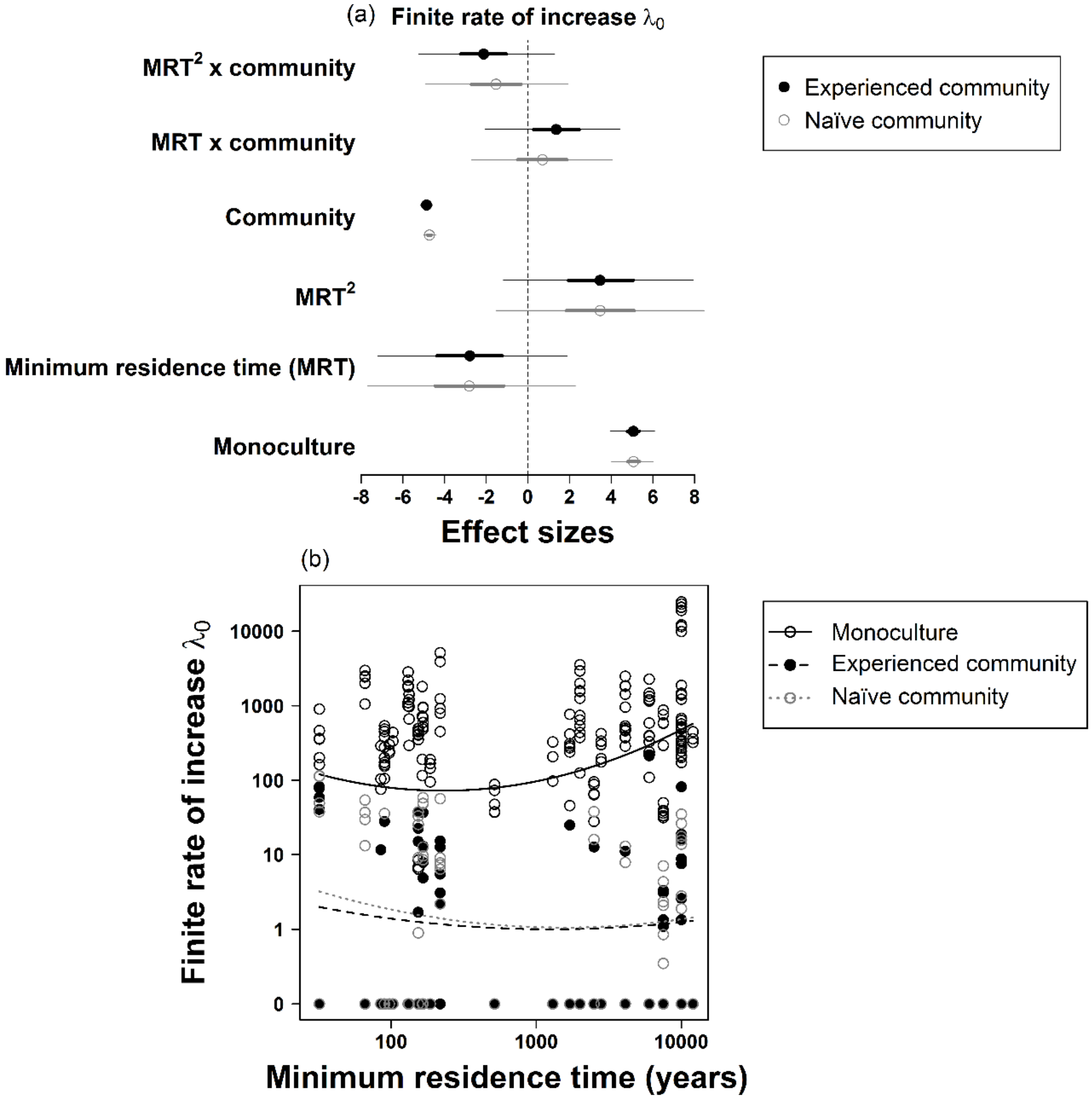

Figure 2.3: Effects of minimum residence time (MRT, linear and quadratic term), competition treatment (monoculture vs. experienced/naïve community), and their interaction on the finite rate of increase (λ_0). (a) Effect sizes of the model contrasting monoculture vs. experienced community are shown in black and effect sizes of the model contrasting monoculture vs. naïve community are shown in grey. Note that monoculture effect sizes refer to the intercept of the respective model and the community effect sizes refer to the contrast of monoculture vs. community. Circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals. (b) Predictions of the model contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). The prediction of competition by the naïve community (based on the model contrasting monoculture vs. naïve community) is shown as dotted grey line. Both models have identical effect sizes for monoculture, thus only one prediction is shown. All axes are shown on log-scale.

Under interspecific competition with the experienced community, λ_0 did not show a unimodal response to minimum residence time (MRT) (quadratic MRT-interaction-effect: posterior mean = -2.12, 95% credible interval = -5.10 – 1.35; Fig. 2.3a). Instead, we found a similar response of λ_0 to MRT in both community types: in the experienced and the naïve community, the focal species with longest MRTs in Germany tended to have the lowest λ_0 (Fig. 2.3b). In contrast, in monoculture, λ_0 increased with MRT (Fig. 2.3b). This contradicts our hypothesis of a build-up of biotic resistance by the native (experienced) community over time. The respective models explain a high proportion of variance in (log-transformed) λ_0 (Table 2.1). We also did not find significant interactions between MRT and competition treatment for the other demographic performance measures E_0, F_0, and λ_1 (Supporting Information Chapter 2, Fig. S8 and Fig. S9). Note that in monoculture, the slight decrease at very low residence times before λ_0 increases (Fig. 2.3b) could be due to variation of initial population sizes (as shown in Fig. 2.1) caused by casual neophytes that usually do not have stable populations. In general, the effects of all explanatory variables on all performance measures were estimated to be similar when comparing monocultures to either experienced or naïve communities. The control analyses for λ_0 only including wild populations did not qualitatively change the results (see Supporting Information Chapter 2, Table S5 and Fig. S11). The interaction between competition treatment and MRT (Supporting Information Chapter 2, Fig. S11a) reveals a similar decrease in λ_0 with MRT in both the experienced and naïve community (Supporting Information Chapter 2, Fig. S11b). This further supports our finding that competitive effects of the communities do not vary with residence time of the focal species.

Discussion

By experimentally comparing the population dynamics of 40 alien and native plant species in monocultures and in either experienced or naïve plant communities, we found strong reductions in intrinsic population growth of our focal species under interspecific competition. In line with our first hypothesis, interspecific competition by the communities markedly altered trait effects on population growth (Fig. 2.2; Supporting Information Chapter 2, Fig. S7). However, regarding our second hypothesis, we did not find evidence for a potential build-up of competition-mediated biotic resistance over time. Experienced communities did not exert greater competitive effects if they shared a longer potential co-existence time with the focal species (Fig. 2.3). Moreover, experienced and naïve communities had very similar effects on fitness and population growth, as well as trait-fitness relationships, of the focal species (Fig. 2.3; Supporting Information Chapter 2, Fig. S8). In the following, we discuss the potential causes and consequences of these findings.

Interspecific competition alters trait-fitness relationships in alien plants

In line with our first hypothesis, we found significant differences in the relationships between functional traits and fitness of the focal species between monocultures and communities. Specifically, in monoculture, intrinsic population growth and fecundity decreased with seed mass. This is expected given the trade-off between seed mass and seed number (Moles *et al.* 2004; Supporting Information Chapter 2, Fig. S5). For the same set of Asteraceae species (plus 6 additional neophytes originating from North America), Brendel *et al.* (2021) previously detected a strongly negative relationship between seed mass and population growth in monocultures. We confirm this relationship for our somewhat smaller species set, although it levels off at high seed mass values (Fig. 2.2b). In contrast, under interspecific competition, regardless of the community type, large-seeded focal species showed highest values of intrinsic population growth and fecundity (Fig. 2.2b and Supporting Information Chapter 2, Fig. S7d, respectively). This matches the hypothesis of Dietz & Edwards (2006), who postulated that during the invasion process, alien plants experience divergent selection in low- vs. high-competition environments. Trait values enabling high fecundity and fast spread (e.g., low seed mass) are advantageous in low-competition ruderal habitats but become disadvantageous under high interspecific competition.

Indeed, we found such a seed-mass-mediated trade-off between population growth in low- vs. high-competition habitats. As expected from intra- and interspecific selection for ruderality in low competition, Brendel *et al.* (2021) showed that seed mass of the Asteraceae species converged with increasing residence time towards values that maximized population growth (λ_0) and consequently, λ_0 increased with their residence time. We also show this advantage of low seed mass in conditions of low competition. However, under intense interspecific competition with the communities, low seed mass instead leads to fitness reductions (Fig. 2.2b and Supporting Information Chapter 2, Fig. S7d), with many of our focal species (being mostly ruderal, annual species) not persisting over two years in the experimental communities. Indeed, we did not find such a trait-mediated trade-off for population growth rate in the second year (λ_1; see Supporting Information Chapter 2, Fig. S7). Given the limited size of the mesocosms, λ_1 strongly depended on population size after the first year and thus on λ_0.

Variation in population size after the first year is thus likely to obscure effects of traits and interspecific competition. Hence, the finding of λ_0 more clearly suggests that divergent selection on functional traits can be imposed by interspecific interactions between species (Colautti *et al.* 2017) and invasion success might strongly depend on the ability to respond to natural selection (Lee 2002). Thus, the expansion and impact of many alien plants may be limited because spread through low-competition habitats (whereby disturbed sites near human settlements often being the first habitats to be colonized; McNeely 2005) requires different traits than establishment in high-competition habitats. This finding has important implications for management of plant invasions. It suggests that the invaders of high concern are those species that are able to escape the trait-mediated trade-off between performance under low and high competition and are therefore successful both at spreading rapidly in disturbed areas and at expanding into habitats of high competition. A possible escape mechanism that allows species with high seed mass to spread rapidly in low-competition environments may be seed dispersal by mobile animals (Nathan *et al.* 2008). On the other hand, small-seeded species can increase their competitive ability if they are allelopathic or modify ecosystem properties by altering fire regimes or fixing atmospheric nitrogen.

Our results have furthermore important implications for community assembly and the co-existence between alien and native species. In a recent study by Maron *et al.* (2021), small-seeded species with high fecundity increased their abundance in low competition more than large-seeded species with low fecundity, but showed a reduced tolerance to high interspecific competition. This seed mass-mediated trade-off in competitive ability, which has also been shown in our study, furthermore balanced abundances of high- and low-fecundity species in a perennial grassland community and hence strongly contributed to species co-existence (Maron *et al.* 2021). Moreover, Laughlin *et al.* (2020) recently pointed out the importance of establishing links between functional traits and intrinsic population growth rates in order to advance community ecology. They call for functional community ecologists to become demographers and our study is one of the first to follow this call.

No evidence for a build-up of competition-mediated biotic resistance by experienced native communities

We expected that experienced communities would exert stronger competition on species with high MRT than naïve communities. However, although experienced communities developed somewhat higher cover than naïve ones (Supporting Information Chapter 2, Fig. S2), they did not exert stronger competition (Fig. 2.3). In fact, both community types had surprisingly similar effects on all performance measures (Fig. 2.3 and Supporting Information Chapter 2, Fig. S8). Thus, competition-driven limits to the population growth of the studied alien plants seem to be independent of co-evolutionary history with the native community.

This finding contradicts the expectation that over time, native communities adapt to the presence of alien species and build up biotic resistance to them(Lau 2006; Strauss *et al.* 2006; Saul *et al.* 2013; Saul & Jeschke 2015). Our results also contradict previous empirical studies that showed higher resistance of experienced natives than naïve natives to competition with invaders (Oduor 2013). However, most studies measured only short-term growth differences rather than population dynamics, focused on highly abundant invasive plants (Goergen *et al.* 2011; Gibson *et al.* 2018), and did not test whether residence time (i.e., length of co-existence time) increases biotic resistance of native species. Here, we included both common invaders (established neophytes) and less abundant aliens (casual neophytes) and covered a wide range of residence times (i.e., co-existence times between native communities and invaders), but did not find evidence that co-evolutionary history generally determines the strength of competition-mediated biotic resistance of native communities. Thus, only highly abundant and competitive invader species rather than alien plants in general may present a large enough selective pressure to cause adaptation of native communities to new invaders. Alternatively, studies that did not find an effect of increased biotic resistance with eco-evolutionary experience may simply be less likely published because of a publication bias. Also, some empirical studies may falsely attribute increased performance of experienced natives (or reduced performance of invaders growing with experienced natives) to a build-up of biotic resistance due to confounding factors in observational studies or limitations of the experimental design that do not allow to conclusively demonstrate such a mechanism. On the other hand, in our experiment we could only test a limited set of native species in our experimental communities. Competitive response of native species in relation to eco-evolutionary experience with alien species may, however, be native species-specific. For instance, Mealor & Hild (2007) conducted a common garden experiment and showed that the native grass *Sporobolus airoides* consistently displayed a positive response (i.e., higher survival) to long-term co-existence with the invader *Acroptilon repens*, whereas the performance of the native grass *Hesperostipa comata* originating from invaded communities was not different from *H. comata* collected from non-invaded communities. Hence, in our communities, only specific native species may have evolved competition-mediated biotic resistance to the presence of the invaders while others did not. This might have caused the net competitive effect of the communities to be independent of co-existence time with the invaders. It is also likely that a build-up of biotic resistance can more easily be detected at population level (albeit only covering considerably shorter timescales). For instance, in a pairwise competition experiment, Germain *et al.* (2020) showed that population growth of the invasive grass *Bromus hordeaceus* was more restricted by the native grass *Vulpia microstachys* originating from populations that have a history of co-existence with the invader compared to non-invaded populations. Finally, as in our experiment we only were able to test competitive effects of native plant species, it is possible that other components of biotic resistance such as parasitism, herbivory or plant-soil feedbacks are more important in limiting invasion success.

In a multi-species common-garden experiment with a smaller set of focal Asteraceae species, Sheppard & Schurr (2019) measured how survival and reproduction respond to competition by a (different) community. They found that competitive effects increased with residence time and suggested that this arises from a build-up of biotic resistance by the native community. Furthermore, in a pairwise competition experiment, Sheppard & Brendel (2021) found that native Asteraceae tended to perform better with Asteraceae neighbours of increasing residence time (consistent with an increase in biotic resistance at the level of individual species), but only under certain soil conditions. However, our finding that naïve communities have similar competitive effects as experienced ones contradicts these findings. The weak decrease in fitness with residence time in both communities may be explained by a priori competitive ability of the focal species correlating with residence time. Accordingly, trait-fitness relationships were also highly similar in both communities. Our study thus shows how the inclusion of a naïve community for a more robust test advances knowledge about the relevance of competition-mediated biotic resistance.

Conclusions

We here for the first time show that seed mass has opposing effects on population growth of alien plant species under high vs. low competition. This shows that the expansion and impact of invaders are limited by a seed-mass-mediated trade-off between spread in low-competition habitats vs. establishment in high-competition habitats. Invaders that are likely to escape this functional trade-off should be of highest management concern. Furthermore, we provide a robust test of competition-mediated biotic resistance by comparing the effect of experienced and naïve communities on population dynamics (cf. Laughlin *et al.* 2020) across a large set of species over two years. We here did not find any evidence that in our study system, an increase of competitive effects by native communities (as one aspect of biotic resistance) over time may limit population growth of alien species. Our results that expand on previous studies on interactions between alien and native species (Sheppard & Schurr 2019; Brendel *et al.* 2021) thus advance both a fundamental understanding of limits to the success of alien plants and the management of alien plant invasions.

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Chapter 3

Competitive ability of native and alien plants: effects of residence time and invasion status *

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*This chapter refers to a manuscript published in *NeoBiota*:

Sheppard, C.S. & **Brendel, M.R.** (2021). Competitive ability of native and alien plants: effects of residence time and invasion status. *NeoBiota 65*, 47-69. (https://doi.org/10.3897/neobiota.65.63179)

Publisher: Pensoft (https://pensoft.net/)

Format and layout were adapted as a matter of consistency.

Abstract

Competition is commonly thought to underlie the impact of plant invasions. However, competitive effects of aliens and competitive response of natives may also change over time. Indeed, as with time, the novelty of an invader decreases, the accumulated eco-evolutionary experience of resident species may eventually limit invasion success. We aimed to gain insights on whether directional changes in biotic interactions over time or more general differences between natives and aliens, for instance, resulting from an introduction bias, are relevant in determining competitive ability. We conducted a pairwise competition experiment in a target-neighbour design, using 47 Asteraceae species with residence times between 8 years-12,000 years in Germany. We first tested whether there are differences in performance in intraspecific competition amongst invasion status groups, that is casual and established neophytes, archaeophytes or native species. We then evaluated whether competitive response and effects depend on residence time or invasion status. Lastly, we assessed whether competitive effects influence range sizes. We found only limited evidence that native target species tolerate neighbours with longer potential co-existence times better, whereas differences in competitive ability were mostly better explained by invasion status than residence time. Although casual neophytes produced most biomass in intraspecific competition, they had the weakest per-capita competitive effects on natives. Notably, we did not find differences between established neophytes and natives, both of which ranked highest in interspecific competitive ability. This lack of differences might be explained by a biased selection of highly invasive or rare native species in previous studies or because invasion success may result from mechanisms other than interspecific competitive superiority. Accordingly, interspecific per-capita competitive effects did not influence range sizes. Further studies across a broader range of environmental conditions, involving other biotic interactions that indirectly influence plant-plant interactions, may clarify when eco-evolutionary adaptations to new invaders are a relevant mechanism.

Introduction

Biological invasions are a major driver of global change, posing a threat to native species, communities, and ecosystems (Simberloff *et al.* 2013; Pyšek *et al.* 2020). For plant invasions, competition is the most commonly invoked mechanism by which alien species impact natives (Levine *et al.* 2003). Understanding whether alien species benefit from higher interspecific competitive ability and whether the resulting local dominance is linked to large-scale invasion success, is thus crucial for conservation management. According to Parker *et al.* (1999), an invader's potential impact is the product of abundance, per-capita effect, and range size. It has long been suggested that locally-abundant species are generally also the ones that are widespread (Lawton 1993) and that rare species are competitively inferior (Griggs 1940). Accordingly, some studies have found that alien species with higher local interspecific competitive ability may also reach larger range sizes (Milla *et al.* 2011; Sheppard 2019), although other studies with native species have not consistently found such an effect (e.g., Lloyd *et al.* 2002). Additionally, performance in intraspecific competition may also be an important determinant of invasion success, given that alien species often dominate in dense monospecific stands.

Given its importance for invasion success and impacts, competition amongst aliens and natives has long been studied (Vilà & Weiner 2004). However, a neglected aspect of competition experiments, so far, is the possibility that competitive effects of aliens and competitive response of natives to aliens might change over longer timescales. As a result of eco-evolutionary changes following the introduction of a new species, the performance and potential impacts of an invader may depend on its residence time; that is, the time since introduction to a new area. In fact, one of the most consistent findings in invasion biology is the importance of residence time, particularly for increasing range sizes (Pyšek & Jarošík 2005; Williamson *et al.* 2009; Pyšek *et al.* 2015). Beyond affecting range sizes, residence time also has consequences for other ecological and evolutionary processes affecting the invader and resident plant communities (e.g., Lankau *et al.* 2009; Lankau 2011; Dostál *et al.* 2013; Gruntman *et al.* 2017). With increasing residence time, an invader may adapt to its new environment, such as to new climate conditions (Colautti & Barrett 2013), increasing population growth and spread. Conversely, as the novelty of an invader and of the biotic interactions between invader and resident competitors and antagonists decreases over time, the accumulated eco-evolutionary experience of resident species may eventually limit population growth and spread of invaders (Hawkes 2007; Saul *et al.* 2013; Sheppard & Schurr 2019; Germain *et al.* 2020).

As competition for limiting resources may act as a selection pressure, plants with a history of co-existence may have developed niche differentiation or reached a balance in competitive abilities through adaptive evolution (Thorpe *et al.* 2011). Hence, evolutionary changes in competitive ability with residence time may be important for long-term changes in invasion success. From the invader perspective, competitive effects may increase, for instance, when, due to a release from natural enemies, invaders invest less in defence and instead more in competitive ability (evolution of increased competitive ability hypothesis, Blossey & Nötzold 1995). In contrast, evolutionary responses of native species to invaders are less frequently considered and most evidence involves animals (Strauss *et al.* 2006). Thereby, high impacts of alien species are frequently explained by the native species being naïve with regards to the novel threat (which, however, can be overcome over time, for example, Bytheway & Banks 2019). The few studies investigating evolutionary adaptation to competition between plants have mostly focused on invasive plants that produce allelochemicals (Callaway *et al.* 2005; Lankau 2012; Dostál *et al.* 2013). In this regard, the novel weapons hypothesis posits that invaders may succeed because they have novel weapons to which native species are not adapted (Callaway & Aschehoug 2000). However, native species may also learn to tolerate such novel weapons over time, in which case they should show stronger competitive responses with length of co-existence time. For instance, native grasses growing for 20-30 years with *Centaurea maculosa* in North America, tolerate the allelochemicals better than native grasses of the same species from uninvaded habitats (Callaway *et al.* 2005). Overall, a meta-analysis of 53 comparisons from 14 experimental studies showed that experienced natives (plants from populations growing with the invader) had higher levels of growth and reproduction than naïve natives (plants from populations that have not yet experienced invasion) (Oduor 2013). Germain *et al.* (2020) recently demonstrated that such gained experience in a native annual grass, which led to increased competitive ability, can, in turn, reduce invasion growth rate of an invasive annual grass considerably.

Differences in competitive ability between invader and resident species are not necessarily only the result of such gradual directional changes in competitive interactions. Instead or additionally, there may be a priori differences in competitive ability that result from an introduction bias. This means that alien species are not a random sample of all plants of the world. Indeed, alien species tend to have a stronger human association and may, hence, be more adapted to human-modified environmental conditions (Buckley & Catford 2016). Furthermore, species deliberately introduced and grown for ornamental or horticultural purposes (which represent the majority of established alien plants in Europe, Lambdon *et al.* 2008) tend to be strong competitors or have a ruderal strategy, rather than being tolerant to stressful abiotic conditions (Guo *et al.* 2019). In contrast to the neophytes, the archaeophytes (alien plants introduced before Columbus' discovery of the Americas in 1492) are ruderal or segetal species, originating from drier and warmer regions of the Fertile Crescent and tend to be adapted to more extensive traditional land use (Chytrý *et al.* 2008; Zając *et al.* 2009). Such an introduction bias may thus result in a priori differences in competitive ability between native, neophyte and archaeophyte species. Indeed, meta-analyses have shown that invasive neophyte species possess traits that distinguish them from native species and which may confer higher competitive ability (Ordonez *et al.* 2010; van Kleunen *et al.* 2010). Although generally fewer studies considered archaeophytes, they have been shown to differ in traits compared to natives (Knapp & Kühn 2012). Nevertheless, it has also been argued that common natives which are successful in human-disturbed habitats may display similar traits as alien species (Thompson & Davis 2011). The concept of discrete "invasion status" categories (such as casual, established, invasive aliens vs. natives; Blackburn *et al.* 2011) is often employed in invasion biology and can be helpful in highlighting such differences amongst groups because of an introduction bias. However, invasion status groups are sometimes also used as a proxy for effects of residence time. If these latter mechanisms are relevant, such discrete categories may, however, not fully account for directional changes during the process of biological invasions, whereby such eco-evolutionary mechanisms may be better described by residence time as a continuous gradient (Sheppard & Schurr 2019).

In this study, we aimed to gain insights into whether continuous residence time or categorical invasion status may explain differences in competitive ability between natives and aliens better and whether any such differences have consequences for large-scale invasion success (i.e., if species with higher competitive ability reach larger range sizes). Thereby, we specifically aimed to test if we find directional changes in competitive ability over time, consistent with an increase in biotic resistance of native species to newly-introduced species. Alternatively, we considered whether we rather find evidence for more general differences amongst invasion status groups, resulting either from an introduction bias or other non-directional eco-evolutionary processes. To this end, we conducted a pairwise competition experiment with 47 Asteraceae species along an "alien-native species continuum", including species along a continuous gradient of residence times (Sheppard & Schurr 2019) and also representing the four discrete invasion status categories of casual neophytes, established neophytes, archaeophytes, and native species in Germany. Such multi-species experiments, although still rarely used in ecology, are very useful in searching for general patterns and mechanisms (van Kleunen *et al.* 2014). We studied pairwise competition of five native target species with 47 alien and native neighbour species, varying in residence times from 8 years to 12,000 years. This enabled us to assess whether tolerance (competitive response) of native species to competition from neighbours increases with their length of potential co-existence time, as expected if native species gain eco-evolutionary experience and increase biotic resistance to newly-introduced alien species. Additionally, given the potential importance of intraspecific competition for invasion success, we also assessed performance of each neighbour species.

Overall, we thus address the following research questions: 1) Does performance in intraspecific competition depend on invasion status? Note that in this first question we did not test for effects of residence time since no interspecific interactions were involved (i.e., no variation in potential co-existence times). 2) Does interspecific competitive ability (competitive response of five native targets and competitive effects of all 47 alien and native neighbours) depend on residence time or invasion status? 3) Do interspecific competitive effects (and residence time) influence range size?

Materials and Methods

Alien-native species continuum

Our study focused on 47 species of annual Asteraceae along an alien-native species continuum (Sheppard & Schurr 2019) (see Supporting Information Chapter 3, Fig. S1), representing species of increasing residence times between 8 years-12,000 years in Germany (including 10 casual neophytes, 15 established neophytes, 15 archaeophytes, and 7 natives). We limited our study system to one family so that we could focus on effects of residence time and invasion status within phylogenetically-related species of the same life form (annuals) and habitat (open vegetation, ruderal and segetal habitats). We chose Asteraceae because they are one of the largest plant families globally and highly represented in plant invasions. We chose annual species because this enabled us to not only measure plant performance in terms of biomass, as usually done in competition experiments, but also total seed production, which serves as the best proxy for individual fitness, given that annuals are typically monocarpic. Minimum residence time (MRT), which is used as a proxy for the date of first introduction of a species to a new area, was extracted from various databases (Sheppard & Schurr 2019). Usually, we used seed material collected from a previous experiment conducted at the same location in 2016, where individuals had been growing in low density monoculture mesocosms (Brendel *et al.* 2021). Thus, we minimised potential performance differences arising from maternal effects. If this seed material was not available, we used the original seed material collected in 2015, whereby five species had been collected from wild populations in Baden-Württemberg and one species originated from a botanical garden (see Supporting Information Chapter 3, Table S1, for further details).

Target-neighbour competition experiment

In March 2017, we set up a pairwise competition experiment at a field station of 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). The experiment was set up in a target-neighbour design, whereby we focused on five native Asteraceae as target species (*Crepis pulchra, Hypochaeris glabra, Lapsana communis, Pulicaria vulgaris,* and *Senecio viscosus*) and all 47 species as neighbours. The five targets were grown in pots as single individuals, in intraspecific competition and in interspecific competition with all other 46 Asteraceae species, which vary in their MRT and invasion status in Germany. Thereby, we had a single target individual in the middle of the pot, surrounded by multiple individuals of one neighbour species.

The pots were placed in ten rows and each target-neighbour combination was usually replicated four times (for the total number of replicates per species combination see Supporting Information Chapter 3, Table S1,). Target-neighbour pots were set up in a fully randomised design. In total, we initially established 904 pots, of which the 20 pots with single targets and the 20 pots with intraspecific competition amongst targets as well as 804 out of the 864 pots in the target-neighbour design had surviving individuals of both species per pot at harvest. The pots had a volume of 15-litre (0.08 m^2 soil surface area, 33 cm upper diameter, 26 cm lower diameter, 24.5 cm height) and were filled with local field soil. Prior to filling the pots, we added a layer of expanding clay to improve drainage. The pots were constantly watered throughout the growing season with an automatic drip-irrigation system and received a maximum of 1.1 litres per day during the warmest period of the year. We weeded the pots before sowing and regularly throughout the experiment.

Targets and neighbours were established from seeds. As we included such a large number of neighbour species that vary in their growth rates, we aimed for constant strength (in terms of biomass production, rather than number of individuals) of neighbour competition across species. We determined the required number of seeds to be sown for each neighbour species, based on data on the average biomass production and establishment rates from a previous experiment in 2016 (Brendel *et al.* 2021; see Supporting Information Chapter 3, Appendix S1, for further details). In mid-May, 3-5 seeds of the target species were added to the centre of each pot to establish the target individuals. At the same time, the species-specific amount of seeds for the neighbour species was sown around the pot centre. All seeds were covered with a thin layer of sand. We also established additional germination trays in the greenhouse to grow seedlings of the target species as back-up for transplanting (see Supporting Information Chapter 3, Appendix S1, for further details).

After setting up the target-neighbour combinations, we noticed that the pots were filled with two different soil types (which was not part of the planned design of the experiment): the field soil originated from two separate deliveries from the same company (Glaser Recycling GmbH, Mönsheim, Germany) and soil analyses indicated that these two deliveries were comparable in soil texture, but differed in nutrient contents. Specifically, we had a nutrient-poor (NO_3^- 5.48 mg/kg, NH_4^+ 0.27 mg/kg, P 3.06 mg/kg, with a pH value of 8 and total carbon content 1.58%) and a nutrient-rich (NO_3^- 10.19 mg/kg, NH_4^+ 0.89 mg/kg, P 4.28 mg/kg, with a pH value of 7.7 and total carbon content 2.85%) soil. The soils had a sandy loamy texture (nutrient-poor type: 76% sand, 10% clay and 14% silt; nutrient-rich type: 66% sand, 16% clay and 18% silt). As having two different soil types was not a planned part of the experiment and pots had been allocated in a completely randomised manner, the target-neighbour combinations were spread unevenly between the two soil types: of the surviving pots, most pots were of the nutrient-poor type (647 pots, 16 of which are single targets), with only 21% (177 pots, four of which are single targets) in the nutrient-rich type. One species, *Carthamus tinctorius*, only occurred in the nutrient-rich soil. Having twice the amount of plant available nitrogen highly influenced biomass production during the season and, hence, we usually analysed data originating from the two soil types separately.

Four weeks after sowing, we assessed the germination success of target and neighbour species. In pots where both the target and neighbour species germinated, we thinned out the target species to one single individual. If the target did not germinate, we transplanted a target species individual from the germination trays. If the neighbour did not germinate, we re-sowed the neighbour species. Pots, in which target and neighbour still did not establish following these measures, were removed from the experiment (see Supporting Information Chapter 3, Appendix S1).

Data collection

To measure performance of targets and neighbours, we harvested aboveground biomass by mid-October 2017 (at least 17 weeks after sowing) and dried it at 70°C for 72 hours before weighing. For the neighbours, we also counted the number of established individuals and the total number of flower heads (capitula) per pot as a proxy for reproductive output. For target individuals, reproductive output was measured more precisely, using the total seed mass produced per individual in each pot. The experimental period was long enough to allow seed production of all target species, whereby approximately two thirds of all target individuals produced seeds. To measure seed production, we collected seeds during the experiment from ideally ten intact capitula of each target individual, from which we determined the average seed mass per capitulum. Before harvesting each target individual at the end of the experiment, we counted the number of its vital capitula, to then calculate the total seed mass produced.

In addition to the experimental data, we collected data on range sizes in Germany for each species. We obtained these data from the database of FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. (www.deutschlandflora.de). This database records species occurrence in each of four quadrants of a grid cell of 10 x 6 arc minutes. We counted the number of occupied quadrants per grid cell for each species. The proportion of occupied cells for each species represents its range size in Germany (Sheppard & Schurr 2019).

Statistical analyses

We analysed all data in R 4.0 (R Core Team 2020). To address the first question of whether performance in intraspecific competition depends on invasion status, we only focused on neighbour performance, assuming that the single target individual had no relevant competitive effect on its many neighbours. Except in the analysis of establishment success, to ensure this assumption was justified, we excluded all pots where target biomass was larger than neighbour biomass. This occurred in 76 out of 527 cases in the nutrient-poor and in 13 out of 156 in the nutrient-rich soil. We included all pots with surviving neighbours, which were not re-sown a second time. This resulted in 43 species for establishment and 41 species for biomass and number of capitula per pot. We were interested in pot-level performance of neighbours as a better measure for overall invasion success. For this first question of addressing intraspecific performance of neighbour species, we analysed the data of both soil types combined, but included soil type as an explanatory variable. We analysed establishment rates (the number of successfully established neighbour individuals by the end of the experiment compared to number of seeds sown) by means of a generalised linear mixed model with binomial distribution. Square-root-transformed aboveground biomass per pot and log(x+1)-transformed total number of capitula per pot were analysed with a linear mixed effects model. Fixed effects included the categorical variables invasion status (a factor with four levels: casual neophyte, established neophyte, archaeophyte or native), soil type (a factor with two levels: nutrient-poor and nutrient-rich) and their interaction. Species was included as a random effect in all models. As the number of seeds sown and seed mass differed between species, we included the log-transformed total seed mass sown per pot as a covariate in all analyses. This covariate should account for initial differences in propagule pressure, as well as potentially higher establishment success for larger seeds and density-dependent thinning for higher seed numbers. We tested significance of the explanatory variables by means of likelihood ratio tests.

For the following questions, we conducted all analyses separately for the two different soil types, because biomass production greatly differed between soil types (see "Competition pressure"). Some of the analyses could only be done for the pots with nutrient-poor soil, for which we had considerably more replicates (for species-specific sample sizes see Supporting Information Chapter 3, Table S1). To address the second question of whether competitive response of targets or competitive effects of neighbours depend on residence time or invasion status, we used two approaches. First, to explore the native targets' tolerance to competition (competitive response), we used a linear mixed effects model to investigate the effect of neighbour biomass on target aboveground biomass and total seed mass, depending on either MRT or invasion status and their interaction with neighbour biomass. Given that the native targets have the longest MRTs, the neighbour MRT here represents the length of potential co-existence times between native targets and neighbours. Aboveground target and neighbour biomass were square-root-transformed in all analyses to meet model assumptions, while the total seed mass was log(x+0.001)- and MRT log-transformed. Given that seed production was possible (the individuals survived and all target species produced seeds at least in some instances), we included the zero values in this analysis. We included random effects of target and neighbour species identity. Models using the explanatory variable MRT versus invasion status were compared via the Akaike Information Criterion (AIC), while the significance of the interaction between MRT (or invasion status, respectively) and neighbour biomass was tested with likelihood ratio tests. To ensure that effects are not due to targets being differently affected by transplanting or re-sowing, we conducted a control analysis excluding all pots with transplanted target individuals and/or re-sown neighbours.

Second, we estimated the competitive effect of each neighbour species on the targets. For each neighbour species separately, square-root-transformed neighbour biomass was regressed against square-root-transformed target biomass (across all five target species), including all data from interspecific competition in the nutrient-poor soil (for species-specific sample sizes see Supporting Information Chapter 3, Table S2). The slope of this regression represents the strength of the competitive effect. We then tested in a linear model if the competitive effect of the 46 neighbour species (*Carthamus tinctorius* had to be excluded as it only occurred in nutrient-rich soil) was related to log-transformed MRT or invasion status, again comparing the two models via AIC. To account for the fact that the species-specific regressions varied in their sample sizes and goodness of fit, we weighted the regressions by the inverse of the squared standard error of the slope. However, to highlight the effect of weighing, we below also show the results of non-weighted regression. Due to a lack of data points, competitive effects were not estimated for the nutrient-rich soil type.

To address the third research question of whether interspecific competitive effects influence range size when accounting for MRT, we assessed in another weighted regression model whether per-capita competitive effects influence range size. Range size was defined as the logit-transformed proportion of area occupied in Germany and we included log-transformed MRT as a covariate. Per-capita competitive effects were again derived from the slope of the species-specific regressions described above and we used the inverse of the squared standard error of the slope as weights.

Results

Competition pressure

The number of neighbour individuals in the nutrient-poor soil type ranged between 1 and 22 (median 4, mean 5.1), except for the casual neophyte *Callistephus chinensis*, which reached up to 53 individuals. Nevertheless, this species was within the range of neighbour biomass covered by other species: neighbour biomass ranged from 0.01-15.6 g (median 4.0 g, mean 4.7 g). In the nutrient-rich soil type, between 1 and 33 (for *C. chinensis*, up to 42) neighbour individuals established (median 5, mean 6.0). Neighbour biomass in the nutrient-rich soil ranged from 0.21-68.3 g (median 16.2, mean 19.5 g). Target species were usually negatively affected by competition, whereby their biomass production greatly varied depending on neighbour species (see Supporting Information Chapter 3, Fig. S2).

Performance in intraspecific competition

Establishment success was not affected by the interaction between soil type and invasion status (χ^2_{3df} = 4.44, P = 0.218), with the full model only explaining 9.9% (marginal R^2; 85.7% with random effects, i.e., conditional R^2) of variance in the data (Fig. 3.1a). We then tested for significance of the main effects in a reduced model without the interaction. Neither the main effects of soil type (χ^2_{1df} = 0.88, P = 0.349) nor invasion status (χ^2_{3df} = 5.03, P = 0.170) were significant, nor even the covariate total seed mass sown.

However, the interaction between soil type and invasion status was highly significant for aboveground biomass (Fig. 3.1b; χ^2_{3df} = 64.5, $P < 0.001$), with the model explaining 74.1% (87.5% with random effects) of the variance. In separate models for the two soil types, differences in invasion status were highly significant (nutrient-poor soil type: χ^2_{3df} = 31.83, $P < 0.001$, with marginal R^2 of 45.4% and conditional R^2 of 72.7%; nutrient-rich soil type: χ^2_{3df} = 21.43, $P < 0.001$, with marginal R^2 of 38.3% and conditional R^2 of 69.1%). While biomass was generally considerably higher in the nutrient-rich soil, in both soil types, casual neophytes produced most biomass and natives the least and this difference was more pronounced in nutrient-rich soil (Fig. 3.1b). Note that these results remained qualitatively similar when removing *C. chinensis* from the analysis, given that this was the casual neophyte that established in considerably higher number of individuals than other species.

For number of capitula, the interaction between soil type and invasion status was not significant (Fig. 3.1c; χ^2_{3df} = 6.15, P = 0.104). The model explained 18.1% (90.2% with random effects) of variance in the data. Testing for significance of the main effects in a reduced model without the interaction showed that more capitula were produced in the nutrient-rich soil (χ^2_{1df} = 266.49, $P < 0.001$), while the effect of invasion status was not significant (χ^2_{3df} = 5.99, P = 0.112), although the data suggest that established neophytes and natives tended to produce more capitula compared to casual neophytes and archaeophytes.

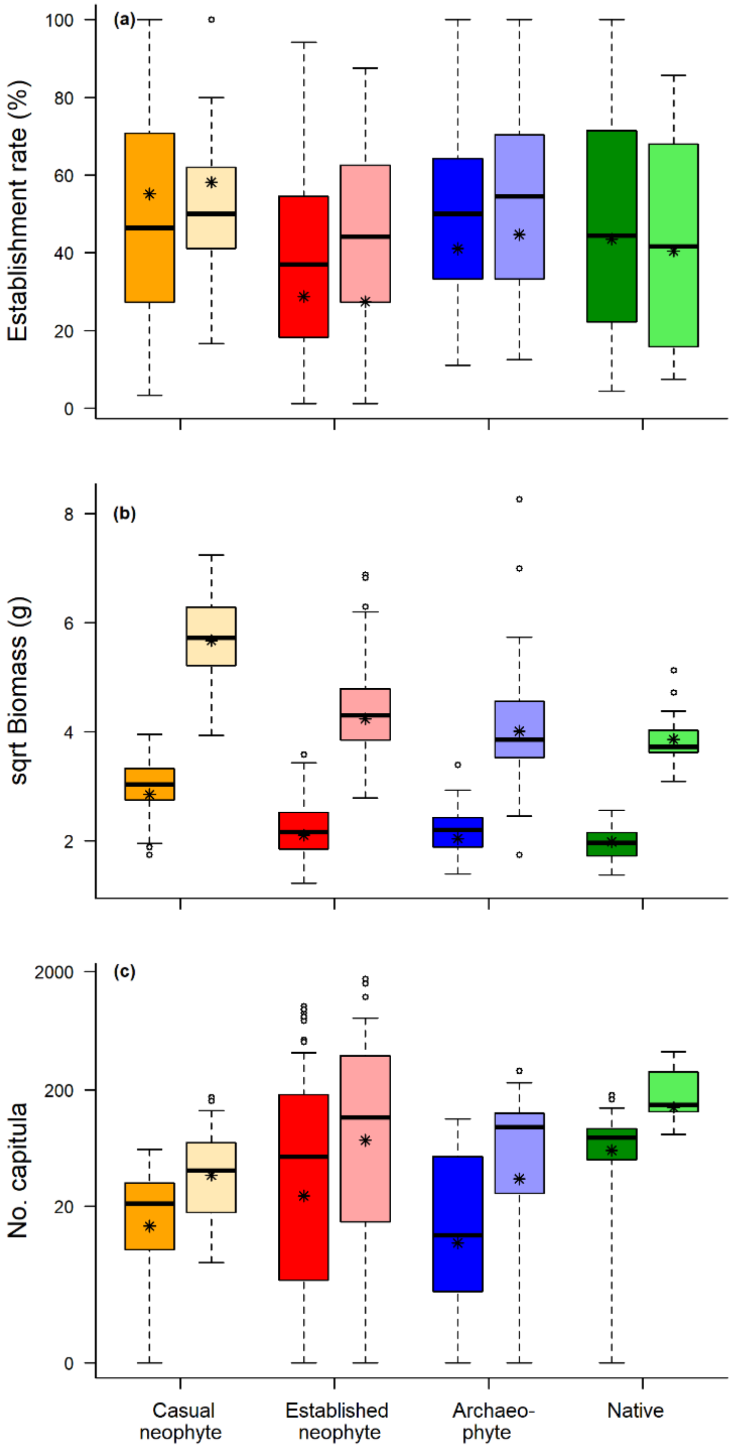

Figure 3.1: Performance in intraspecific competition at pot-level depending on invasion status and soil type (left bars in darker colours show the nutrient-poor and right bars in lighter colour the nutrient-rich soil type). Performance is shown as (a) establishment success (n = 527/156 in the nutrient-poor/nutrient-rich soil type), (b) square-root-transformed aboveground biomass per pot (n = 451/143) and (c) total number of capitula per pot (shown on a log-scale, n = 449/143). The asterisks show the mean performance per invasion status group and soil type.

Competitive response and competitive effects

The models testing the effect of invasion status instead of minimum residence time (MRT) on competitive responses resulted in lower AIC and thus better model performance for both aboveground biomass and total seed mass of native targets in the nutrient-poor soil (Table 3.1).

Table 3.1: Models analysing effects of neighbour biomass on target performance depending on minimum residence time (MRT) or invasion status. For each target performance measure (aboveground biomass and total seed mass, sample sizes for the nutrient-poor and nutrient-rich soil type in parentheses), differences in the Akaike Information Criterion (ΔAIC), explained variance (marginal R^2 and, in parentheses, conditional R^2) and results of likelihood ratio tests (LRT, χ^2 with degrees of freedom and *P*-values) for the interaction between MRT and neighbour biomass or invasion status and neighbour biomass, are shown. Analyses were done separately for the nutrient-poor and nutrient-rich soil type.

Model	**Soil type**	**Target biomass (n = 615/168)**			**Target total seed mass (n = 607/167)**		
		ΔAIC	**R^2**	**LRT**	**ΔAIC**	**R^2**	**LRT**
MRT	Nutrient-poor	6.12	58.4 (71.6)	$\chi^2_{1df} = 3.34$, $P = 0.067$	2.75	13.3 (55.6)	$\chi^2_{1df} = 0.98$, $P = 0.322$
Invasion status	Nutrient-poor	0	59.6 (72.4)	$\chi^2_{3df} = 15.67$, $P = 0.001$	0	14.9 (56.0)	$\chi^2_{3df} = 5.62$, $P = 0.132$
MRT	Nutrient-rich	3.20	47.7 (68.4)	$\chi^2_{1df} = 3.33$, $P = 0.068$	0	19.1 (47.3)	$\chi^2_{1df} = 2.07$, $P = 0.150$
Invasion status	Nutrient-rich	0	49.6 (72.3)	$\chi^2_{3df} = 13.04$, $P = 0.005$	1.07	22.6 (49.6)	$\chi^2_{3df} = 7.24$, $P = 0.065$

Thereby, we did not find directional changes in competitive ability in respect to target biomass (i.e., only a marginally significant interaction between MRT and neighbour biomass; Fig. 3.2a). Instead, we found a significant interaction between neighbour biomass and invasion status (Fig. 3.2b): native targets generally showed lowest tolerance to competition from natives and established neophytes and were least affected by competition from casual neophytes. For target seed mass, the direction of effects was the same as for biomass (Fig. 3.2c and d), but the interactions were not significant (Table 3.1). The control analysis without transplanted targets or re-sown neighbours resulted in qualitatively similar effects (see Supporting Information Chapter 3, Fig. S3).

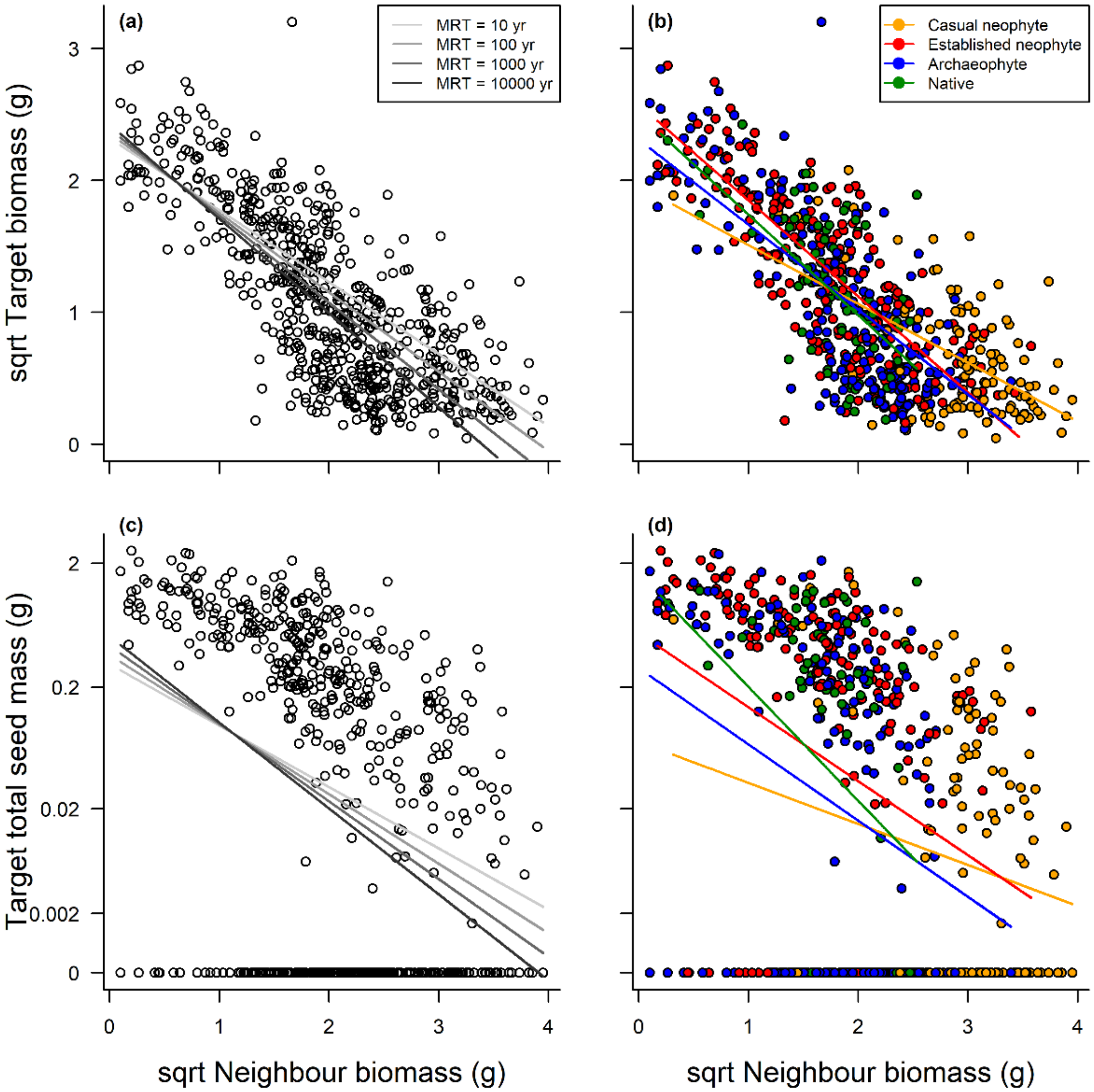

Figure 3.2: Effects of square-root-transformed neighbour biomass on target performance: (a, b) square-root-transformed aboveground biomass (n = 615) and (c, d) total seed mass (shown on a log-scale, n = 607), depending on (a, c) minimum residence time (MRT) or (b, d) invasion status in the nutrient-poor soil. To illustrate the interaction between continuous MRT and neighbour biomass in (a, c), a few representative values were chosen.

In the nutrient-rich soil (Fig. 3.3), for total seed mass of targets, the model with MRT resulted in lower AIC (Table 3.1). This model predicted higher tolerance of native targets to competition from neighbour species with higher MRT (in line with the hypothesis of increasing biotic resistance over time, Fig. 3.3c, although note that the interaction between MRT and neighbour biomass was not significant). Conversely, predictions for the invasion status models were similar to the nutrient-poor soil (Fig. 3.3b and d).

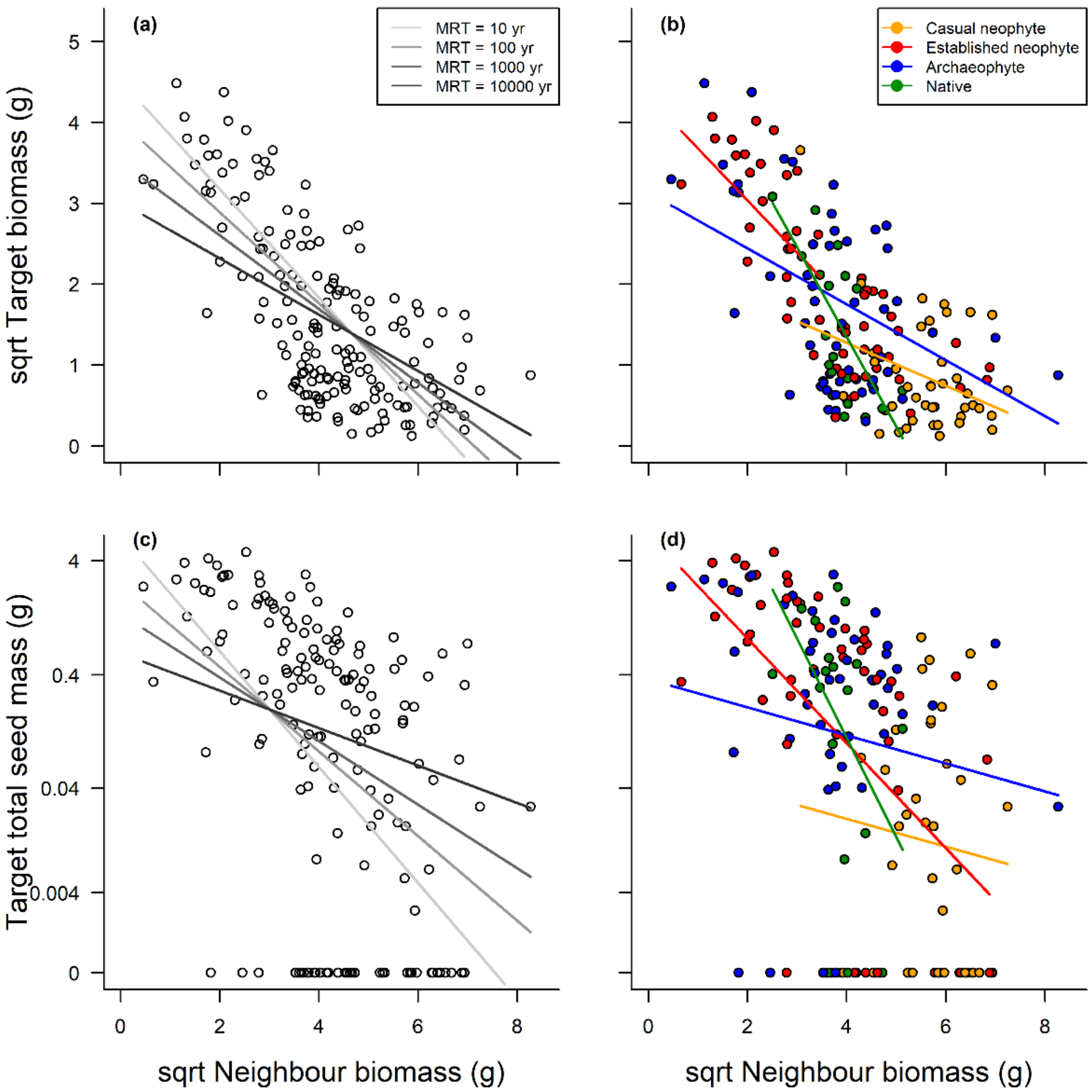

Figure 3.3: Effects of square-root-transformed neighbour biomass on target performance: (a, b) square-root-transformed aboveground biomass (n = 168) and (c, d) total seed mass (shown on a log-scale, n = 167), depending on (a, c) minimum residence time (MRT) or (b, d) invasion status <u>in the nutrient-rich</u> soil. To illustrate the interaction between continuous MRT and neighbour biomass in (a, c), a few representative values were chosen.

The regression models to determine competitive effects of the 46 species ranged in R^2 from 0.5-87.7% (mean 41.6%, median 41.9%), with 33 species having *P*-values lower than 0.05 (see Supporting Information Chapter 3, Table S2). MRT had a negative effect on the slope (competitive effect) of these species-specific regressions ($F_{1,44} = 8.20$, $P = 0.006$), explaining 15.7% of variance in the data (whereas, if using non-weighted regression, effect size was weaker and not significant). Hence, species with longer residence times have larger competitive effects (Fig. 3.4a). However, the invasion status model was better with a difference in AIC (ΔAIC) of 12.05, showing a highly significant effect of invasion status ($F_{3,42} = 9.54$, $P < 0.001$, Fig. 3.4b) and explaining 40.5% of variance in the data (however, without weighting, only half the variance was explained for the invasion status model which was still better by ΔAIC = 3.72). Casual neophytes had the weakest, established neophytes and natives the strongest competitive effects (Fig. 3.4b).

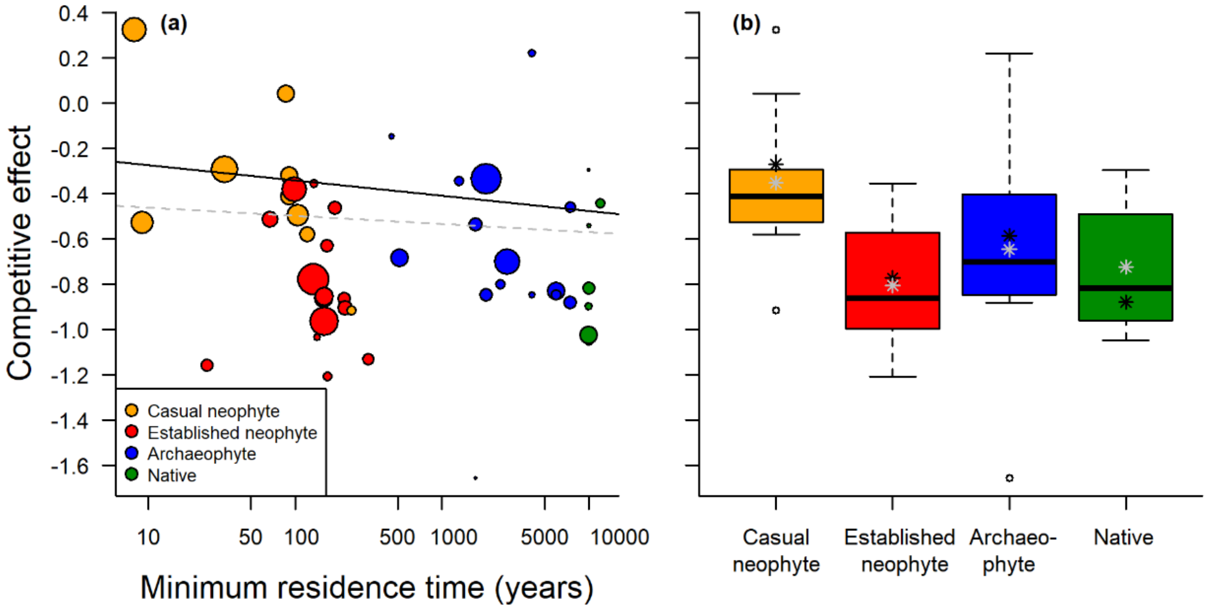

Figure 3.4: Effects of (a) minimum residence time or (b) invasion status on the competitive effect (slope of species-specific regressions). In (a), size of circles shows the square root of the inverse of the standard error of the slope to illustrate weights of data points. The grey dashed line shows the regression line without weighting for comparison. In (b), the asterisks show the mean competitive effect per invasion status group (in black, in grey for the model without weighting).

Competitive effect and range size

When controlling for the highly significant positive effect of MRT on range size ($F_{1,43} = 69.33$, $P < 0.001$, Fig. 3.5a), the slope (per-capita interspecific competitive effect, whereby lower values indicate stronger effects) of the species-specific regressions did not significantly affect range sizes in Germany ($F_{1,43} =$ 0.25, $P = 0.618$, Fig. 3.5b; although, without weighting, there was a marginally significant negative effect, meaning that more competitive species tended to have larger range sizes). The model explained 61.8% of variance in range sizes.

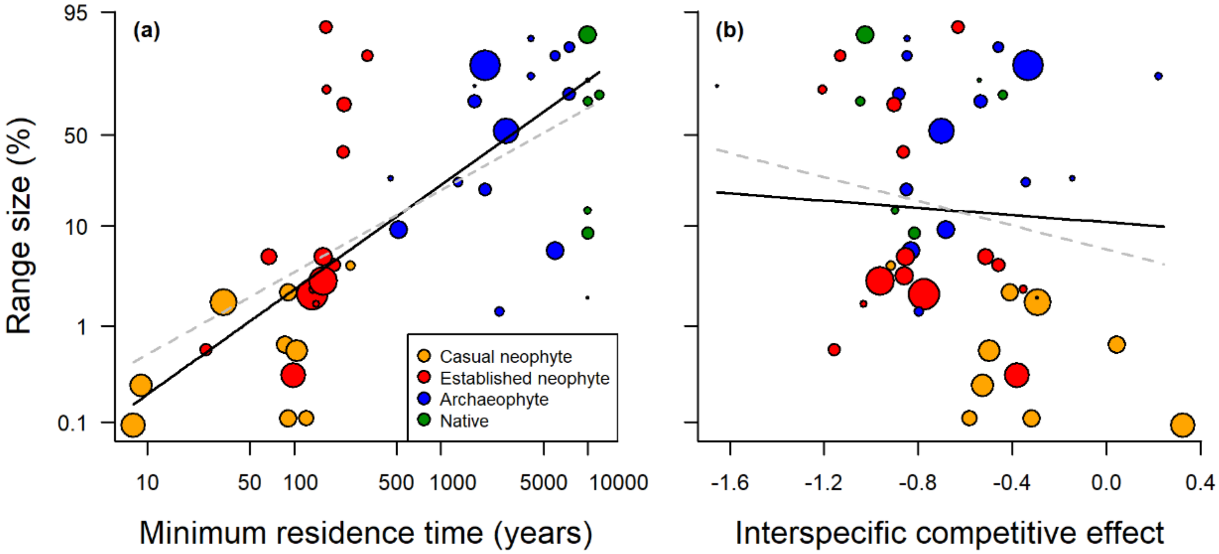

Figure 3.5: Effects of (a) minimum residence time (MRT) and (b) interspecific competitive effect (slope of species-specific regressions) on range size in Germany (model predictions shown with the other explanatory variable fixed at its mean). Size of circles show (a, b) the square root of the inverse of the standard error of the slope to illustrate weights of data points. The grey dashed lines show regression lines without weighting for comparison.

Discussion

Competitive ability in relation to residence time: is there evidence for directional eco-evolutionary changes in competitive ability?

Our results showed that interspecific competitive ability was generally better explained by categorical invasion status compared to continuous residence time. However, total seed production of targets tended to be less affected by competition with neighbours the longer their potential co-existence times in the nutrient-rich soil. This pattern is consistent with the hypothesis of increasing eco-evolutionary experience (Saul *et al.* 2013) of targets leading to higher biotic resistance to newly-introduced species over time. Thereby, total seed production greatly varied in our experiment from no seeds at all to a large reproductive output. Given that seed production serves as the best measure of individual fitness for annual species, this variation in response to competition should thus have direct consequences on native population growth and persistence.

Invasions provide a natural experiment with which we can test if plant-plant interactions can drive evolution (Thorpe *et al.* 2011). Provided that competition is important for fitness and that there is genetic variation in traits related to competitive ability, we may expect adaptation to new competitors over time as a result of natural selection (Lankau 2011). From the perspective of a native plant community (consisting of perennial ruderal grassland species, no Asteraceae), rather than pairwise interactions, Sheppard & Schurr (2019) previously found evidence of increasing biotic resistance to invasion by Asteraceae species of increasing residence times. There are several explanations why, in this study, we only found limited evidence of such an effect. First, context-dependence is clearly important, as highlighted by the contrasting results from the two soil types. Other studies have also found that, in contrast to the competitive effect, competitive response was not consistent with nutrient levels or neighbour identity (Wang *et al.* 2010). Second, eco-evolutionary changes in competitive ability may simply not be relevant enough in contrast to *a priori* differences: even under strong selective forces, there are factors constraining adaptation, such as plasticity, spatial heterogeneity in selective forces, gene flow, lack of additive genetic variance, negative genetic correlations or unfavourable demography and population structure (Strauss *et al.* 2006; Thorpe *et al.* 2011). Third, instead of, or additionally to, adaptive responses of native plant species to novel competitive interactions, other eco-evolutionary changes in biotic interactions may decrease (or increase) invader performance over time (e.g., Lankau *et al.* 2009; Dostál *et al.* 2013; Gruntman *et al.*

2017; Aldorfová *et al.* 2020), potentially confounding effects. Finally, there are some limitations with our multi-species approach, because not all study species are necessarily bound to co-occur, meaning that the neighbour's residence time is only a proxy for length of co-existence time with the native target. To minimise this issue, we used a large set of study species, so that individual species pairs should have limited effects on the results, and selected species from the same habitats and sourced them in the same region as far as was possible. Nevertheless, even when finding a pattern consistent with our hypothesis. such as in the nutrient-rich soil, we cannot prove that it results from evolutionary adaptation over time. For this, we would need to experimentally manipulate the presence of alien species and compare performance of naïve and experienced native genotypes (Strauss *et al.* 2006), which considerably limits the temporal scale that can be studied. Hence, to better understand changes in competitive interactions with increasing length of co-existence time, our approach should be combined with studies on population differences within a species (e.g., Germain *et al.* 2020), whereby to provide conclusive evidence, experiments ideally would be coupled with genetic analyses.

Differences in performance and competitive ability depending on invasion status

The finding that invasion status mostly better explained differences in competitive ability compared to residence time might be because of *a priori* differences between species types due to an introduction bias. Although invasion status can also serve as a proxy for residence time, our results do not support increasing biotic resistance by native species to newly-introduced species as a mechanism, because we did not find directional effects: archaeophytes generally ranked intermediate, with both natives and established neophytes performing best, whereby native targets showed the lowest tolerance to competition from these two groups. Besides introduction bias, these differences might arise from other eco-evolutionary processes that are more specific to certain invasion status groups (e.g., evolution of increased competitive ability hypothesis; Blossey & Nötzold 1995). However, we here did not find support for the often-invoked hypothesis that established alien species have higher competitive ability than natives, which may have several reasons. Recent meta-analyses on pairwise plant interactions between natives and aliens found such higher competitive ability only in particular cases which we did not test here: invasive alien species had greater competitive effects on native species than on non-invasive alien species (Kuebbing & Nuñez 2016) and alien plants were better response competitors than native plants (whereas in line with our results, they did not have larger competitive effects than natives; Golivets & Wallin 2018). In addition, as previously suggested, whether aliens and natives differ may also depend on the types of alien and native species comparisons are made (Vilà & Weiner 2004). For instance, in a multi-species experiment, Zhang & van Kleunen (2019) quantified competitive outcomes between 48 pairs of 17 annual natives and established alien neophytes. They found that common aliens (defined as species that are widespread and locally abundant, only two categories: common or rare) were not more competitive than common natives, but only than rare natives. Furthermore, that aliens themselves are not a uniform category is shown by the substantial differences between casual and established aliens in our study, which may also have important management implications.

Most studies to date did not consider casual neophytes. Indeed, Kuebbing & Nuñez (2016) hypothesised that interaction patterns including casuals may likely differ from established or invasive aliens, but they did not include casuals in their meta-analysis due to the lack of studies available. Casual aliens, as a category, may be more variable in performance than other groups since they have only passed through the transport and introduction stage of the invasion, but not yet through subsequent filters determining establishment and spread (Blackburn *et al.* 2011). This group includes species that are casual because they did not have enough time to establish, which is indicated by the generally lower residence times (see Supporting Information Chapter 3, Fig. S1) and are described by the concept of lag phases (Aikio *et al.* 2010) or invasion debt (Rouget *et al.* 2016). This group, however, also includes species that are not successful enough to establish and hence will disappear again with time, representing failed invasions. Thus, it may not be surprising that this group was found to have the weakest per-capita interspecific competitive effects. One species, *Bidens ferulifolia*, may even facilitate other species, a finding and potential mechanisms that should be further investigated in future studies. The finding that casual neophytes, as a group, produced the highest biomass in intraspecific competition may be because weak competitors generally tolerate intraspecific competition better than interspecific competition (Stoll & Prati 2001). The high biomass production of casual aliens in intraspecific competition also did not lead to higher reproductive output, which could explain why casual neophytes were not yet able to establish self-sustaining populations, even when establishment success did not differ amongst invasion status groups. However, we note that, due to our experimental design that aimed for similar competition pressures amongst species in terms of aboveground biomass production, achieved population densities differed between species due to differing number of seeds sown and additionally differed between replicates due to varying establishment success. Although we corrected for these differences in propagule pressure in our analysis, density-dependence may limit inference of our results. Additionally, since we did not have a true intraspecific competition treatment for the majority of species, the target species may still have had an effect on its neighbours.

Finally, the archaeophytes had the weakest competitive effects after the casual neophytes and an intermediate rank in terms of the native species tolerance to these neighbours. Archaeophytes generally occur in similar habitats to neophytes, but have quite different introduction histories (Chytrý *et al.* 2008). Their weaker competitive ability may also explain, to some extent, why some archaeophytes are threatened nowadays due to the intensifications in land use. Although they are alien species, their threatened status may be unfortunate, since, as segetal weeds, they are valued for their function in increasing biodiversity in agricultural landscapes (Zając *et al.* 2009).

Scaling up: relationships between competitive effect and range size

Invasion success may also result from other mechanisms than interspecific competitive superiority. According to the Parker equation, the impact of an invader is the product of abundance, per-capita competitive effects and range sizes (Parker *et al.* 1999). As several studies have shown before for alien species, residence time strongly influenced range sizes (Pyšek & Jarošík 2005; Williamson *et al.* 2009; Pyšek *et al.* 2015). When testing whether large-scale success is associated with local success, we found that per-capita interspecific competitive effects did not influence range sizes. Although a couple of studies previously found that more competitive alien species reach larger range sizes (Milla *et al.* 2011; Sheppard 2019), there are numerous explanations why this might not be the case. Particularly for species with limited residence time, range sizes may depend more on dispersal ability or human introductions. Furthermore, range sizes may also be influenced by herbivory or pollinators (Svenning *et al.* 2014). We consider it unlikely that variation in the size of potentially suitable habitat may mask effects, as the choice of species was based on similar habitat preference, whereby ruderal and segetal habitats are widespread across Germany. Furthermore, although the species originate from different parts of the world, the species' potentially suitable habitat in Germany, based on climatic niches, is high according to estimates from a previous study (i.e., larger than 90%, calculated using Mahalanobis distances, including all focal species, except four, Sheppard & Schurr 2019).

However, a study on the whole German flora showed that the traits that influence range sizes differed amongst neophytes, archaeophytes, and natives (Knapp & Kühn 2012), in which case we may not expect to find a consistent effect across the whole alien-native species continuum considered here.

Furthermore, the lack of association between competitive ability and range size may also indicate that our species are r-selected, with fast growth and with it spread in non-competitive environments (Dietz & Edwards 2006). This is a strategy frequently observed in annual species of ruderal habitats, such as we studied here. In fact, for an almost identical set of study species, we previously found evidence for intra- or interspecific selection towards ruderality with increasing residence time: annual Asteraceae species with lower seed mass had higher finite rates of increase and, consistent with selection, species with long residence times had low seed mass (Brendel *et al.* 2021).

Conclusions

Using an alien-native species continuum to investigate pairwise competition amongst 47 Asteraceae species, in this study, we found little evidence of directional changes in competitive ability over long timescales. Large-scale invasion success was also not explained by small-scale competitive ability. Further, despite the well justified reasons to argue that human-mediated invasions differ from natural colonisation (Wilson *et al.* 2016), we here did not find differences specifically between established neophytes and natives in terms of intra- and interspecific competitive ability. However, there may be other *a priori* differences resulting from an introduction bias and other mechanisms resulting from different eco-evolutionary processes by which the aliens can utilise their novelty to impact on natives that we did not consider here. Further studies across a broader range of environmental conditions, involving other biotic interactions that may indirectly influence plant-plant interactions, may shed light on the contexts in which eco-evolutionary adaptations to new invaders are a relevant mechanism.

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General Discussion

In Chapter 1, I showed that mismatches in functional traits, specifically seeds mass, rather than mismatches in climate between the area of origin and the introduced area, present important constraints to population growth of alien plants in ruderal and segetal habitats. The strong negative relationship between seed mass and finite rate of increase (λ_0) resulted in directional selection (intra- or interspecific), leading to a convergence of seed mass to low values with increasing residence time. In accordance with this selection for small seeds, also population growth increased with residence time. In Chapter 2, I investigated the role of interspecific competition with native communities for relationships between functional traits and population growth of alien plants. I did not find evidence that native communities build-up competition-mediated biotic resistance over time and thereby limit population growth of alien plants. Instead, seed mass mediated a strong trade-off between population growth of alien plants in low vs. high competition. Particularly, in line with results of Chapter 1, small seeds were beneficial for population growth in low-competition ruderal/segetal habitats, while in high-competition habitats of semi-natural communities, high seed mass led to an increase in population growth. In Chapter 3, I tested whether the response of native target plants to competition with alien plants depends on residence time and whether competitive effects differ between invasion status groups. I found only little evidence for a higher tolerance of native target individuals to neighbouring alien plants with increasing residence time, which is in line with Chapter 2 and the lack of a temporal increase in competition-mediated biotic resistance. Both established neophytes and natives showed a similarly high interspecific competitive ability and species' range sizes were not influenced by per-capita competitive effects. This might indicate that other mechanisms than interspecific competitive superiority, maybe adaptations to low-competition habitats, are more important for range sizes and determining invasion success.

In the following paragraphs, I will link these findings by putting them in a broader context and discuss their implications for ecology and evolution of alien plants. I will furthermore give some suggestions for invasive species management and finish off with an agenda for future research in plant invasion ecology.

In order to understand and predict what determines invasion success, it is crucial to study interactions between abiotic constraints and biotic resistance (Byun *et al.* 2015) and their effects on demographic processes (Von Holle *et al.* 2003), for instance the ability to increase in population growth when rare (Lodge 1993). Additionally, the study of long-term patterns of invasions, where historical range extensions of native species should be treated in the same context as the introduction of species into their new ranges, can gain further insights into the various components that lead to invasion success (Von Holle *et al.* 2003). This is because abiotic constraints and biotic resistance may act synergistically and their effects may also vary depending on the point in time during the invasion process (D'Antonio 1993). In my research, I followed these theoretical considerations by using an alien-native species continuum (including neophytes, archaeophytes, and natives) and focussing on demographic processes across habitats that vary from low intraspecific to high interspecific competition to reflect the interplay between abiotic and biotic constraints. I demonstrated that long-term population dynamics of alien plants are strongly shaped by environmental selection of functional traits that increase fitness in habitats of low intraspecific competition and the associated trait-mediated trade-offs in competitive ability when introduced to habitats of high interspecific competition.

Abiotic constraints to population growth of alien plants can arise from mismatches in climate between the area of origin and the introduced area (Braasch *et al.* 2019). Based on the assumption that invasive species conserve their climatic niche after being introduced (Liu *et al.* 2020), any deviance from the climate in the area of origin should thus result in a performance decrease, respectively, more similar conditions to the climate in the area of origin should lead to a performance increase (see Colautti *et al.* 2009; Colautti & Barrett 2013). However, my results showed that in lieu of climatic distances in temperature, mismatches in functional traits determine population growth under local climatic conditions in the introduced area. In other words, specific functional traits, low seed mass in particular, led to highest population growth. On a broader scale, this might reflect a mismatch between the distribution of species and their climatic niche optima (Carscadden *et al.* 2020). In this context, a discrepancy between species distribution (based on climatic conditions) and their performance and may well be the result of functional traits allowing them to persist even in sub-optimal climatic conditions (Lian *et al.* 2022). At least, this was found for tree species with a wide geographic distribution (Lian *et al.* 2022). In the case of my study, the possession of functional traits that the introduced (ruderal/segetal) habitats select for, might have led to a stronger adaptive advantage of alien plants than originating from a similar climate.

The performance of invasive species is strongly determined by functional traits that directly relate to fitness (Drenovsky *et al.* 2012). Furthermore, if the possession of particular functional traits results in a fitness advantage caused by novel selection pressures in the introduced range, this should lead to evolution of traits (Keller & Taylor 2008). Indeed, the strong relationship between seed mass and intrinsic rate of increase in my study revealed such a trait evolution. Particularly, with increasing residence time, seed mass of alien plants converged to values that increased their population growth under local environmental conditions in the introduced range. Consequently, this directional selection (either within or between species) led to an increase of population growth with residence time. Despite this clear trait selection as a mechanism for invasion success shown here, some authors did not find differences in functional traits along the invasion continuum (from naturalized to invasive alien plants) to be dependent on residence time, covering a range of residence times from few decades to approx. 200 years (Gallagher *et al.* 2015). However, to detect such a link between adaptation through trait evolution and invasion success as in my study, the timescale covered needs to be sufficiently long enough (from decades to millennia) and selection pressures need to be strong enough. Moreover, temporal variation may occur in trait-environment relationships of alien plants (Milanović *et al.* 2020), in traits determining invasiveness in native communities (Catford *et al.* 2019), and in selection pressures affecting growth and fitness of alien plants (Gong *et al.* 2022). Nevertheless, only a few studies, in addition to the present one, investigated how relationships between functional traits and alien plant fitness are determined by changes in selection pressures that follow the invasion process.

The dynamics of invasion are strongly influenced by biotic interactions between alien and native species (Hui *et al.* 2020). In this context, native species can be expected to gain eco-evolutionary experience to the presence of the invader and thereby increase their biotic resistance over time (Lankau *et al.* 2009; Saul *et al.* 2013). To detect such temporal dynamics, it is crucial to go a step further than testing biotic resistance of one specific community that only presents a snapshot in time and thereby a limitation to infer invasion mechanisms (Ernst *et al.* 2022). Studies that investigate the performance of alien species in a novel/non-analogue community (i.e., a novel combination of species that do not currently co-occur) compared to an analogue community should thus advance the understanding of biotic resistance of native communities (Renault *et al.* 2022). In my study, I adapted this theoretical approach and comparted fitness of alien plants in a community of varying length in co-existence times with a community that never co-existed with the alien plants and is thus naïve to their presence. This allowed me to dissect competition-mediated biotic resistance of native communities in relation to their co-evolutionary history with alien plants from inherent competitive ability of alien plants determining their success in native communities. Instead of increased biotic resistance of native communities over time, I found a trait-mediated trade-off in competitive ability of alien plants to determine their success in native communities. This finding is linked the results of Guo *et al.* (2022a) who showed that differences in adaptation strategies between ruderal vs. competitor depend on the stage of invasion. Specifically, such changing roles of adaptation strategies can occur due to differential selection regimes when alien species spread from disturbed sites of initial establishment, where a ruderal strategy might be favoured (Alpert *et al.* 2000; Dietz & Edwards 2006) into more natural habitats that select for higher competitive abilities (Duyck *et al.* 2007; Tayeh *et al.* 2015). Indeed, in my study, ruderal/segetal habitats of low intraspecific competition, often being the habitats of first colonization (McNeely 2005), selected for low seed mass in alien plants, whereas in semi-natural grasslands of high interspecific competition, a high seed mass increased population growth. This trade-off in life-history strategies may not only be apparent within a system of annual Asteraceae, but might also be applicable to other systems and across different life-forms. For instance, in novel immature ecosystems of urban areas (e.g., ruderal communities on vacant land), annual non-native herbs that reproduce by seeds benefitted of reduced competition by native species, whereas in novel mature ecosystems (e.g., emerging urban forests), highest establishment was found for non-native perennial species that exclusively reproduce clonally (Knapp *et al.* 2022). Furthermore, the seed-mass-mediated trade-off in competitive ability found in my study is also in accordance with globally consistent patterns that traits generate trade-offs between performance with competition vs. performance without competition (Kunstler *et al.* 2016). Moreover, such a trait-based differentiation in competitive ability, especially given the strong links between seed mass and demographic rates (Rees *et al.* 2001), also shown in my study, is suggested to stabilize species coexistence in native plant communities (Turnbull *et al.* 2004; Maron *et al.* 2021) and thus most likely also between native and alien plants.

My findings clearly show a strong role of competition as a mechanism for invasion success in terms of population growth but not in terms of range sizes. Hence, further determinants that are involved in and affect species interactions need to be considered when explaining limits to population growth and spread of alien plants. Although alien plants often appear to be more competitive than native plants (Vilà & Weiner 2004; Kuebbing & Nuñez 2016; Golivets & Wallin 2018), I did not find that established neophytes exert greater interspecific competition than natives. This is in line with results of Zhang & van Kleunen (2019) who showed that common alien plants are more competitive than rare natives but not than common natives. Despite that two out of my seven native study species appear on the list of endangered native species in Germany, namely *Hypochaeris glabra* and *Pulicaria vulgaris* (Metzing *et al.* 2018), they performed well in the experiments. Furthermore, in my study, a stronger tolerance of native species to competition of alien species with longer residence times, suggesting an increase in eco-evolutionary experience, was only present in nutrient-rich conditions and not at low nutrient levels. This might well be the result of shifts in competitive interactions due to additional nutrients, as increased resource availability can lead to enhanced competitive ability of invasive plants relative to native plants (Vasquez *et al.* 2008; He *et al.* 2012). Specifically, a pattern where competitive effects of alien plants on native plants weaken with residence time can occur, if species with shorter residence times (i.e., neophytes) exploit additional resources more efficiently (e.g., due to rapid nutrient uptake capacity; see Vasquez *et al.* 2008) and thus exert stronger competition compared to species with longer residence times (i.e., archaeophytes and natives). However, different nutrient treatments do not necessarily lead to differences in competitive outcomes between native and alien plants (Wandrag *et al.* 2023). Wandrag *et al.* (2023) suggested that niche partitioning can override interspecific competition in determining the distribution of alien and native plants. Indeed, in my study, interspecific competitive abilities did not explain range sizes of alien and native plants in Germany. In contrast, for a larger set of Asteraceae species in Germany (including neophytes, archaeophytes, and natives), differences in competitiveness (based on the C-coordinate of Grimes's CSR strategies; see Grime 1974, 1977) influenced range sizes (Sheppard & Schurr 2019). However, Vicente *et al.* (2014) found that environmental conditions and dispersal limitations can override effects of Grimes's CSR strategies and residence time in determining regional patterns of alien plant invasions. Nevertheless, results of a recent meta-analysis by Sheth *et al.* (2020) revealed only limited ability to infer the relative importance of dispersal ability and environmental heterogeneity as determinants of geographic range sizes in plants. For a better understanding of range expansions in plants, they suggested, like in my study, to merge approaches from macroecology and evolutionary ecology.

Last but not least, functional traits that are related to competitive abilities of alien plants are also linked to their dispersal abilities. In particular, small-seeded species are good colonizers and typically disperse over long distances, while large-seeded species are more limited in their dispersal but can reach high local abundances as they are good competitors (Carboni *et al.* 2018; Palma *et al.* 2021). This link is crucial for understanding dynamics of plant invasions as dispersal together with population growth determines the rate of spread (Skellam 1951) that is furthermore key to predicting and managing potential impacts of invasions (With 2002; O'Reilly-Nugent *et al.* 2016). In my study, the selection for small seeds with increasing residence time, leading to increased population growth under local environmental conditions, in combination with the strong seed-mass-mediated trade-off in competitive ability, might help to explain limits to population growth and spread of alien plants. For instance, recently introduced alien plants that possess large seeds are limited in population growth and dispersal, but might be competitive enough to establish in more natural habitats outside their first colonization sites (e.g., ruderal/segetal habitats). In contrast, species with longer residence times that experienced selection for small seeds, increased their population growth and might be better dispersed over long distances, but are limited in establishing and persisting in natural habitats due to their low competitive ability. Hence, alien plants of highest management concern that may become the most critical invaders are those species that are able to escape the seed-mass mediated trade-off in competitive ability. Indeed, Molina-Montenegro *et al.* (2012) suggest trait combinations that break the trade-off between dispersal and competitive ability may allow species to successfully establish in new communities (i.e., "the ideal weed"; *sensu* Baker 1974). A mechanism by which alien plants can escape the seed-mass mediated trade-off in competitive ability is animal dispersal. Intriguingly, epizoochorous dispersal traits were found to be positively associated with global plant naturalization (Moyano *et al.* 2022). Furthermore, the combination of greater competitive abilities with enhanced dispersal abilities is a strong determinant of invasion success in plant communities (Vedder *et al.* 2021). Thus, management practices should particularly focus on avoiding the introduction of species that display such characteristics (Vedder *et al.* 2021). Moreover, as my research showed, such an active management approach is especially important, given that an increase in biotic resistance of native communities over time may not always present a desired invasion barrier, not even over long timescales. In addition to animals, also humans can act as a dispersal agent of alien plant propagules by increased foot and motor traffic that facilitates population expansion (Lemke *et al.* 2019). This becomes especially problematic at sites with high tourism within protected areas (Aththanayaka *et al.* 2023) or in protected areas embedded in agricultural landscapes (Boscutti *et al.* 2018), as agricultural production practices can lead to unintentional introduction an spread of invasive alien plants (Brundu *et al.* 2011). Additionally, in agricultural landscapes, human activities to combat biodiversity loss, for instance the establishment of hedgerows, act as a selective filter for animal-dispersed alien plants (Boscutti *et al.* 2018). In the light of my results, this underlines the importance of integrating invasive species management into the design and implementation of biodiversity measures and related ecosystem services (Gallardo *et al.* 2019).

For future research in plant invasion ecology, it is of utmost importance to gain deeper insights into how eco-evolutionary responses of native communities to alien plants and performance of alien plants in native communities are determined by residence time. Specifically, it is crucial to further disentangle whether eco-evolutionary processes are driven by changes of the invaders, changes of the native communities or a combination of both. In other words, how does residence time shape the relative importance of changes in inherent characteristics of alien plants (i.e., due to trait selection) to changes in native communities (i.e., due to a gain in eco-evolutionary experience). In this context, the role of intra- vs.- interspecific selection for both alien plants and native community species needs to be more deeply investigated. Particularly, it is necessary to understand to which degree alien plants adapt to novel abiotic and biotic conditions as a result of selection and become invasive compared to alien plants that fail to adapt and depend on repeated introductions for their persistence. From the perspective of native communities, it is necessary to understand whether a gain in eco-evolutionary experience is related to different adaptation abilities between species, for instance, via selection of species that are able to withstand allelochemicals of invaders (Callaway *et al.* 2005) or within species, for instance, due to a continuous exposure of populations to allelochemicals of invaders (Lankau 2012).

In order to answer the above-mentioned research questions, I suggest that future experiments should include the following components. A reciprocal experiment in the native and introduced range of invasive species allows to investigate interactions with their new vs. old neighbours, respectively, species that are native to communities from the origin and the introduced range of invasive species. In this way, one can compare if co-existence time similarly determines population growth in communities of the native and introduced range of invaders. In this context, a reciprocal transplantation of native community species is also required to disentangle effects of abiotic factors from biotic interactions. Furthermore, the re-introduction of genotypes of invaders from the new range to communities of their native range allows to test, if the absence time from the native range determines interspecific interactions in the same manner as residence time in introduced range. This should be based on a multi-species approach to cover a continuum of populations with increasing residence/absence times, ideally across the same plant family and life history strategy (e.g., annual). Particularly, one would suggest that the longer absence time from the native range, the more novel the re-introduced population appears to their old neighbours. Thus, the novelty might result in increased population growth due to reduced competition by the old neighbours. In the same way, one would suggest that the longer the residence time in the introduced range, the less novel the invader population appears to their new neighbours, leading to a decrease in population growth due to enhanced competition by the new neighbours. Hence, one might be able to assess a general rule for biotic interactions depending on residence time, respectively, co-existence time between invaders and native communities based on the loss (old neighbours) or gain (new neighbours) in eco-evolutionary experience. The reciprocal approach on population level should furthermore be complemented by a comparison of specific species pairs of casual and established neophytes (in the introduced range) for a given residence/absence time. This will help to understand changes in the relative importance of inherent characteristics of invaders to eco-evolutionary experience of communities, respectively, the degree to which selection in the new range is determining invasion success.

In addition to a reciprocal component of experiments, future research should also focus on native communities in the introduced range that follow the invasion route. In this context, invasive species can lead to rapid evolutionary changes of native species, for example, *Pseudechis porphyriacus* (black snakes) native to Australia evolved resistance to toxins of the introduced species *Bufo marinus* (cane toad) within 67 years (Phillips & Shine 2006). Particularly, it is necessary to investigate differences and similarities in community compositions between the leading edge of an invasion front and the core range. If, for instance, a specific native species is similarly abundant both at the leading edge and the core range, this might indicate that this particular species is able to adapt to the presence of the invader. In order to determine the adaptation potential due to intraspecific selection, one should thus compare the responses of genotypes of such a native species from the leading edge and the core range to invader presence. To further delineate the role of interspecific selection in native communities due to invader presence, the response of a species that is similarly abundant at the leading edge and the core range should be compared to the response of a species that is abundant at the leading edge but absent from or reduced in abundance at the core range.

Lastly, future research should also focus on other aspects and dimensions of biotic resistance of native communities and their interactions with residence time. It seems very likely that, for instance, increased herbivory due to a loss of the novelty of the invader acts over different time scales and is triggered by a different strength of selection pressures (e.g., abundance of invaders) than effects of soil pathogens and also competition-induced biotic resistance in plant-plant interactions studied here. By combining experimental macroecology with approaches of functional and community ecology, my study strongly advanced the understanding of mechanisms of limits to population growth and spread of invaders and provides a fundamental basis for the agenda of future research in invasion ecology.

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Supporting Information Chapter 1

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

Alien-native species continuum

Table S1: The 46 Asteraceae species (nomenclature according to the Plant List, http://www.theplantlist.org, Kalwij 2012), the number of mesocosms per population (seeds from wild populations and botanical gardens as indicated by city), the median (°C) and the amplitude (K) for the temperature variables (T_{max} corresponds to bio5: maximum temperature of the warmest month, T_{min} corresponds to bio6: minimum temperature of the coldest month in the WorldClim dataset; Hijmans *et al.* 2005) of the species' native range distribution, and species- specific references for the distribution data from the Global Biodiversity Information Facility database (GBIF, http://gbif.org).

	Mesocosms$_{\text{population}}$	**Median (amplitude)**		
Species	**pop.1 / pop.2 / pop.3**	**T_{max}**	**T_{min}**	**GBIF citation**
Anthemis arvensis L.	2_{wild} / 2_{wild} / 2*	28.0 (12.4)	1.5 (10.5)	GBIF.org (23 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.xbtcqz
Anthemis cotula L.	$2_{\text{Berlin-Dahlem}}$ / $2_{\text{Hohenheim}}$ / 2_{Konstanz}	28.7 (12.0)	1.0 (10.4)	GBIF.org (23 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.f7japw
Artemisia annua L.	2_{Bonn} / 2_{Dresden} / 2_{Konstanz}	30.0 (18.1)	-1.4 (39.6)	GBIF.org (20 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.r2rvc6
Bidens ferulifolia (Jacq.) Sweet	2_{Bonn} / 2_{Dresden} / $2_{\text{Hohenheim}}$	29.4 (12.0)	2.8 (15.5)	GBIF.org (05 June 2020) BIF Occurrence Download https://doi.org/10.15468/dl.5awrn4
Bidens pilosa L.	4_{Dresden} / $2_{\text{Hohenheim}}$	29.6 (15.8)	11.5 (20.8)	GBIF.org (21 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.tzyqus
Calendula arvensis M.Bieb.	2_{wild} / 1_{wild} / 2_{wild}	30.7 (11.2)	3.8 (8.9)	GBIF.org (26 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.dhrflc
Calendula officinalis L.	2_{wild} / 2_{wild} / 2_{wild}	28.0 (9.5)	2.1 (9.0)	GBIF.org (26 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.7ugytl
Callistephus chinensis (L.) Nees	1_{wild} / 2_{Dresden} / $2_{\text{Tuebingen}}$	28.3 (15.5)	-7.4 (22.1)	GBIF.org (21 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.zt1g1v

Table S1: (Continued).

	Mesocosms$_{\text{population}}$	**Median (amplitude)**		
Species	**pop.1 / pop.2 / pop.3**	**T_{max}**	**T_{min}**	**GBIF citation**
Carthamus lanatus L.	4_{Dresden}	28.0 (11.1)	1.2 (9.6)	GBIF.org (22 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.yocvtz
Carthamus tinctorius L.	2_{Bonn} / 4_{Halle}	33.3 (11.9)	-4.4 (14.1)	GBIF.org (04 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.rqcdfg
Centaurea diffusa Lam.	2_{wild} / 2_{wild} / 2_{wild}	27.7 (10.1)	-2.0 (9.9)	GBIF.org (22 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.hcvhzl
Centaurea solstitialis L.	$2_{\text{Berlin-Dahlem}}$ / 4_{Dresden}	26.8 (10.9)	0.3 (10.7)	GBIF.org (25 March 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.pg5ne2
Cosmos bipinnatus Cav.	2_{wild} / 2_{wild} / 2_{wild}	27.1 (12.2)	3.4 (13.4)	GBIF.org (02 April 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.dp3yh0
Cota austriaca (Jacq.) Sch.Bip.	$3_{\text{Hohenheim}}$ / 3_{Potsdam}	25.4 (8.5)	-4.9 (11.3)	GBIF.org (04 June 2020) GBIF Occurrence Download https://doi.org/10.15468/dl.tr2qa2
Crepis capillaris (L.) Wallr.	2_{wild} / 2_{wild} / 2_{wild}	29.4 (12.4)	2.6 (10.5)	GBIF.org (28 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.dmtonh
Crepis pulchra L.	4_{Dresden} / 2_{Konstanz}	24.3 (5.8)	-1.3 (6.1)	GBIF.org (28 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.tlhp2j
Crepis setosa Haller f.	6_{Dresden}	24.5 (8.0)	0.0 (7.5)	GBIF.org (03 April 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.sxoy9g
Crepis tectorum L.	6**	21.7 (4.4)	-3.2 (6.3)	GBIF.org (28 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.fhf94p
Cyanus segetum Hill.	4_{wild} / 2_{wild} / 2_{wild}	27.4 (8.1)	-0.4 (8.8)	GBIF.org (28 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.ppethy
Dittrichia graveolens (L.) Greuter	2_{wild} / 2_{wild} / 2_{wild}	26.1 (11.8)	1.1 (11.2)	GBIF.org (15 April 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.9p2bdf
Erigeron annuus (L.) Pers.	2_{wild} / 2_{wild} / 2_{wild}	28.4 (10.9)	-8.5 (20.0)	GBIF.org (17 April 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.sx7vm3
Erigeron canadensis L.	2_{wild} / 2_{wild} / 2_{wild}	29.5 (13.7)	-5.4 (39.0)	GBIF.org (15 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.axi7di
Erigeron sumatrensis Retz.	6_{wild}	28.7 (17.5)	14.0 (18.4)	GBIF.org (15 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.ap1nlm
Galinsoga parviflora Cav.	2_{wild} / 2_{wild} / 2_{wild}	27.5 (14.5)	4.7 (19.5)	GBIF.org (16 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.h6hog3
Galinsoga quadriradiata Ruiz & Pav.	2_{wild} / 2_{wild} / 2_{wild}	26.5 (17.0)	9.0 (17.5)	GBIF.org (16 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.7cpoeo

Table S1: (Continued).

	Mesocosms$_{population}$	**Median (amplitude)**		
Species	**pop.1 / pop.2 / pop.3**	**T_{max}**	**T_{min}**	**GBIF citation**
Glebionis coronaria (L.) Cass. ex Spach	2_{wild} / 2_{wild} / 2_{wild}	28.9 (12.9)	4.8 (9.8)	GBIF.org (15 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.fte8gxn
Glebionis segetum (L.) Fourr.	2_{wild} / 2_{wild} / $2_{Dresden}$	29.3 (12.1)	4.2 (8.2)	GBIF.org (29 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.fgclxf
Gnaphalium uliginosum L.	4_{wild} / 2_{wild} / 2_{wild}	22.0 (5.8)	-2.5 (8.3)	GBIF.org (29 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.dreift
Guizotia abyssinica (L.f.) Cass.	2_{Bonn} / $2_{Dresden}$ / $2_{Hohenheim}$	29.0 (6.6)	10.3 (5.7)	GBIF.org (17 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.lxff46
Helminthotheca echioides (L.) Holub	2_{wild} / 2_{wild} / 2_{wild}	28.8 (11.6)	3.6 (9.3)	GBIF.org (29 September 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.kyzjcx
Hypochaeris glabra L.	$6_{Dresden}$	22.8 (5.6)	-2.3 (7.4)	GBIF.org (04 October 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.hc25si
Iva xanthiifolia Nutt.	$2_{Dresden}$	27.9 (10.3)	-11.1 (17.4)	GBIF.org (21 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.w7rwrq
Lactuca serriola L.	2_{wild} / 2_{wild} / 2_{wild}	28.8 (11.6)	2.2 (11.9)	GBIF.org (05 October 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.zjekdc
Lactuca virosa Habl.	$2_{Hohenheim}$	27.2 (8.9)	0.6 (10.3)	GBIF.org (05 October 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.6315gi
Lapsana communis L.	2_{wild} / 2_{wild} / 2_{wild}	22.2 (6.1)	-2.2 (8.6)	GBIF.org (05 October 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.mlkyra
Matricaria chamomilla L.	2_{wild} / 2_{wild} / 2_{wild}	29.5 (11.4)	2.4 (11.6)	GBIF.org (06 October 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.ayqzzo
Matricaria discoidea DC.	2_{wild} / 2_{wild} / 2_{wild}	26.0 (18.0)	-9.1 (35.2)	GBIF.org (23 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.kxpek6
Pulicaria vulgaris Gaertn.	2_{wild} / 2_{wild} / 2_{wild}	23.4 (5.3)	-1.3 (7.2)	GBIF.org (27 December 2016) GBIF Occurrence Download https://doi.org/10.15468/dl.ljkcth
Rudbeckia hirta L.	2_{wild} / $2_{Dresden}$ / $2_{Hohenheim}$	28.8 (12.8)	-8.6 (28.8)	GBIF.org (24 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.dhlzy5
Senecio viscosus L.	2_{wild} / 2_{wild}	21.8 (5.6)	-2.9 (7.7)	GBIF.org (09 January 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.uzuqah
Senecio vulgaris L.	2_{wild} / 2_{wild} / 2_{wild}	29.1 (11.9)	2.4 (9.9)	GBIF.org (09 January 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.mhuh2n
Sigesbeckia serrata DC.	$6_{Dresden}$	26.9 (11.6)	1.3 (14.1)	GBIF.org (27 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.d2zuwv
Silybum marianum (L.) Gaertn.	2_{Bonn} / $2_{Rostock}$	28.6 (13.0)	1.8 (11.3)	GBIF.org (27 May 2019) GBIF Occurrence Download https://doi.org/10.15468/dl.nmfwif

Table S1: (Continued).

Species	**Mesocosms$_{population}$** **pop.1 / pop.2 / pop.3**	**Median (amplitude)** **T$_{max}$**	 **T$_{min}$**	**GBIF citation**
Sonchus asper (L.) Hill	2_{wild} / 2_{wild} / 2_{wild}	29.1 (12.1)	3.2 (10.8)	GBIF.org (09 January 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.ywvikx
Sonchus oleraceus (L.) L.	2_{wild} / 2_{wild} / 2_{wild}	28.7 (11.9)	2.9 (9.8)	GBIF.org (09 January 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.xdiuav
Tripleurospermum inodorum (L.) Sch.Bip.	3_{wild} / 2_{wild} / 2_{wild}	26.5 (8.0)	0.7 (11.0)	GBIF.org (10 January 2017) GBIF Occurrence Download https://doi.org/10.15468/dl.mpdkus

* seeds received from commercial seed supplier Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany) in 2015

** seed source from botanical garden in Tuebingen and grown for one generation at Hohenheim

(both were treated as botanical garden populations and therefore removed for control analyses)

Experimental design

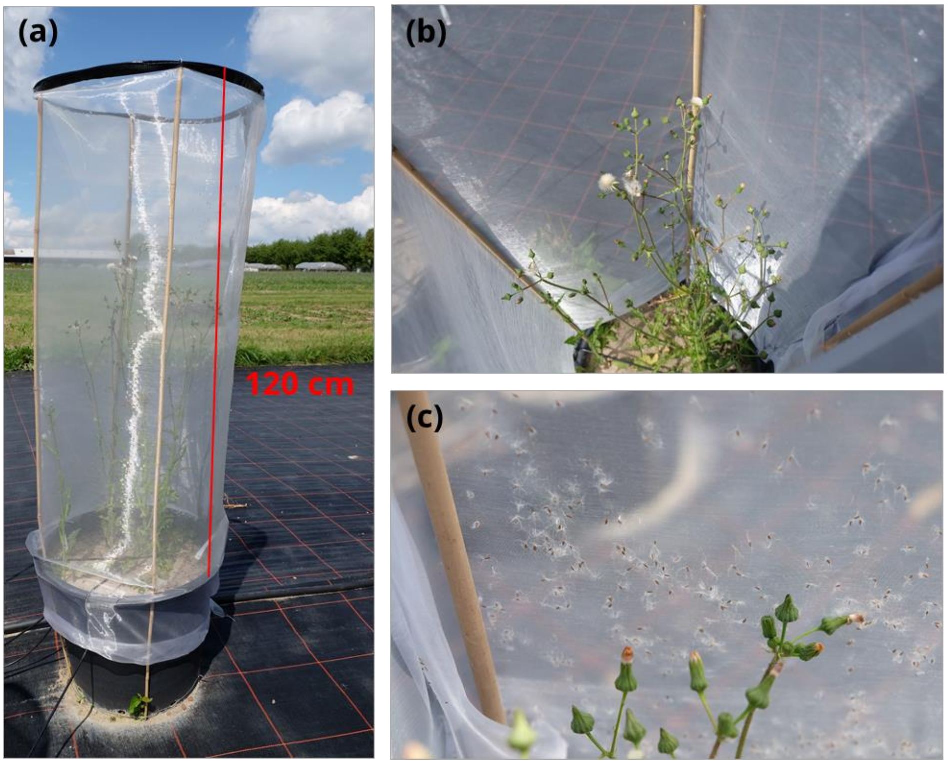

Figure S1: (a) Example of an open-top organza fabric, surrounding a *Sonchus asper* mesocosm, which retains the developed seeds (b and c).
Photo credits: (a-c) – ©Huw Cooksley

Climatic distance

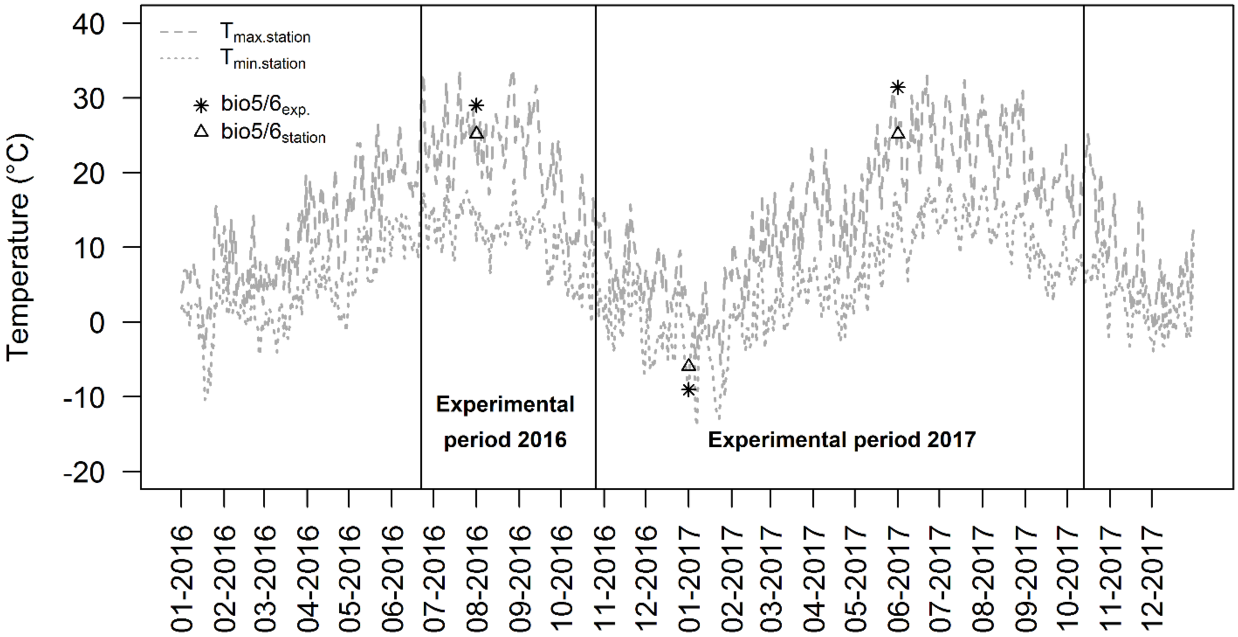

Figure S2: Maximum (T_{max}) and minimum (T_{min}) daily temperature values (from January 1st, 2016, to December 31st, 2017, measured at 2 m above the ground) at the weather station in proximity to the common garden facility (i.e., "local" conditions). The experimental period in 2016 (first day of sowing seeds on June 22nd until last day of assessment on October 26th) and in 2017 (October 27th, 2016, until last day of assessment on October 13th, 2017) are additionally indicated. The average maximum temperature of the warmest month (bio5) in 2016 was 25.17 °C (in August) measured at the weather station (triangle) and 29.02 °C after correcting for the experimental effect (adding the average difference between data-logger measurements in the field and mesocosm; asterisk). In 2017, the corresponding bio6 variable (average minimum temperature of the coldest month) was -5.92 °C and -9.03 °C in January, respectively. The bio5 variable in 2017 was 25.13 °C and 31.42 °C in June, respectively.

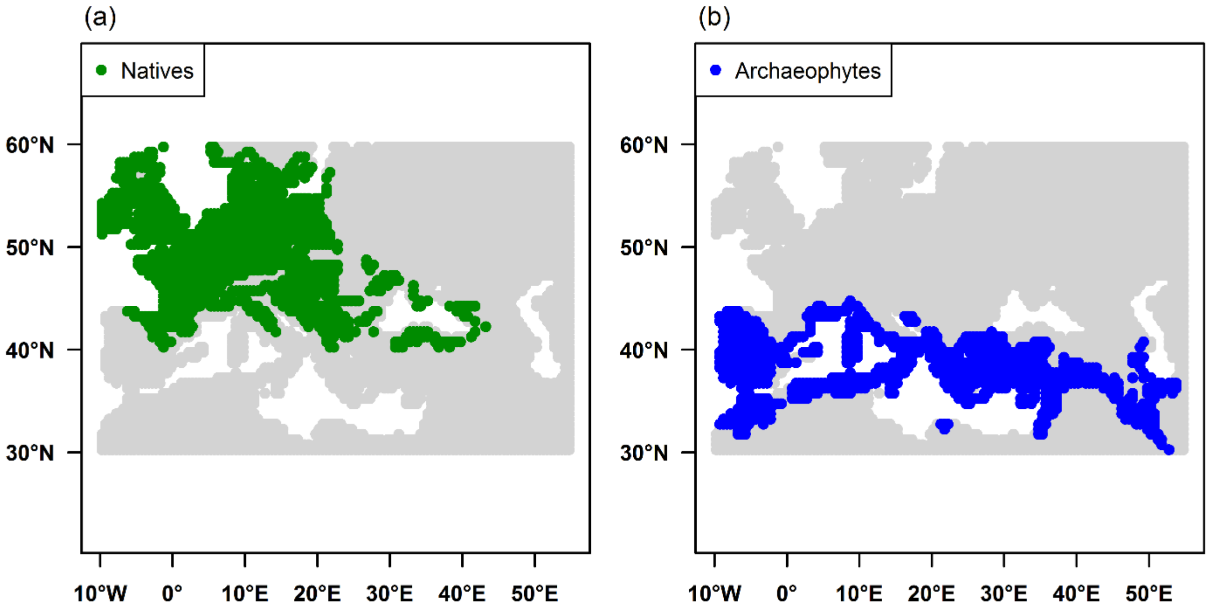

Figure S3: Native ranges of the (a) native and (b) archaeophyte Asteraceae study species. The native ranges are based on the Köppen-Geiger climate classification (Kottek *et al.* 2006). (a) For natives, we used the classification “Cfb” (warm temperate, fully humid, warm summer) within a defined spatial extent (latitudes between 30°N and 60°N and longitudes between 10°W and 55°E) to cover temperate Central Europe. (b) 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) to cover the Mediterranean basin and the Fertile Crescent.

Appendix S1: Functional trait measurements

The average seed mass was determined at population-level before the start of the experiment by weighing 6 batches of 20 seeds with a high-precision balance (accuracy of 10^{-4} g). In late June 2016, we transplanted six seedlings (previously grown in the same soil as used for the mesocosms in germination trays for six weeks in greenhouses next to the common garden facility) of each study species into two empty mesocosms to measure maximum height and specific leaf area (SLA) at population-level. Whenever feasible, we evenly assigned the populations to the six individual plants (i.e., three populations leading to two individuals each per mesocosm). At the end of October 2016, we measured the height of 531 transplanted individuals (that survived from initially 534 individuals). During August 2016, we collected two leaves from each individual with at least four fully developed leaves (516 individuals). All leaves were scanned and their area was measured using ImageJ2 (Rueden *et al.* 2017). Afterwards, the leaves were dried (at 70°C for 72 hours) and weighed to calculate SLA (mm^2/mg) at population-level. Due to low germination rates, we could only measure five individuals for *Cyanus segetum* per mesocosm and did not have any transplanted individuals to measure for *Crepis tectorum*. For the latter species, we thus used the individuals developed from seeds. We sampled two leaves in three random mesocosms and measured the tallest individual in each mesocosm. For 16 populations (of 13 species) used to assess demographic performance, no matching transplants were available. We thus used the corresponding species-level average of SLA and maximum height.

Results of analyses for effects of climatic distance

Table S2: 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}; or minimum temperature of the coldest month: local temperature in the common garden minus median temperature in the native range, ΔT_{min}), minimum residence time (MRT), and T_{max} or T_{min} amplitude on establishment (E_0), fecundity (F_0), and population growth rate in the second year (λ_1). We compared eight models (using the Deviance Information Criterion, DIC): with or without linear effects of ΔT (quadratic relationships with apex either fixed at $\Delta T = 0$ K or flexible), with or without interactions between the ΔT terms and MRT, and with or without MRT.

Demographic performance measure	Climatic distance	MRT	ΔT-MRT interaction	DIC	ΔDIC	Mean R² (95% credible interval)		Mean phylogenetic signal (95% credible interval)	Sample size (species, populations, mesocosms)
						marginal	conditional	Pagel's lambda	
Establishment E_0	yes (flexible apex)	yes	yes	6434.15	0.75	0.21 (0.03, 0.35)	0.72 (0.56, 0.88)	0.24 (0.0005, 0.62)	46, 115, 264
		yes	no	6434.09	0.69	0.16 (0.02, 0.35)	0.70 (0.54, 0.88)	0.23 (0.0007, 0.61)	
	yes (apex = 0)	yes	yes	6433.78	0.38	0.19 (0.01, 0.36)	0.70 (0.52, 0.86)	0.23 (0.0005, 0.61)	
		yes	no	6433.87	0.47	0.14 (< 0.01, 0.32)	0.70 (0.52, 0.87)	0.23 (0.0005, 0.60)	
	yes (flexible apex)	no	no	6434.01	0.61	0.11 (< 0.01, 0.25)	0.70 (0.52, 0.86)	0.29 (0.0006, 0.62)	
	yes (apex = 0)	no	no	6433.90	0.50	0.10 (< 0.01, 0.24)	0.69 (0.52, 0.87)	0.29 (0.0002, 0.64)	
	no	yes	no	6433.69	0.29	0.09 (< 0.01, 0.24)	0.68 (0.49, 0.86)	0.26 (0.0005, 0.61)	
	no	no	no	6433.40	0.00	0.03 (< 0.01, 0.12)	0.69 (0.49, 0.86)	0.34 (0.0007, 0.64)	

Table S2: (Continued).

Demographic performance measure	Climatic distance	MRT	ΔT-MRT interaction	DIC	ΔDIC	Mean R^2 (95% credible interval)		Mean phylogenetic signal (95% credible interval)	Sample size (species, populations, mesocosms)
						marginal	conditional	Pagel's lambda	
Fecundity F_0	yes (flexible apex)	yes	yes	939.61	1.49	0.25 (0.08, 0.42)	0.70 (0.58, 0.82)	0.44 (0.13, 0.70)	39, 101, 224
		yes	no	939.53	1.41	0.19 (0.02, 0.34)	0.69 (0.55, 0.81)	0.43 (0.001, 0.64)	
	yes (apex = 0)	yes	yes	938.46	0.34	0.17 (0.03, 0.31)	0.71 (0.59, 0.83)	0.49 (0.27, 0.72)	
		yes	no	938.82	0.70	0.13 (0.01, 0.26)	0.70 (0.57, 0.82)	0.48 (0.19, 0.71)	
	yes (flexible apex)	no	no	939.87	1.75	0.15 (0.01, 0.31)	0.68 (0.55, 0.81)	0.42 (0.0007, 0.64)	
	yes (apex = 0)	no	no	939.10	0.98	0.08 (< 0.01, 0.19)	0.69 (0.57, 0.81)	0.47 (0.13, 0.74)	
	no	yes	no	938.12	0.00	0.08 (< 0.01, 0.20)	0.69 (0.56, 0.82)	0.51 (0.27, 0.71)	
	no	no	no	938.86	0.74	0.02 (< 0.01, 0.06)	0.68 (0.56, 0.81)	0.50 (0.21, 0.72)	

Table S2: (Continued).

Demographic performance measure	Climatic distance (top: ΔT_{max}; bottom: ΔT_{min})	MRT	ΔT-MRT interaction	DIC	ΔDIC	ΔDIC*	Mean R^2 (95% credible interval)		Mean phylogenetic signal (95% credible interval)	Sample size (species, populations, mesocosms)
							marginal	conditional	Pagel's lambda	
Population growth rate λ_1	yes (flexible apex)	yes	yes	221.35	1.15	-	0.17 (0.04, 0.32)	0.72 (0.57, 0.84)	0.38 (0.02, 0.66)	39, 94, 199
		yes	no	220. 82	0.62	-	0.13 (0.02, 0.25)	0.70 (0.56, 0.84)	0.36 (0.02, 0.64)	
	yes (apex = 0)	yes	yes	220.63	0.43	-	0.11 (0.01, 0.23)	0.71 (0.58, 0.85)	0.37 (0.01, 0.65)	
		yes	no	220.51	0.31	-	0.10 (< 0.01, 0.20)	0.70 (0.54, 0.82)	0.38 (0.02, 0.66)	
	yes (flexible apex)	no	no	220.56	0.36	-	0.11 (0.01, 0.23)	0.69 (0.55, 0.84)	0.34 (0.02, 0.63)	
	yes (apex = 0)	no	no	220.20	0.00	-	0.08 (< 0.01, 0.17)	0.69 (0.54, 0.83)	0.36 (0.03, 0.66)	
	no	yes	no	220.99	0.79	-	0.05 (< 0.01, 0.14)	0.67 (0.53, 0.80)	0.30 (0.01, 0.60)	
	no	no	no	220.92	0.72	-	0.02 (< 0.01, 0.09)	0.65 (0.50, 0.80)	0.30 (0.01, 0.59)	
	yes (flexible apex)	yes	yes	220.12	1.06	-1.23	0.22 (0.07, 0.39)	0.69 (0.55, 0.83)	0.25 (0.007, 0.56)	
		yes	no	219.20	0.14	-1.62	0.19 (0.04, 0.35)	0.68 (0.54, 0.81)	0.27 (0.01, 0.57)	
	yes (apex = 0)	yes	yes	219.35	0.29	-1.28	0.19 (0.04, 0.35)	0.68 (0.53, 0.81)	0.27 (0.01, 0.57)	
		yes	no	219.06	0.00	-1.45	0.18 (0.04, 0.35)	0.67 (0.52, 0.81)	0.26 (0.006, 0.54)	
	yes (flexible apex)	no	no	219.53	0.47	-1.03	0.14 (0.02, 0.28)	0.67 (0.53, 0.80)	0.25 (0.01, 0.56)	
	yes (apex = 0)	no	no	219.22	0.16	-0.98	0.14 (0.01, 0.28)	0.70 (0.51, 0.79)	0.23 (0.006, 0.54)	
	no	yes	no	219.26	0.20	-1.73	0.12 (< 0.01, 0.26)	0.66 (0.52, 0.80)	0.26 (0.009, 0.55)	
	no	no	no	219.35	0.29	-1.57	0.07 (< 0.01, 0.20)	0.65 (0.49, 0.79)	0.26 (0.009, 0.55)	

*DIC comparison between the models with ΔT_{min} (and T_{min} amplitude) and the equivalent model with ΔT_{max} (and T_{max} amplitude): positive values indicate that the T_{max} model has a higher performance and negative values indicate the T_{min} model has a higher performance.

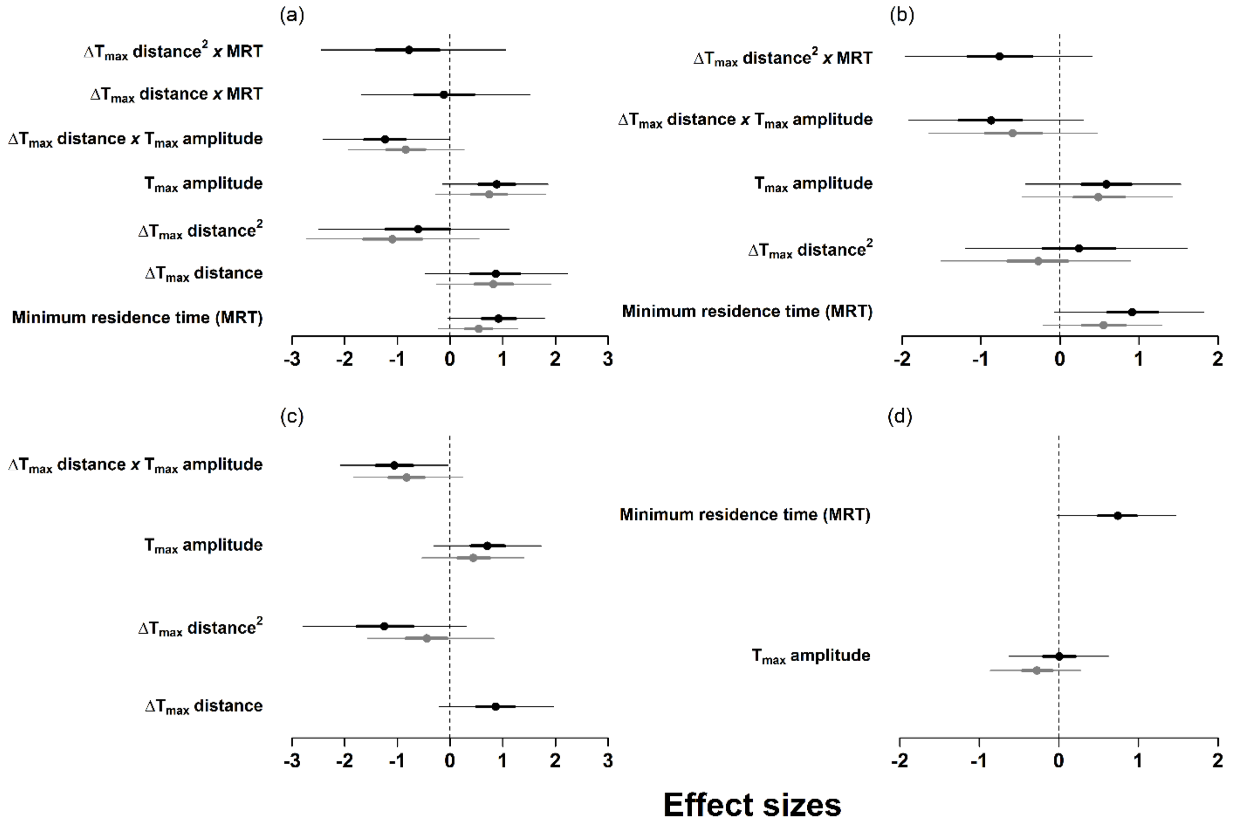

Figure S4: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}), minimum residence time (MRT) and T_{max} amplitude on finite rate of increase (λ_0). (a) The model with linear and quadratic effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (b) The model without linear effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (c) The model only with effects of ΔT_{max} (black: with linear effects; grey: without linear effects). (d) The model only with MRT (black) and the null model (grey). Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

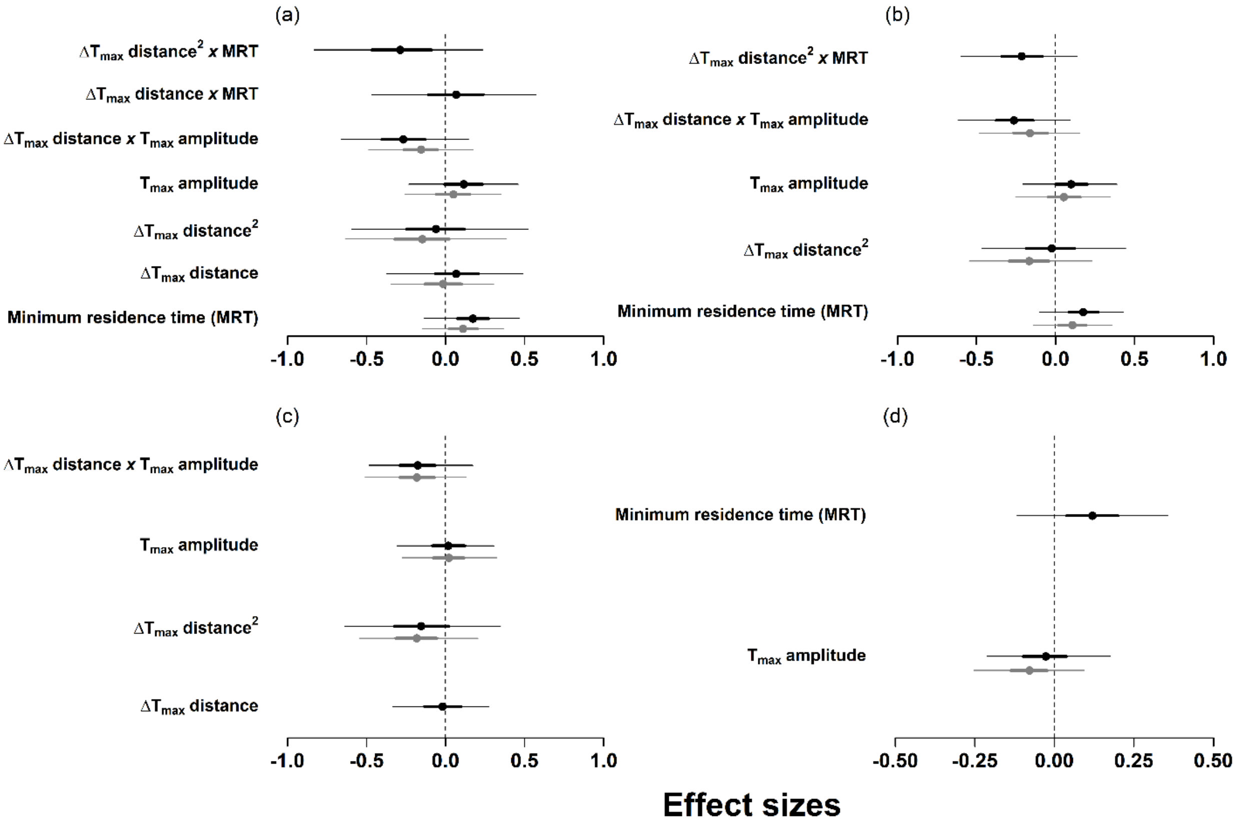

Figure S5: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}), minimum residence time (MRT) and T_{max} amplitude on establishment (E_0). (a) The model with linear and quadratic effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (b) The model without linear effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (c) The model only with effects of ΔT_{max} (black: with linear effects; grey: without linear effects). (d) The model only with MRT (black) and the null model (grey). Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

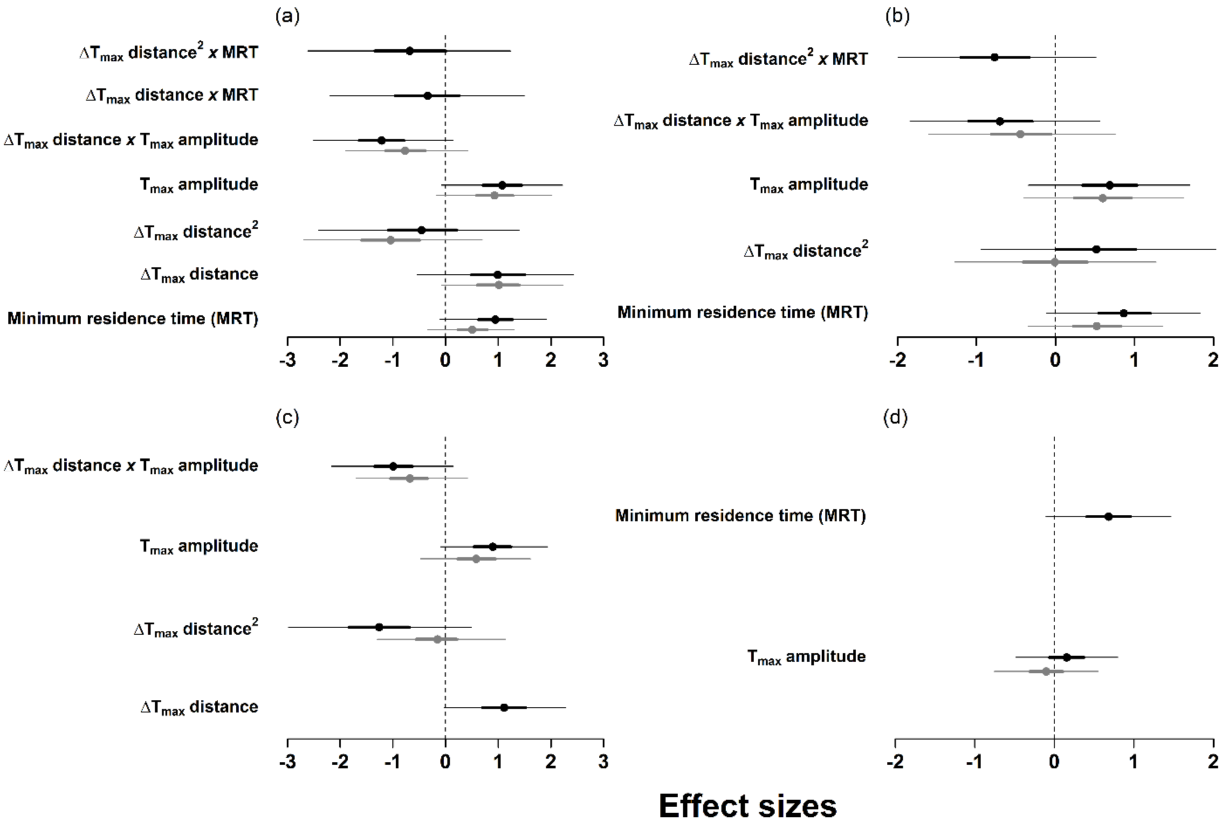

Figure S6: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}), minimum residence time (MRT) and T_{max} amplitude on fecundity (F_0). (a) The model with linear and quadratic effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (b) The model without linear effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (c) The model only with effects of ΔT_{max} (black: with linear effects; grey: without linear effects). (d) The model only with MRT (black) and the null model (grey). Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

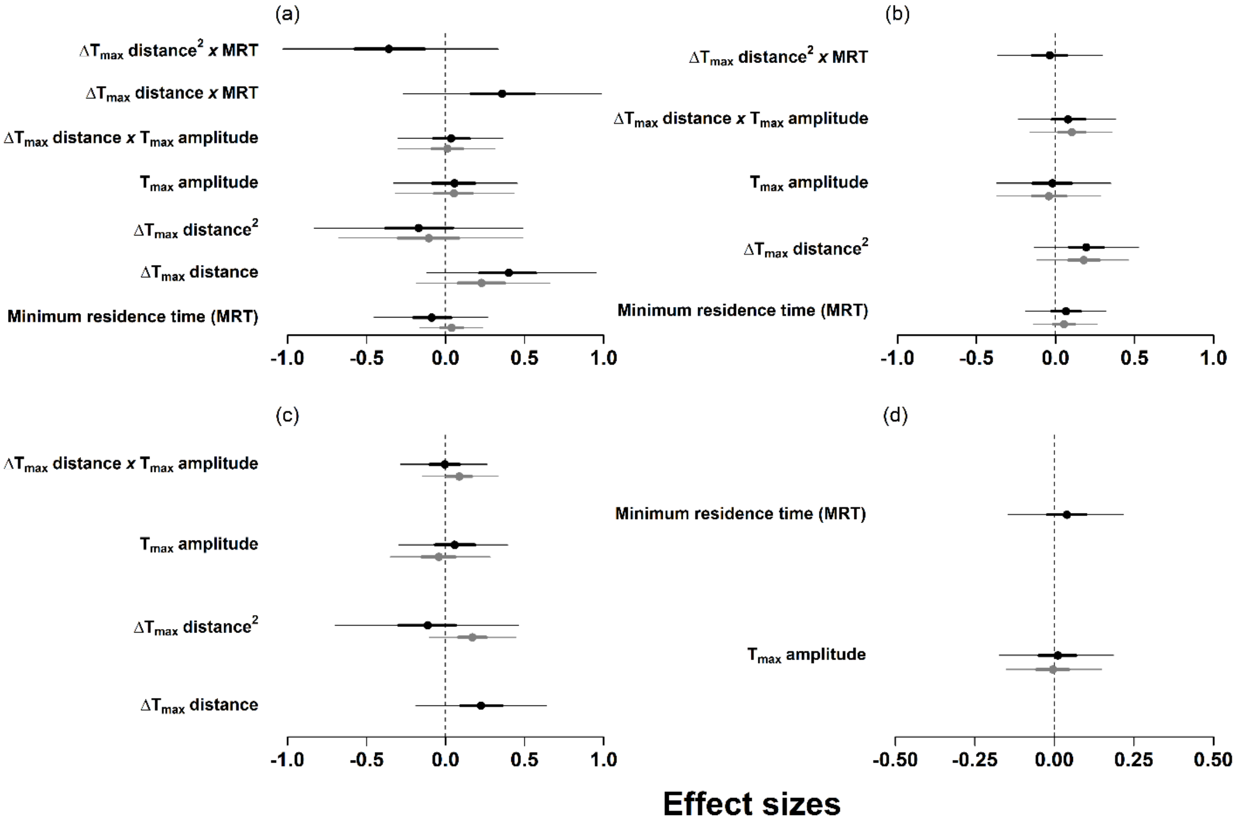

Figure S7: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}), minimum residence time (MRT) and T_{max} amplitude on population growth rate in the second year (λ_1). (a) The model with linear and quadratic effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (b) The model without linear effects of ΔT_{max} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (c) The model only with effects of ΔT_{max} (black: with linear effects; grey: without linear effects). (d) The model only with MRT (black) and the null model (grey). Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

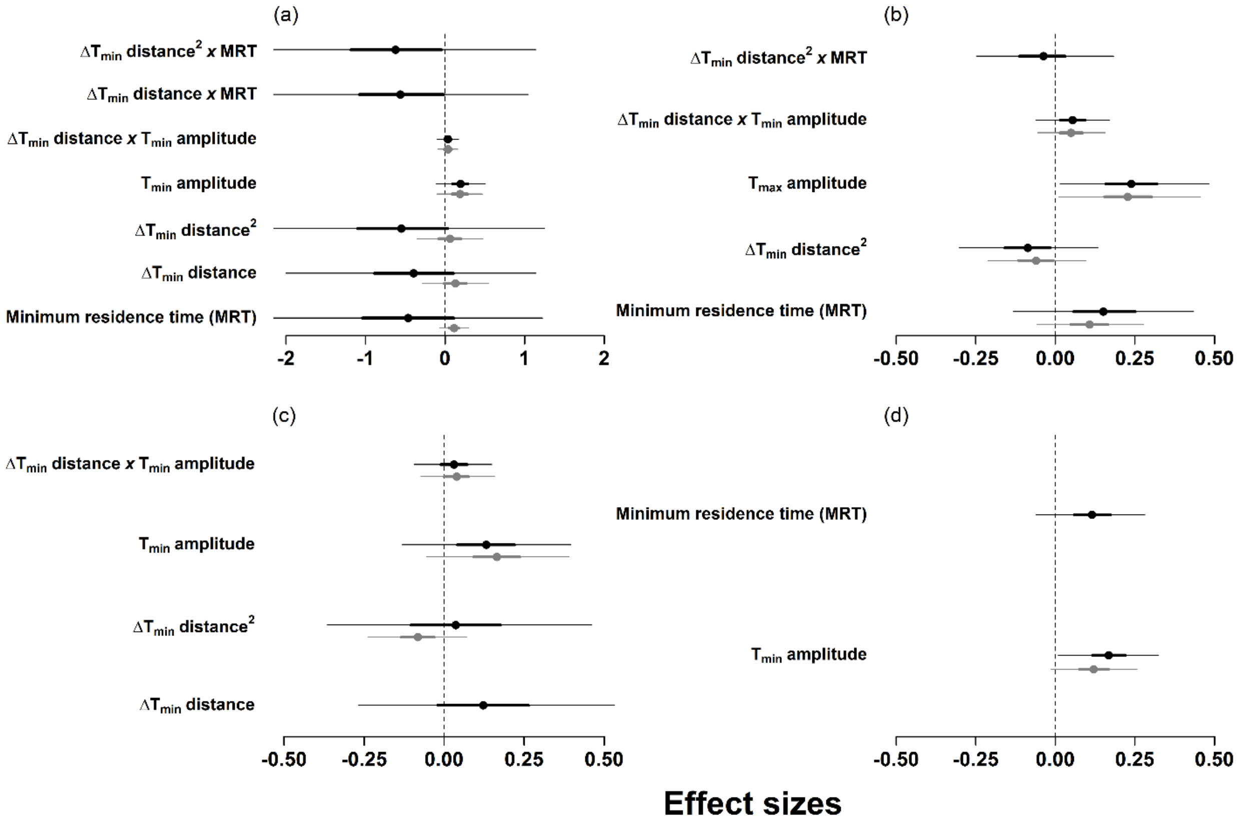

Figure S8: Effects of climatic distance (minimum temperature of the coldest month: local temperature in the common garden minus median temperature in the native range, ΔT_{min}), minimum residence time (MRT) and T_{min} amplitude on population growth rate in the second year (λ_1). (a) The model with linear and quadratic effects of ΔT_{min} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (b) The model without linear effects of ΔT_{min} (black: with ΔT-MRT interaction; grey: without ΔT-MRT interaction). (c) The model only with effects of ΔT_{min} (black: with linear effects; grey: without linear effects). (d) The model only with MRT (black) and the null model (grey). Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

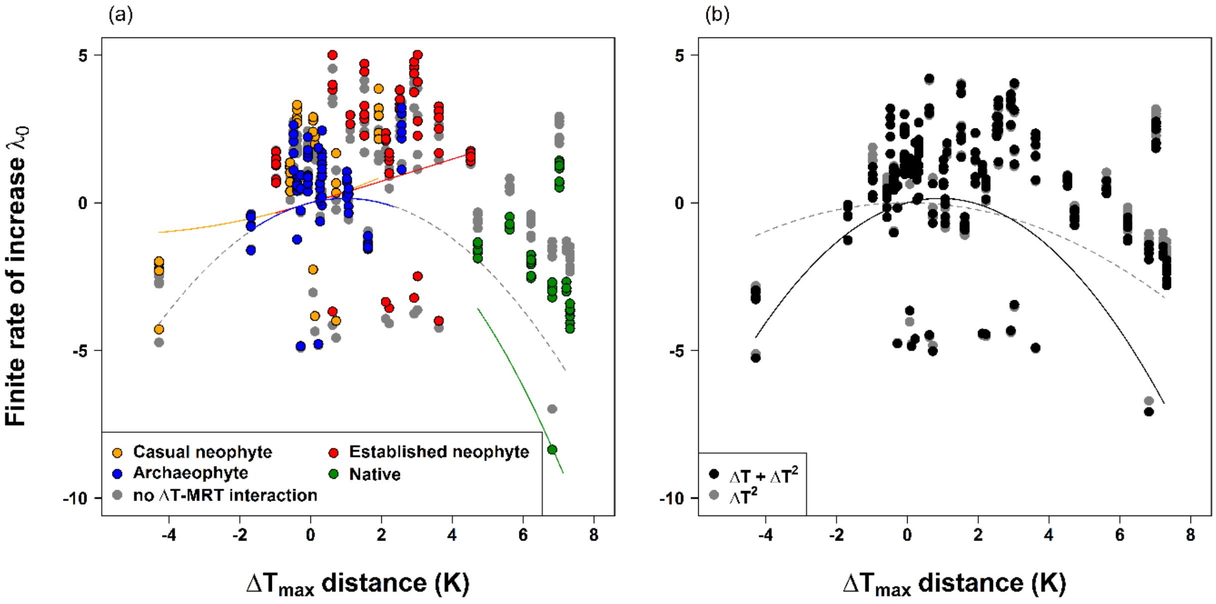

Figure S9: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}) and minimum residence time (MRT) on finite rate of increase (λ_0). (a) The model with linear and quadratic effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the ΔT_{max} terms and MRT 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 ΔT_{max} terms and MRT. (b) The model only with effects of ΔT_{max} (black line: with linear effects; grey line: without linear effects). Note that y-axes depict partial residuals of log-transformed λ_0.

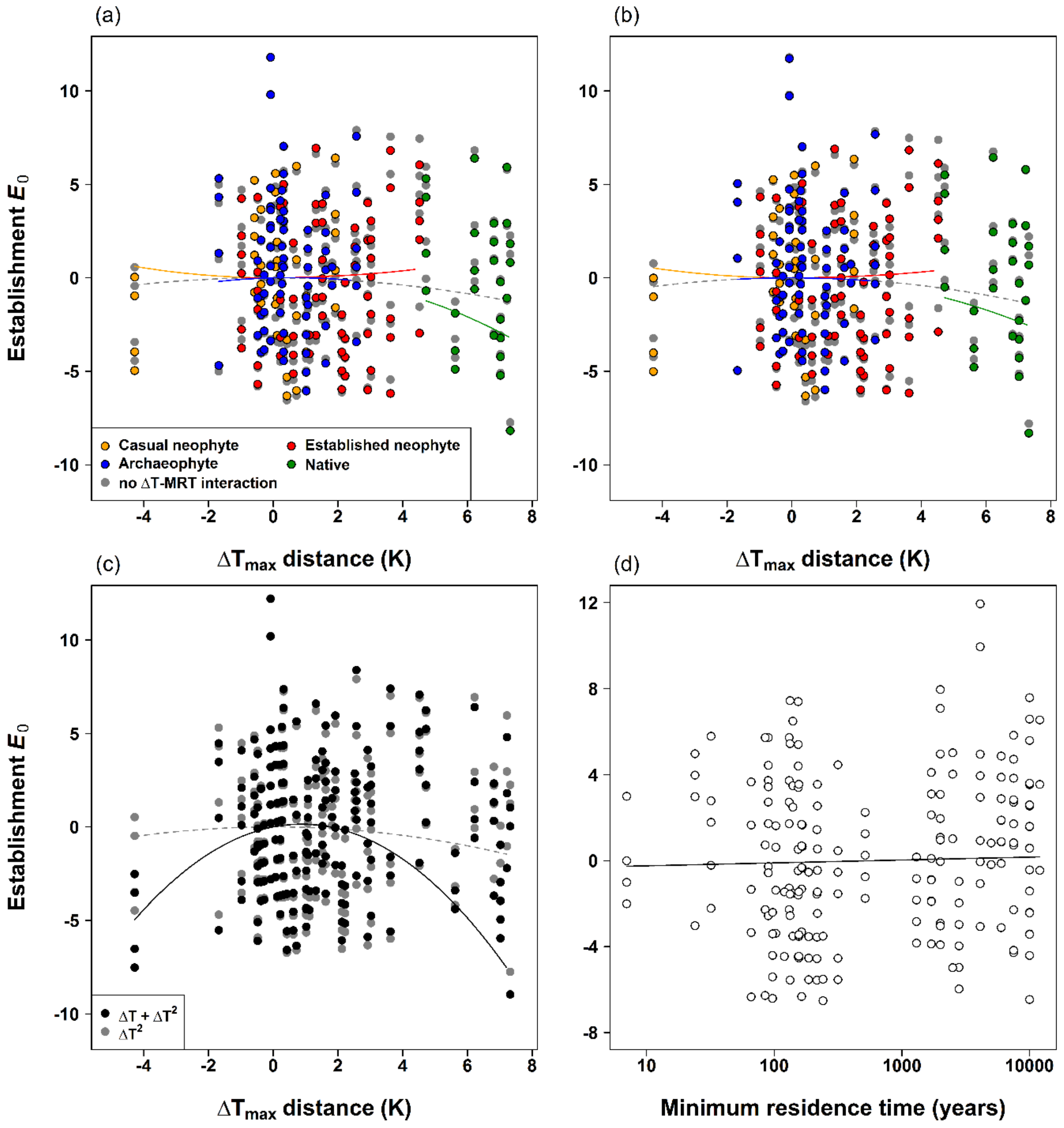

Figure S10: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}) and minimum residence time (MRT) on establishment (E_0). (a) The model with linear and quadratic effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the ΔT_{max} terms and MRT 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 ΔT_{max} terms and MRT. (b) The model without linear effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the quadratic effect of ΔT_{max} and MRT for the median MRT of each introduction status group. The grey line shows predictions of the corresponding model without an interaction between the quadratic effect of ΔT_{max} and MRT. (c) The model only with effects of ΔT_{max} (black line: with linear effects; grey line: without linear effects). (d) The model only with MRT. Note that y-axes depict partial residuals of E_0.

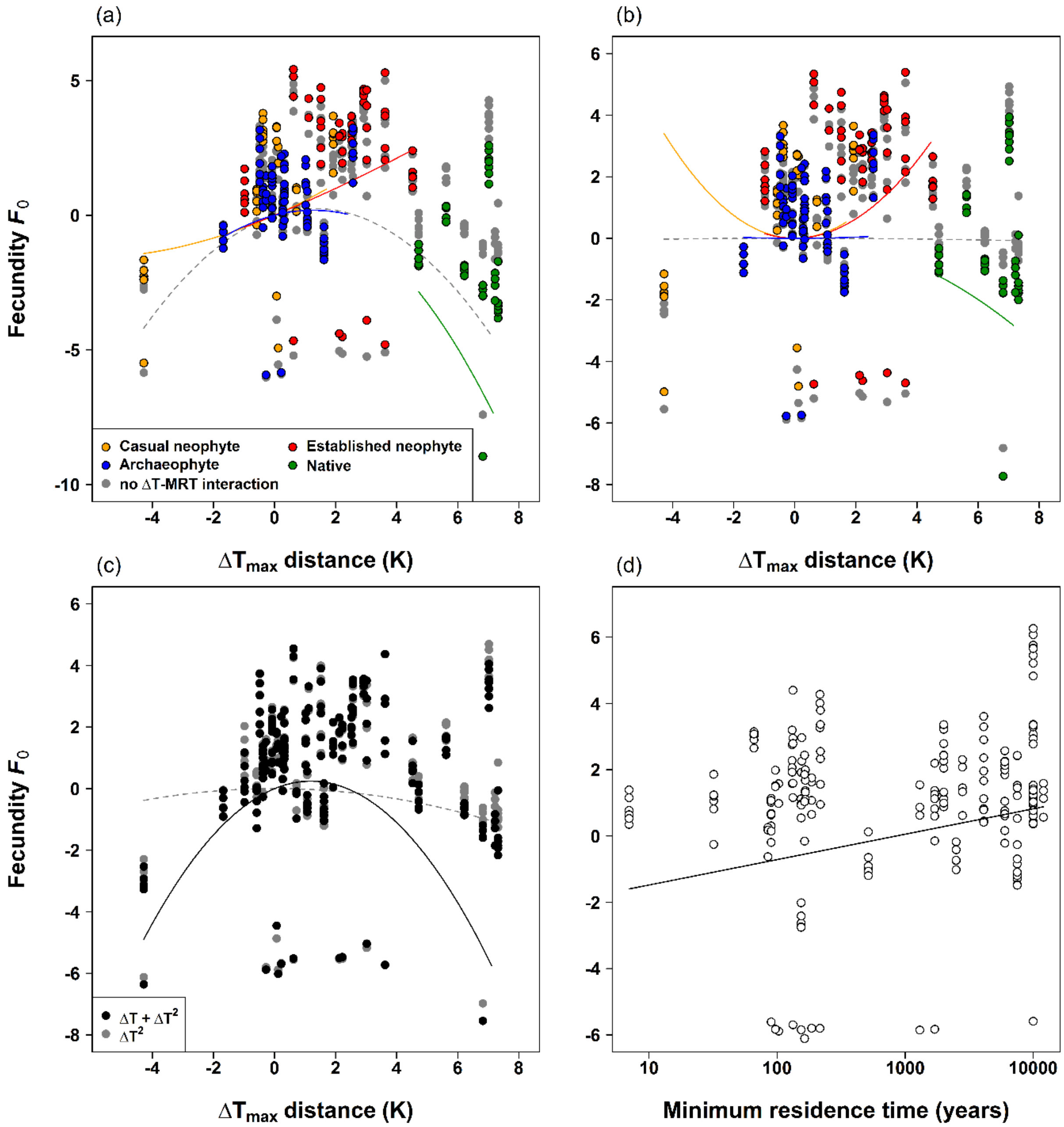

Figure S11: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}) and minimum residence time (MRT) on fecundity (F_0). (a) The model with linear and quadratic effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the ΔT_{max} terms and MRT 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 ΔT_{max} terms and MRT. (b) The model without linear effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the quadratic effect of ΔT_{max} and MRT for the median MRT of each introduction status group. The grey line shows predictions of the corresponding model without an interaction between the quadratic effect of ΔT_{max} and MRT. (c) The model only with effects of ΔT_{max} (black line: with linear effects; grey line: without linear effects). (d) The model only with MRT. Note that y-axes depict partial residuals of log-transformed F_0.

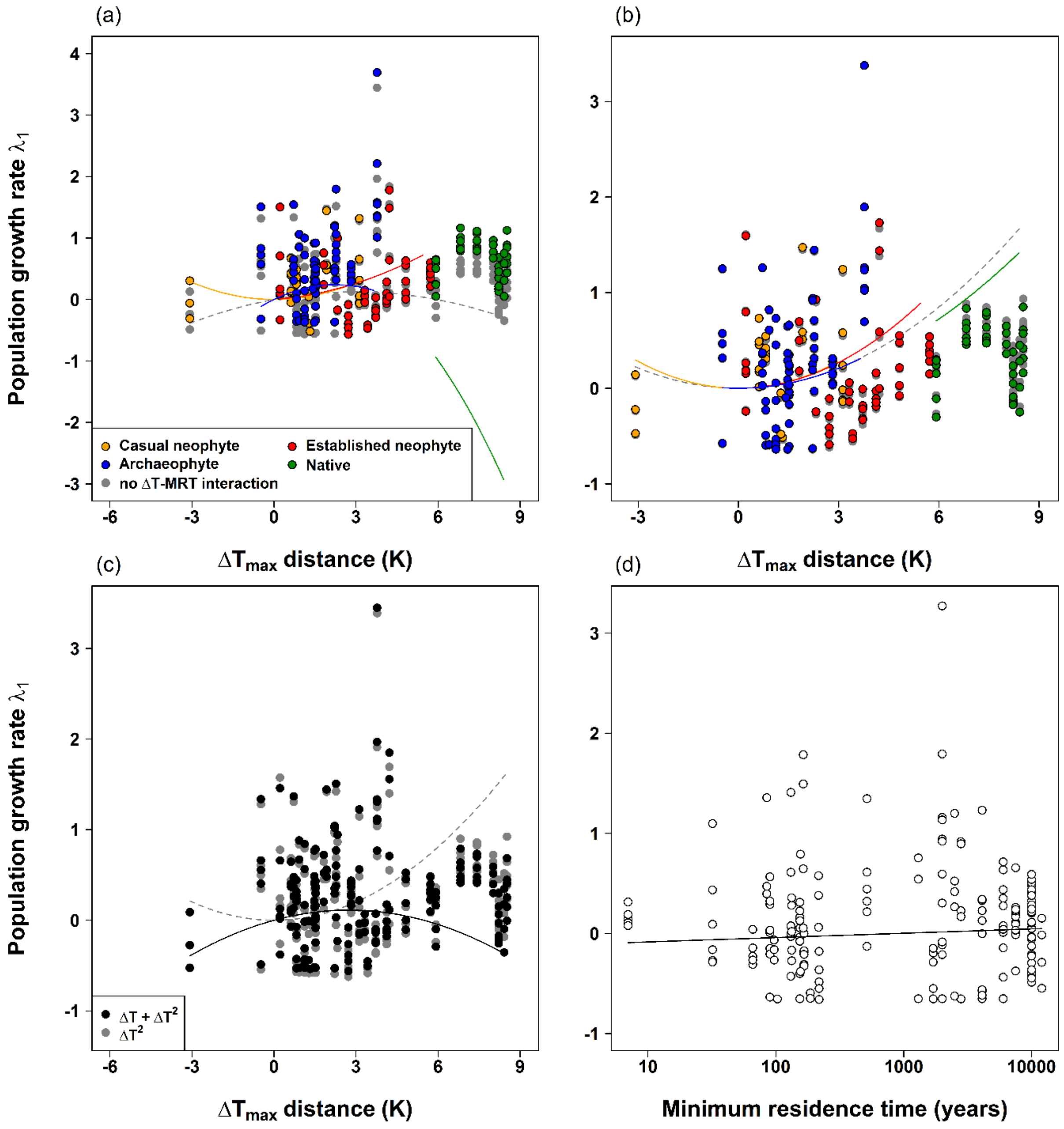

Figure S12: Effects of climatic distance (maximum temperature of the warmest month: local temperature in the common garden minus median temperature in the native range, ΔT_{max}) and minimum residence time (MRT) on population growth rate in the second year (λ_1). (a) The model with linear and quadratic effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the ΔT_{max} terms and MRT 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 ΔT_{max} terms and MRT. (b) The model without linear effects of ΔT_{max}. Coloured lines show predictions of the model including interactions between the quadratic effect of ΔT_{max} and MRT for the median MRT of each introduction status group. The grey line shows predictions of the corresponding model without an interaction between the quadratic effect of ΔT_{max} and MRT. (c) The model only with effects of ΔT_{max} (black line: with linear effects; grey line: without linear effects). (d) The model only with MRT. Note that y-axes depict partial residuals of log-transformed λ_1.

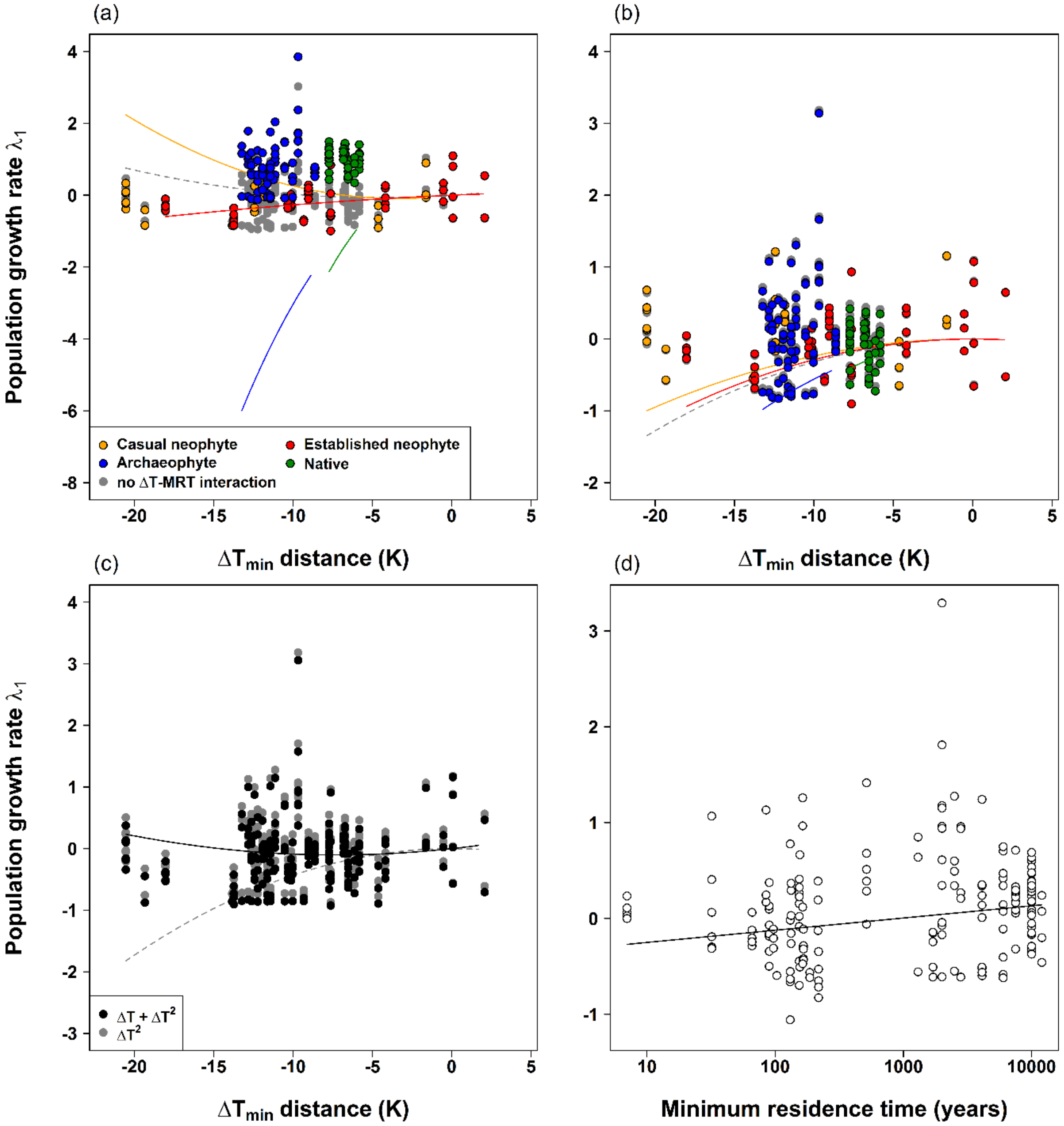

Figure S13: Effects of climatic distance (<u>minimum temperature of the coldest month</u>: local temperature in the common garden minus median temperature in the native range, ΔT_{min}) and minimum residence time (MRT) on population growth rate in the second year (λ_1). (a) The model with linear and quadratic effects of ΔT_{min}. Coloured lines show predictions of the model including interactions between the ΔT_{min} terms and MRT 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 ΔT_{min} terms and MRT. (b) The model without linear effects of ΔT_{min}. Coloured lines show predictions of the model including interactions between the quadratic effect of ΔT_{min} and MRT for the median MRT of each introduction status group. The grey line shows predictions of the corresponding model without an interaction between the quadratic effect of ΔT_{min} and MRT. (c) The model only with effects of ΔT_{min} (black line: with linear effects; grey line: without linear effects). (d) The model only with MRT. Note that y-axes depict partial residuals of log-transformed λ_1.

Relationships between functional traits and the other demographic performance measures

Table S3: Results of models for effects of functional traits (seed mass, maximum height, and specific leaf area [SLA]) on establishment (*E_0*), fecundity (*F_0*), and population growth rate in the second year (λ_1). We tested for linear and quadratic effects of each trait in a full model. 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.

			Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**
Demographic performance measure	**Functional trait**	**Mean effect size (95% credible interval)**	**marginal**	**conditional**	**Pagel's lambda**
Establishment E_0	log(seed mass)	0.02 (-0.10, 0.12)	-	-	-
	log(seed mass)^2	-0.03 (-0.07, 0.007)			
	log(max. height)	-1.46 (-5.46, 2.43)	-	-	-
	log(max. height)^2	0.21 (-0.35, 0.67)			
	log(SLA)	4.96 (-5.44, 17.04)	-	-	-
	log(SLA)^2	-0.64 (-2.46, 0.96)			
	full model	-	0.26 (0.08, 0.47)	0.71 (0.53, 0.87)	0.21 (0.0004, 0.55)
Fecundity F_0	log(seed mass)	**-0.51 (-0.88, -0.07)**	0.15_{par}	-	-
	log(seed mass)^2	0.05 (-0.10, 0.19)			
	log(max. height)	**15.21 (3.02, 26.48)**	0.03_{par}	-	-
	log(max. height)^2	**-1.97 (-3.53, -0.52)**			
	log(SLA)	-9.61 (-56.25, 38.03)	-	-	-
	log(SLA)^2	1.48 (-5.81, 8.33)			
	full model	-	0.25 (0.09, 0.44)	0.68 (0.55, 0.80)	0.42 (0.0009, 0.62)

Table S3: (Continued).

Demographic performance measure	Functional trait	Mean effect size (95% credible interval)	Mean R^2 (95% credible interval) marginal	Mean R^2 (95% credible interval) conditional	Mean phylogenetic signal (95% credible interval) Pagel's lambda
Population growth rate λ_1	log(seed mass)	-0.009 (-0.11, 0.09)	-	-	-
	log(seed mass)^2	-0.02 (-0.05, 0.02)			
	log(max. height)	-0.43 (-3.91, 2.96)	-	-	-
	log(max. height)^2	0.05 (-0.37, 0.51)			
	log(SLA)	1.55 (-9.61, 13.48)	-	-	-
	log(SLA)^2	-0.27 (-2.07, 1.39)			
	full model	-	0.11 (0.02, 0.24)	0.70 (0.56, 0.84)	0.32 (0.02, 0.63)

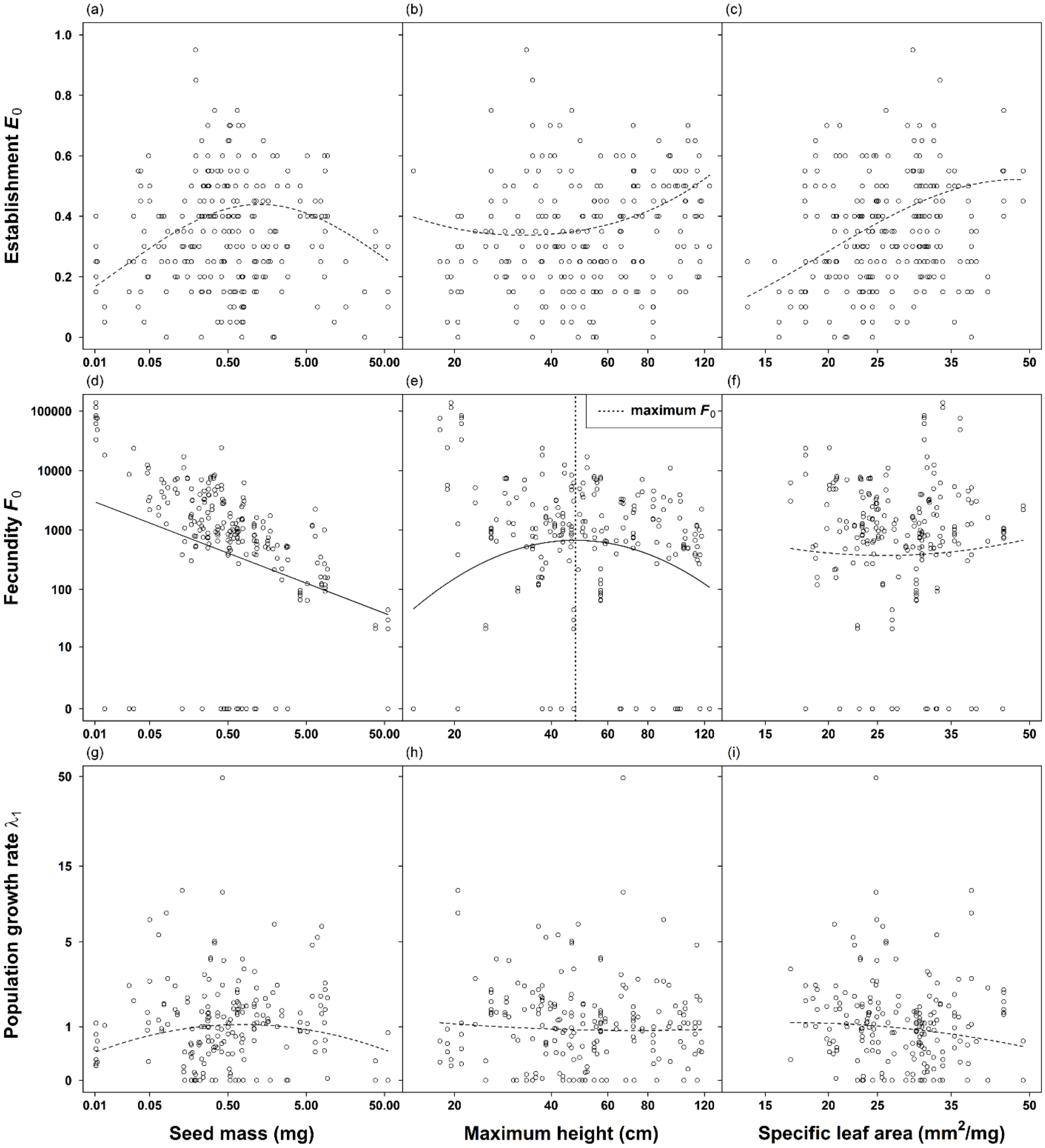

Figure S14: Relationships between functional traits and (a-c) establishment (E_0), (d-f) fecundity (F_0), and (g-i) population growth rate in the second year (λ_1). Predictions are based on the full model (see Table S3 for establishment, fecundity, and population growth rate in the second year) with the other explanatory variables fixed at their mean. Solid lines represent significant trait effects (with 95% credible intervals not overlapping zero), whereas for dashed lines, 95% credible intervals of estimated effects overlap zero. (d) For the smallest seed mass measured (0.01 mg), F_0 is predicted to be highest. (e) The vertical dotted line represents the value of plant height (47.6 cm) that maximizes F_0. All axes (except for establishment) are shown on log-scale.

Appendix S2: Results of control analyses for relationships between functional traits and residence time

Control analysis (only including wild populations) for the relationship between seed mass and minimum residence time (MRT) revealed results similar to the analysis of the full dataset (Fig. S15a; MRT-effect on mean: $t_1 = -3.6$, $P < 0.001$; MRT-effect on SD: $t_1 = -3.7$, $P < 0.001$). The MRT-effect on the mean value of maximum plant height was comparable to the full dataset (Fig. S15b; $t_1 = -2.6$, $P = 0.011$). Although the mean MRT-effect on trait SD was slightly positive, albeit non-significant ($t_1 = 1.09$, $P = 0.281$), the central 95% of the plant height distribution predicted for a maximum MRT of 12,000 years still comprise the plant height value that maximizes λ_0 (Fig. S15b).

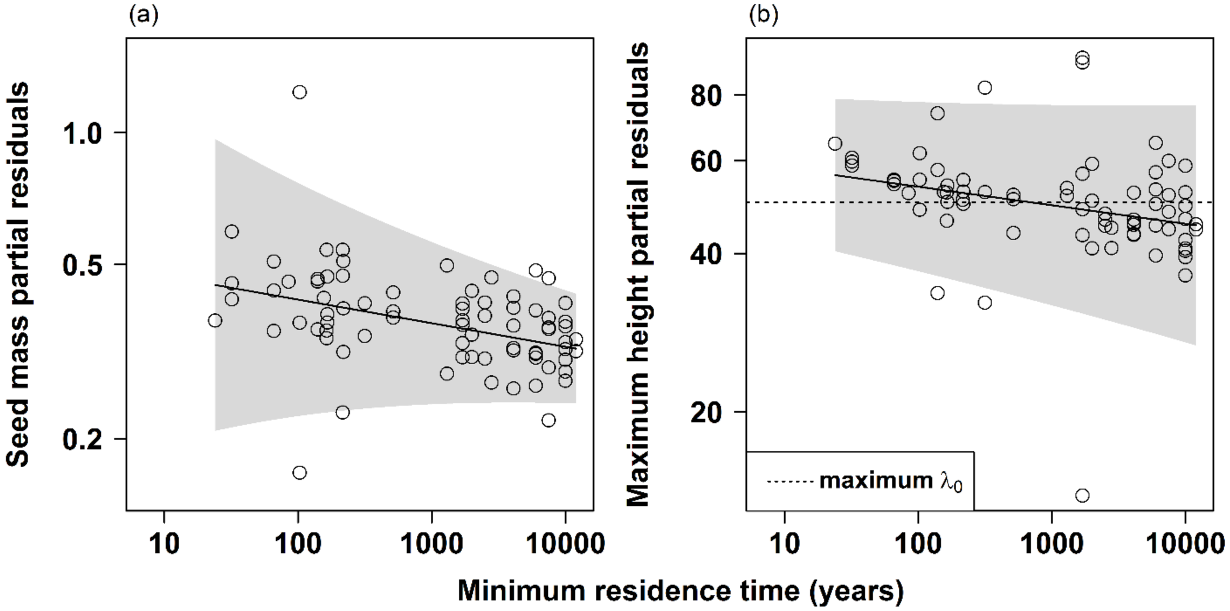

Figure S15: Relationships between (a) seed mass and (b) maximum height and minimum residence time (MRT) for control analyses. Note that y-axes depict partial residuals, which were calculated by subtracting the random effects of species. The solid lines show the effect of MRT on the interspecific trait mean. The shaded areas represent the effect of MRT on the central 95% of the interspecific trait distribution. The horizontal dotted line in (b) represent the value of plant height that maximizes λ_0. All axes are shown on log-scale. Note that these analyses included a considerably smaller set of species (29 species, 78 populations) and thus less continuous gradient of residence times.

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Supporting Information Chapter 2

Alien plant fitness is limited by functional trade-offs rather than a long-term increase in competitive effects of native communities

Alien-native continuum of the Asteraceae species

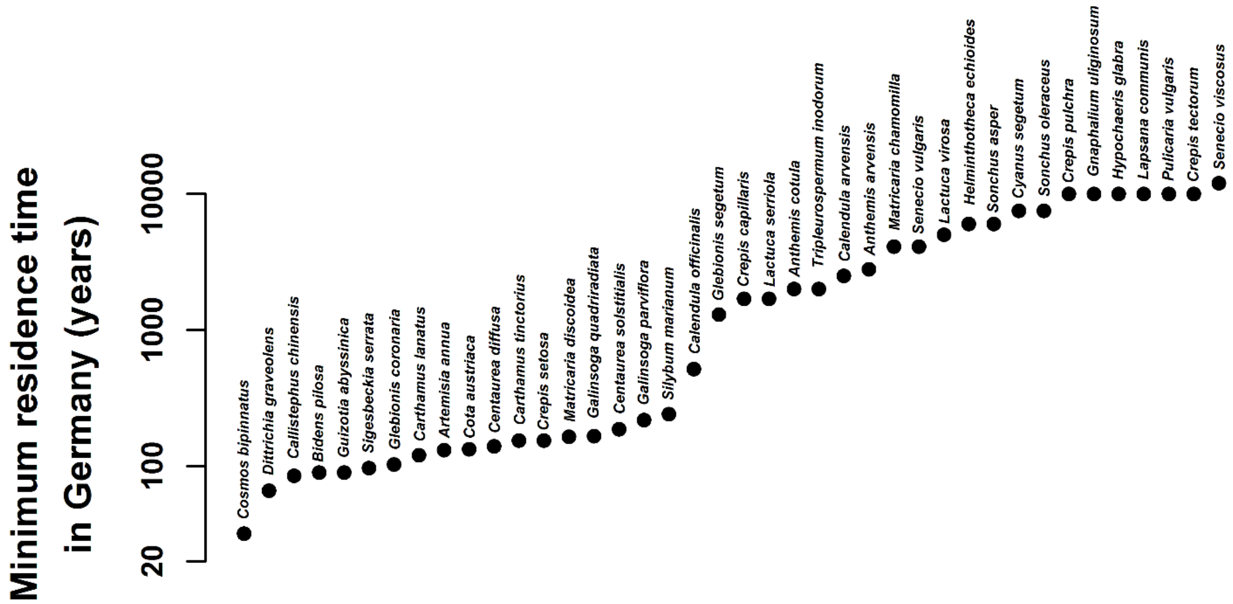

Figure S1: The alien-native continuum of the 40 Asteraceae species varying in their minimum residence time in Germany.

Table S1: The 40 Asteraceae species (nomenclature according to the Plant List, http://www.theplantlist.org, Kalwij 2012) and the number of mesocosms per population (seeds from wild populations and botanical gardens as indicated by city) for monoculture and each community type.

Asteraceae species	Mesocosms per population		
	Monoculture	Experienced community	Naïve community
Anthemis arvensis L.	2_{wild} / 2_{wild} / 2*	2_{wild} / 2_{wild} / 2*	2_{wild} / 2_{wild} / 2*
Anthemis cotula L.	$2_{\text{Berlin-Dahlem}}$ / $2_{\text{Hohenheim}}$ / 2_{Konstanz}	$2_{\text{Berlin-Dahlem}}$ / $2_{\text{Hohenheim}}$ / 2_{Konstanz}	$2_{\text{Berlin-Dahlem}}$ / $2_{\text{Hohenheim}}$ / 2_{Konstanz}
Artemisia annua L.	2_{Bonn} / 2_{Dresden} / 2_{Konstanz}	2_{Bonn} / 2_{Dresden} / 2_{Konstanz}	2_{Bonn} / 2_{Dresden} / 2_{Konstanz}
Bidens pilosa L.	4_{Dresden} / $2_{\text{Hohenheim}}$	4_{Dresden} / $2_{\text{Hohenheim}}$	4_{Dresden} / $2_{\text{Hohenheim}}$
Calendula arvensis M.Bieb.	2_{wild} / 1_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Calendula officinalis L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Callistephus chinensis (L.) Nees	1_{wild} / 2_{Dresden} / $2_{\text{Tuebingen}}$	2_{wild} / 2_{Dresden} / $2_{\text{Tuebingen}}$	2_{wild} / 2_{Dresden} / $2_{\text{Tuebingen}}$
Carthamus lanatus L.	4_{Dresden}	4_{Dresden}	4_{Dresden}
Carthamus tinctorius L.	2_{Bonn} / 4_{Halle}	2_{Bonn} / 4_{Halle}	2_{Bonn} / 4_{Halle}
Centaurea diffusa Lam.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Centaurea solstitialis L.	$2_{\text{Berlin-Dahlem}}$ / 4_{Dresden}	$2_{\text{Berlin-Dahlem}}$ / 4_{Dresden}	$2_{\text{Berlin-Dahlem}}$ / 4_{Dresden}
Cosmos bipinnatus Cav.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Cota austriaca (Jacq.) Sch.Bip.	$3_{\text{Hohenheim}}$ / 3_{Potsdam}	$3_{\text{Hohenheim}}$ / 3_{Potsdam}	$3_{\text{Hohenheim}}$ / 3_{Potsdam}
Crepis capillaris (L.) Wallr.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Crepis pulchra L.	4_{Dresden} / 2_{Konstanz}	4_{Dresden} / 2_{Konstanz}	4_{Dresden} / 2_{Konstanz}
Crepis setosa Haller f.	6_{Dresden}	6_{Dresden}	6_{Dresden}
Crepis tectorum L.	6**	6**	6**
Cyanus segetum Hill.	4_{wild} / 2_{wild} / 2_{wild}	4_{wild} / 2_{wild} / 2_{wild}	4_{wild} / 2_{wild} / 2_{wild}
Dittrichia graveolens (L.) Greuter	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	3_{wild} / 2_{wild} / 2_{wild}
Galinsoga parviflora Cav.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Galinsoga quadriradiata Ruiz & Pav.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 3_{wild} / 2_{wild}
Glebionis coronaria (L.) Cass. ex Spach	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Glebionis segetum (L.) Fourr.	2_{wild} / 2_{wild} / 2_{Dresden}	2_{wild} / 2_{wild} / 2_{Dresden}	2_{wild} / 2_{wild} / 2_{Dresden}
Gnaphalium uliginosum L.	4_{wild} / 2_{wild} / 2_{wild}	4_{wild} / 2_{wild} / 2_{wild}	4_{wild} / 2_{wild} / 2_{wild}
Guizotia abyssinica (L.f.) Cass.	2_{Bonn} / 2_{Dresden} / $2_{\text{Hohenheim}}$	2_{Bonn} / 2_{Dresden} / $2_{\text{Hohenheim}}$	2_{Bonn} / 2_{Dresden} / $2_{\text{Hohenheim}}$
Helminthotheca echioides (L.) Holub	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Hypochaeris glabra L.	6_{Dresden}	6_{Dresden}	6_{Dresden}
Lactuca serriola L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}

Table S1: (Continued).

Asteraceae species	Mesocosms per population		
	Monoculture	**Experienced community**	**Naïve community**
Lactuca virosa Habl.	$2_{\text{Hohenheim}}$	$2_{\text{Hohenheim}}$	$2_{\text{Hohenheim}}$
Lapsana communis L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Matricaria chamomilla L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Matricaria discoidea DC.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Pulicaria vulgaris Gaertn.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 3_{wild} / 2_{wild}	2_{wild} / 1_{wild} / 2_{wild}
Senecio viscosus L.	2_{wild} / 2_{wild}	2_{wild} / 2_{wild}	2_{wild} / 2_{wild}
Senecio vulgaris L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Sigesbeckia serrata DC.	6_{Dresden}	6_{Dresden}	6_{Dresden}
Silybum marianum (L.) Gaertn.	2_{Bonn} / 2_{Rostock}	2_{Bonn} / 2_{Rostock}	2_{Bonn} / 2_{Rostock}
Sonchus asper (L.) Hill	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 3_{wild} / 2_{wild}	2_{wild} / 1_{wild} / 2_{wild}
Sonchus oleraceus (L.) L.	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}
Tripleurospermum inodorum (L.) Sch.Bip.	3_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}	2_{wild} / 2_{wild} / 2_{wild}

* seeds received from commercial seed supplier Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany) in 2015
** seed source from botanical garden in Tuebingen and grown for one generation at Hohenheim
(both cases were removed for control analyses only including wild populations)

Seed mixtures of each community type

Table S2: Composition of the experienced and naïve community, consisting of species native to Central European grasslands and congeneric/confamilial species native to North American grasslands, respectively. Seeds originate from regional seed sources (see explanations below). The number of seeds for each species was adjusted based on the individual seed mass. In total, 477 mg seed weight per mesocosm (on a soil surface of 0.159 m^2) refers to a sowing density of 3 g/m^2. The low germination ability in *Bromus erectus* and *Elymus repens* (personal communication with the commercial seed supplier) explains the relatively higher amount of seeds for these species. As a measure of the range size of the experienced community species in Germany (indicated in parentheses), we calculated the proportion (%) of occupied raster-cells in Germany using the FlorKart, BfN and NetPhyD Netzwerk Phytodiversität Deutschlands e.V. database (www.floraweb.de).

Species composition		**Individual seed mass (mg)**	**Seed number per mesocosm**	**Seed weight per mesocosm (mg)**
Experienced community[1]	**Naïve community**[2]			
Bromus erectus Huds. (59.8 %)	*Bromus kalmii* A.Gray	5.40 / 3.54	29 / 14	156.60 / 49.56
Festuca rupicola Heuff. (15.0 %)	*Festuca paradoxa* Desv.	0.50 / 1.23	20 / 20	10.00 / 24.60
Elymus repens (L.) Gould (99.2 %)	*Elymus canadensis* L.	3.00 / 5.45	29 / 14	87.00 / 76.30
Carex flacca Schreb. (77.5 %)	*Carex bicknellii* Britton & A.Br.	0.83 / 1.67	29 / 20	24.07 / 33.40
Galium verum L. (71.0 %)	*Galium concinnum* Torr. & A.Gray	0.50 / 0.47	50 / 50	25.00 / 23.50
Salvia pratensis L. (56.5 %)	*Salvia lyrata* L.	1.80 / 1.89	25 / 25	45.00 / 47.25
Campanula rapunculus L. (46.0 %)	*Lobelia spicata* Lam.	0.02 / 0.03	100 / 100	2.00 / 3.00
Potentilla argentea L. (80.1 %)	*Potentilla arguta* Pursh	0.10 / 0.12	50 / 50	5.00 / 6.00
Verbascum lychnitis L. (57.1 %)	*Penstemon tubaeflorus* Nutt.	0.10 / 0.31	50 / 50	5.00 / 15.50
Euphorbia cyparissias L. (86.3 %)	*Euphorbia corollata* L.	2.20 / 3.54	25 / 25	55.00 / 88.50
Silene nutans L. (58.2 %)	*Silene regia* Sims	0.30 / 1.23	50 / 25	15.00 / 30.75
Falcaria vulgaris Bernh. (44.1 %)	*Thaspium trifoliatum* (L.) A.Gray	2.00 / 3.15	25 / 25	50.00 / 78.75
		Σ	**482 / 418**	**479.67 / 477.10**

Seed material and information on individual seed mass was obtained from commercial seed supplier [1]Rieger-Hofmann GmbH (Blaufelden-Raboldshausen, Germany; regional seed sources "Regiosaatgut") and [2]Prairie Moon Nursey (Westfield, Wisconsin, USA).

The commercial seed supplier Rieger-Hoffmann provides autochthonous seed material ("Regiosaatgut") from in total 22 regional seed sources across Germany that is mandatory for grassland restoration and in the open landscape (Durka *et al.* 2019).

The commercial seed supplier Prairie Moon Nursey provides seed material produced within the Midwestern prairie ecoregion that is commonly obtained for research on prairie grassland communities (Bauer *et al.* 2012).

Appendix S1: Compositional characteristics of each community type

All community species established and were abundant in the first and the second year of the experiment (only in the experienced community, *Bromus erectus* was present in the first year but absent in the second year, while *Falcaria vulgaris* was absent in the first year and present in the second year; Fig. S2a and b). In the first year of the experiment, *Salvia pratensis* and *Salvia lyrata* were the most abundant forbs in the experienced and naïve community, respectively (Fig. S2a). In the naïve community, *Elymus canadensis* was the most dominant grass (in the first and second year of the experiment), while *Festuca rupicola* and *Carex flacca* reached highest abundances among the grass species in the experienced community (Fig. S2a and b). From the first to the second year of the experiment, *Potentilla argentea* and *Potentilla arguta* increased in abundance in the experienced and naïve community, respectively (Fig. S2b). Additionally, *Penstemon tubaeflorus* showed relatively high abundances in the naïve community (Fig. S2b). The total cover of the communities, which was visually estimated, slightly differed between the experienced and naïve community in the first year (Fig. S2c) but became very similar in the second year (Fig. S2d).

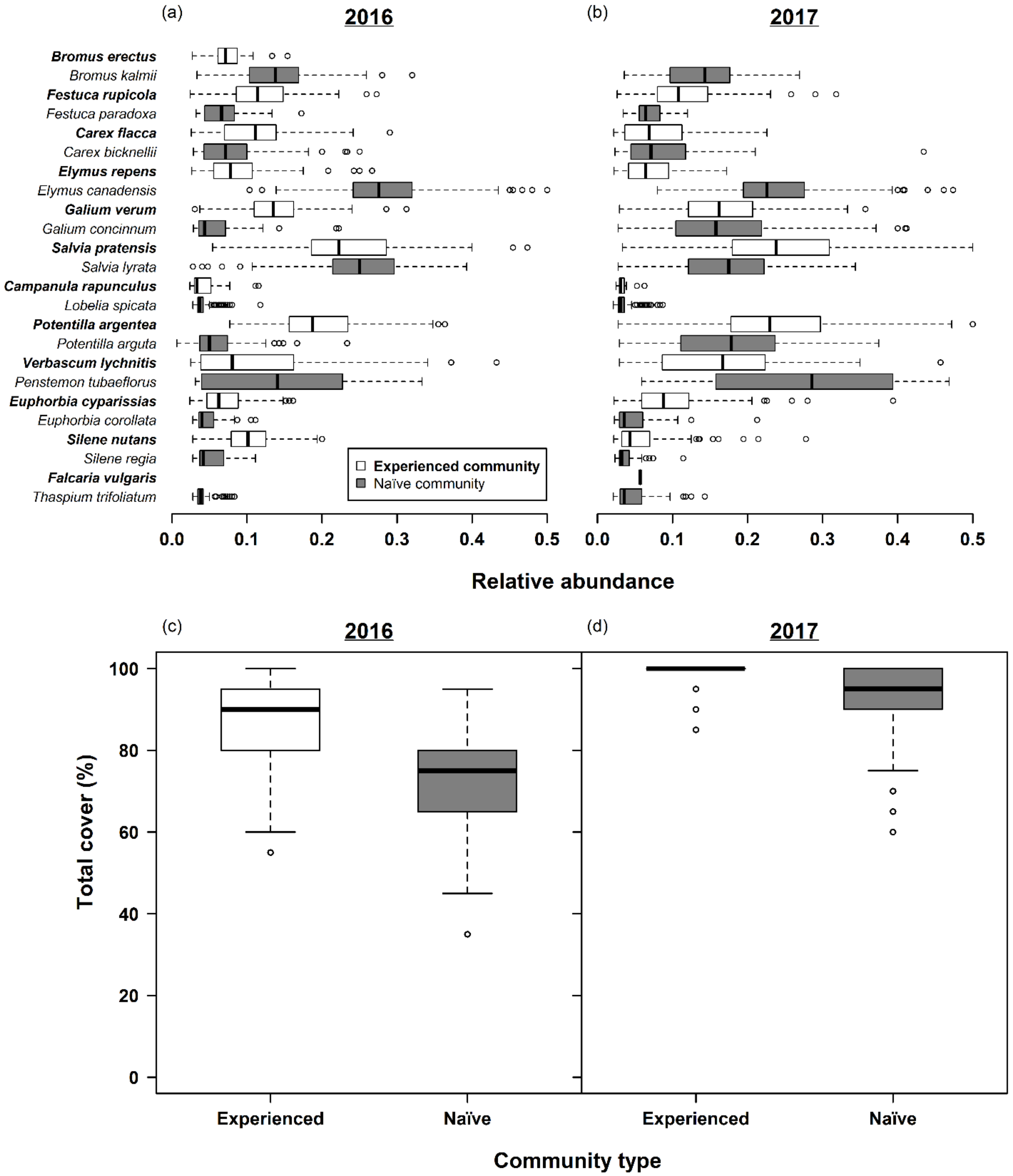

Figure S2: (a and b) Relative abundances of community species and (c and d) total cover of each community type after the first year (2016) and second year (2017). Species of the experienced community (in a and b) are highlighted in bold. Note that *Falcaria vulgaris* was absent in the first year and *Bromus erectus* was absent in the second year. Relative abundances and total cover are based on 236/234 mesocosms for the experienced/naïve community in the first year (corresponding to the analyses of establishment E_0) and 206/204 mesocosms for the experienced/naïve community in the second year (corresponding to the analyses of population growth rate in the second year λ_1).

Experimental design

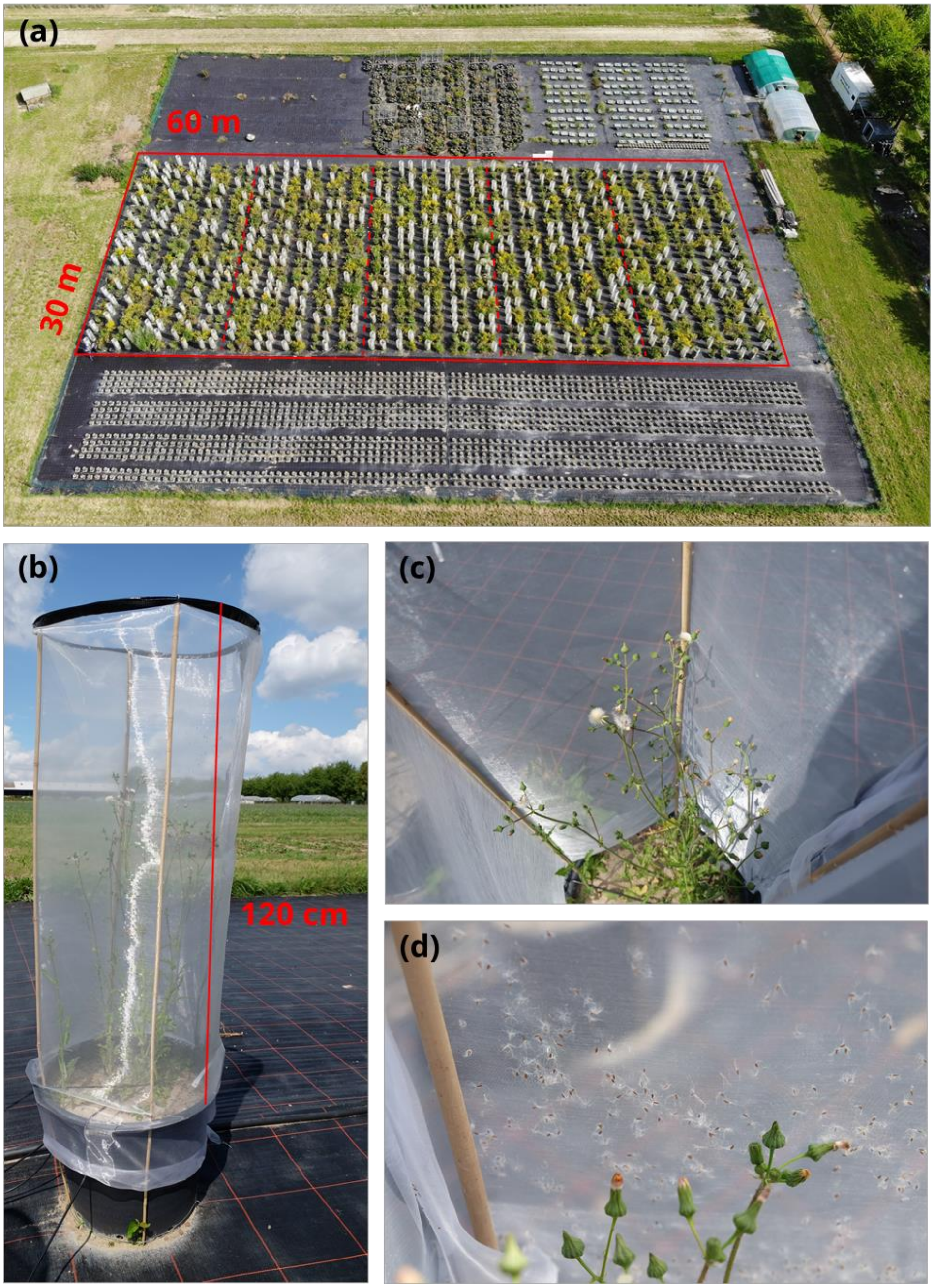

Figure S3: (a) Spatial arrangement of the mesocosms (random block design) used to follow population dynamics (with open-top organza fabric) and for functional trait measurements, showing the common garden experiment in the second year (2017). Note that each block also includes mesocosms used for the experiment of Brendel et al. (2021) (Global Ecology and Biogeography) and another (smaller) experiment not covered by the present study. (b) Example of an open-top organza fabric, surrounding a *Sonchus asper* monoculture mesocosm, which retains the developed seeds (c and d).
Photo credits: (a) – ©Viktoria Ferenc; (b-d) – ©Huw Cooksley

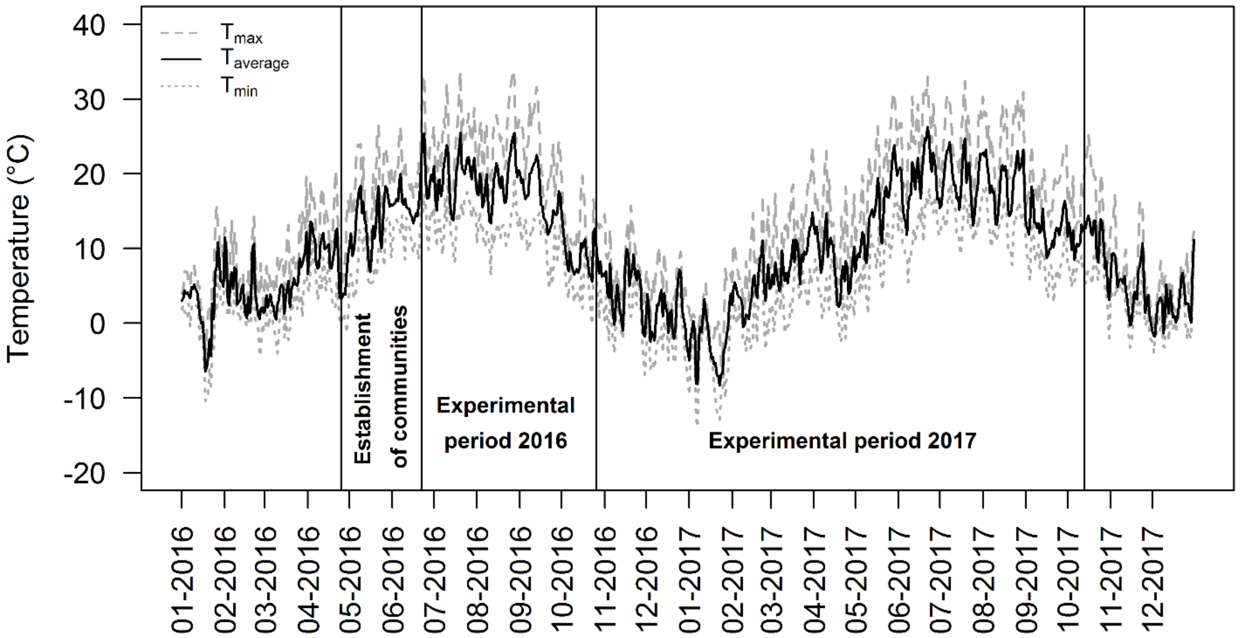

Figure S4: Maximum (T_{max}), average ($T_{average}$) and minimum (T_{min}) daily temperature values (from January 1st, 2016, to December 31st, 2017, measured at 2 m above the ground) at the weather station in proximity to the field site (48° 42' 40.212'' N, 9° 11' 45.384'' E, 389 m a.s.l.), provided by the state institution on agro-meteorology (Agrarmeteorologie Baden-Württemberg, www.wetter-bw.de). The phase of community establishment (first day of sowing the seed-mixture of Central European and North American community species on April 25th until first day of sowing Asteraceae seeds on June 22nd), the experimental period in 2016 (first day of sowing Asteraceae seeds on June 22nd until last day of assessment on October 26th) and the experimental period in 2017 (October 27th, 2016, until last day of assessment on October 13th, 2017) are indicated.

Trade-off between seed mass and seed number of the Asteraceae study species

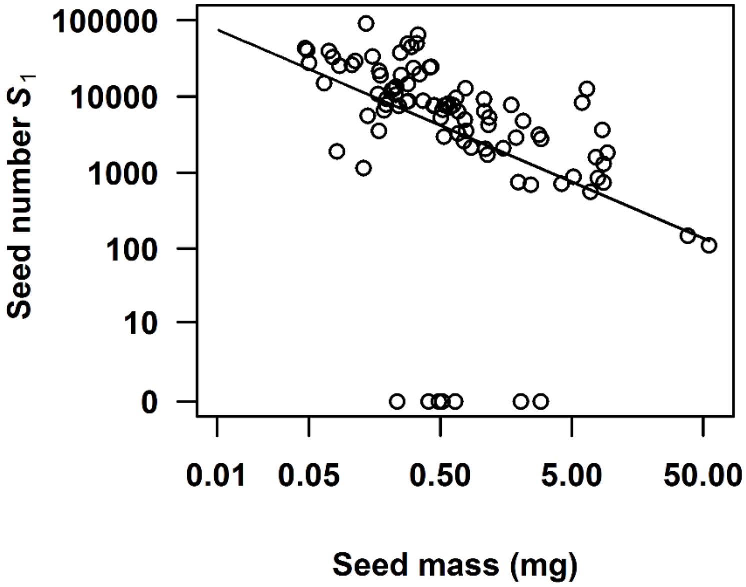

Figure S5: Significant effect of log-transformed seed mass on average log seed number per monoculture mesocosm at population level in the first year of the experiment.

Effects of competition treatment on relationships between functional traits and demographic performance

Table S3: Properties of the models relating establishment (E_0), fecundity (F_0) (in the first year), and population growth rate in the second year (λ_1) to three functional traits (linear and quadratic effect of log-transformed seed mass, maximum height and specific leaf area), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction.

		Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**	
Demographic performance measure	**Interspecific competition with the community**	**marginal**	**conditional**	**Pagel's lambda**	**Sample size (species, populations, mesocosms)**
Establishment E_0	monoculture vs. experienced community	0.43 (0.31, 0.54)	0.75 (0.66, 0.83)	0.18 (0.0004, 0.48)	40, 101, 468
	monoculture vs. naïve community	0.34 (0.22, 0.47)	0.68 (0.59, 0.78)	0.10 (0.0003, 0.32)	40, 101, 466
Fecundity F_0	monoculture vs. experienced community	0.71 (0.64, 0.76)	0.82 (0.80, 0.86)	0.25 (0.001, 0.46)	36, 94, 430
	monoculture vs. naïve community	0.68 (0.61, 0.74)	0.82 (0.79, 0.86)	0.27 (0.002, 0.49)	36, 94, 428
Population growth rate λ_1	monoculture vs. experienced community	0.42 (0.34, 0.49)	0.64 (0.56, 0.71)	0.16 (0.02, 0.34)	36, 87, 394
	monoculture vs. naïve community	0.34 (0.27, 0.41)	0.55 (0.46, 0.64)	0.12 (0.01, 0.29)	36, 87, 392

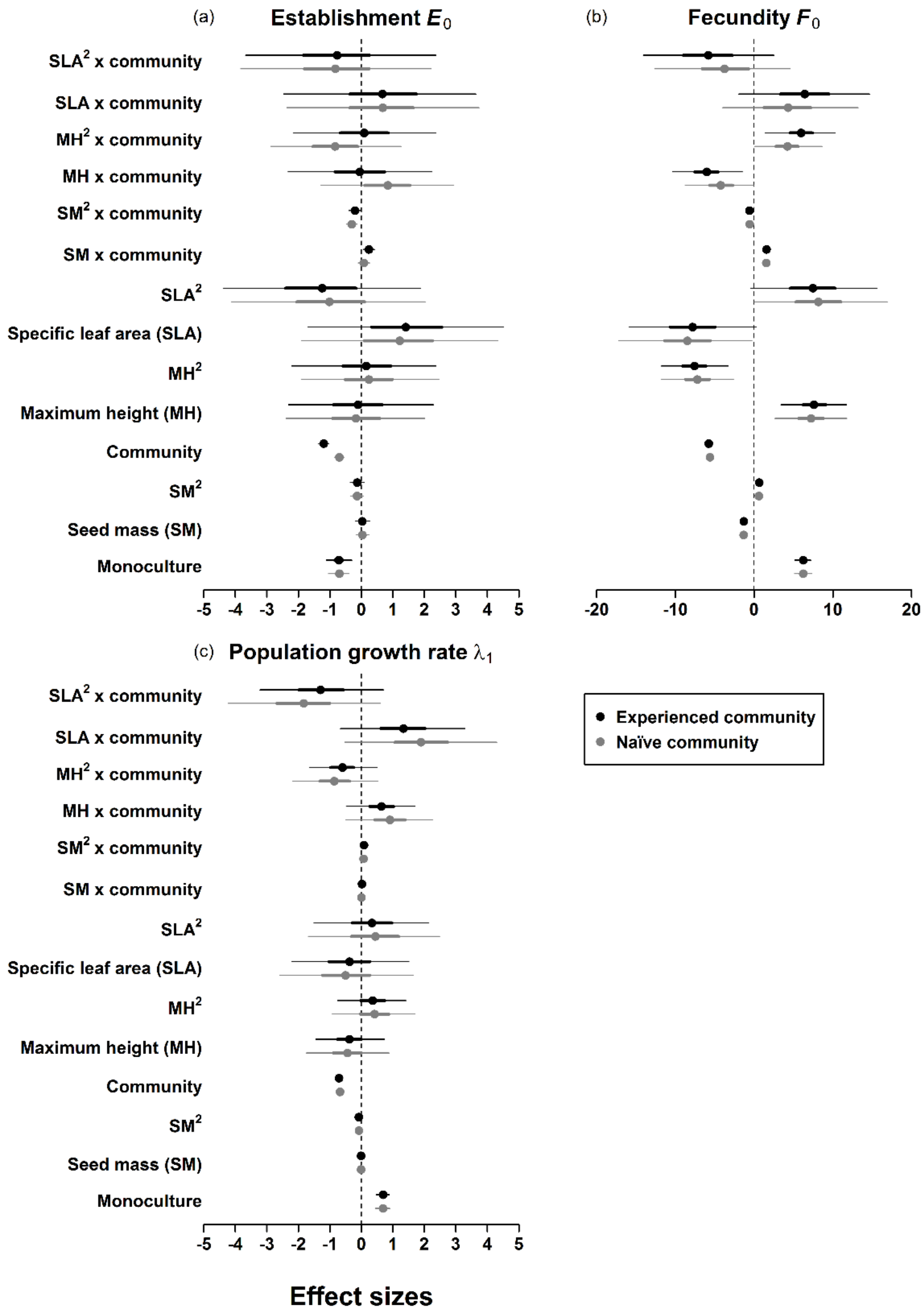

Figure S6: Effects of functional traits (linear and quadratic term of seed mass, maximum height, and specific leaf area), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction on (a) establishment (E_0), (b) fecundity (F_0) (in the first year), and (c) population growth rate in the second year (λ_1). Effect sizes of the models contrasting monoculture vs. experienced community are shown in black and effect sizes of the models contrasting monoculture vs. naïve community are shown in grey. Note that the monoculture effect sizes refer to the intercept of the respective models and the community effect sizes refer to the contrast of monoculture vs. community. Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

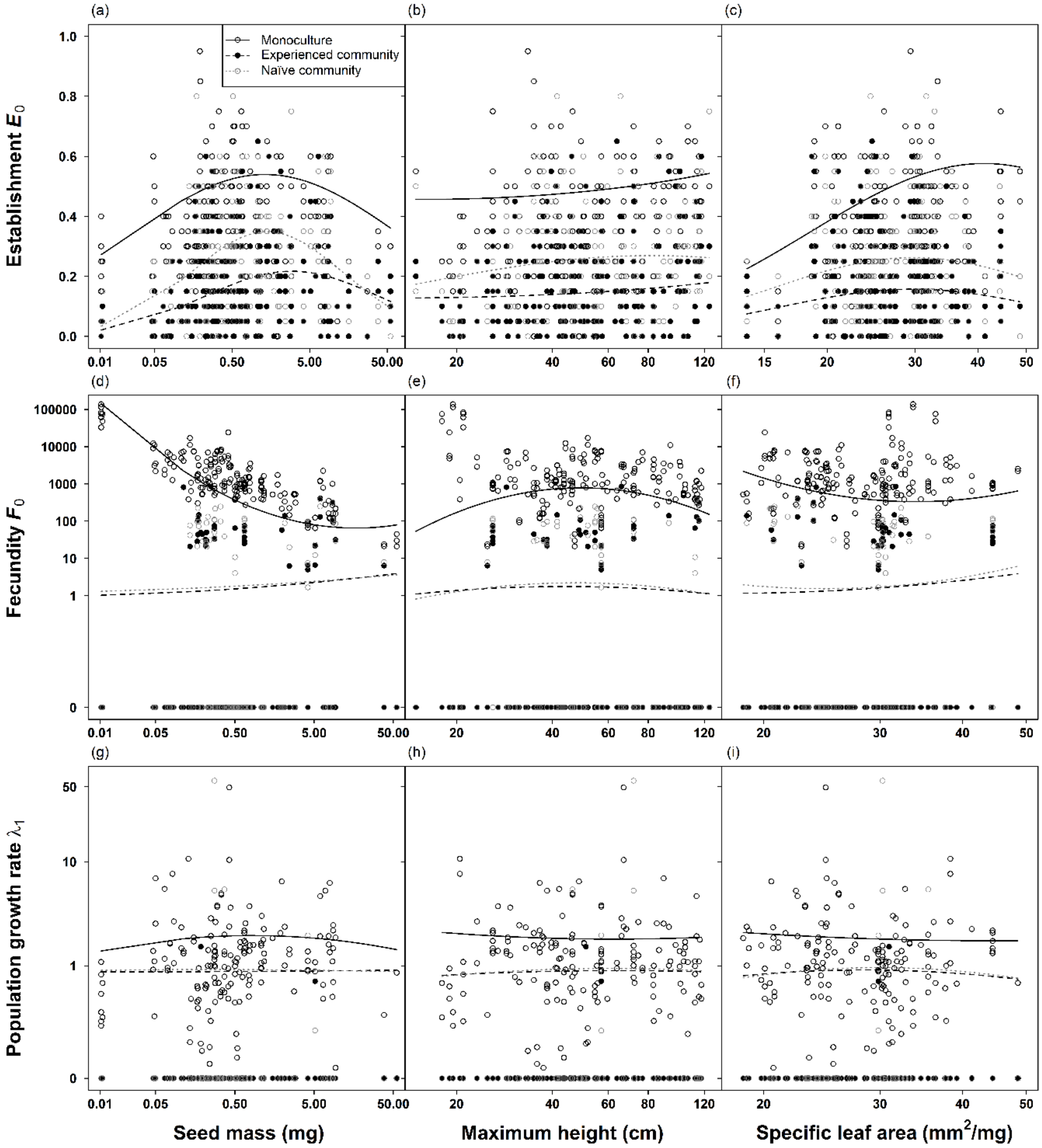

Figure S7: Relationships between functional traits (seed mass, maximum height, and specific leaf area) and (a-c) establishment (E_0), (d-f) fecundity (F_0) (in the first year), and (g-i) population growth rate in the second year (λ_1) in monoculture and the two community types (experienced and naïve community). Predictions are based on the full models with the other explanatory variables set to their mean value (i.e., zero, since the functional traits were scaled and centred, allowing the response of E_0, F_0, and λ_1 to any given trait to be interpreted independently of the other trait variables in the respective model). Predictions of the models contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). Predictions for the naïve community (based on the models contrasting monoculture vs. naïve community) are shown as grey dotted line. For each demographic performance measure, both models have identical effect sizes for monoculture (see Fig. S6), thus only one prediction is shown. All axes (except for E_0) are shown on log-scale. Note that only interactions between functional traits and competition treatment in (a), (d), and (e) are significant.

Results of analyses for effects of residence time, competition treatment, and their interaction on demographic performance

Table S4: Properties of the models relating establishment (E_0), fecundity (F_0) (in the first year), and population growth rate in the second year (λ_1) to minimum residence time, competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction.

Demographic performance measure	Competition treatment	Mean R^2 (95% credible interval) marginal	Mean R^2 (95% credible interval) conditional	Mean phylogenetic signal (95% credible interval) Pagel's lambda	Sample size (species, populations, mesocosms)
Establishment E_0	monoculture vs. experienced community	0.32 (0.22, 0.41)	0.73 (0.64, 0.83)	0.28 (0.001, 0.57)	40, 101, 468
	monoculture vs. naïve community	0.17 (0.10, 0.24)	0.67 (0.55, 0.79)	0.25 (0.001, 0.53)	40, 101, 466
Fecundity F_0	monoculture vs. experienced community	0.63 (0.56, 0.70)	0.76 (0.72, 0.81)	0.21 (0.001, 0.46)	36, 94, 430
	monoculture vs. naïve community	0.61 (0.52, 0.67)	0.76 (0.72, 0.81)	0.20 (0.001, 0.51)	36, 94, 428
Population growth rate λ_1	monoculture vs. experienced community	0.41 (0.33, 0.49)	0.62 (0.55, 0.70)	0.15 (0.02, 0.30)	36, 87, 394
	monoculture vs. naïve community	0.32 (0.24, 0.39)	0.52 (0.44, 0.62)	0.05 (0.001, 0.25)	36, 87, 392

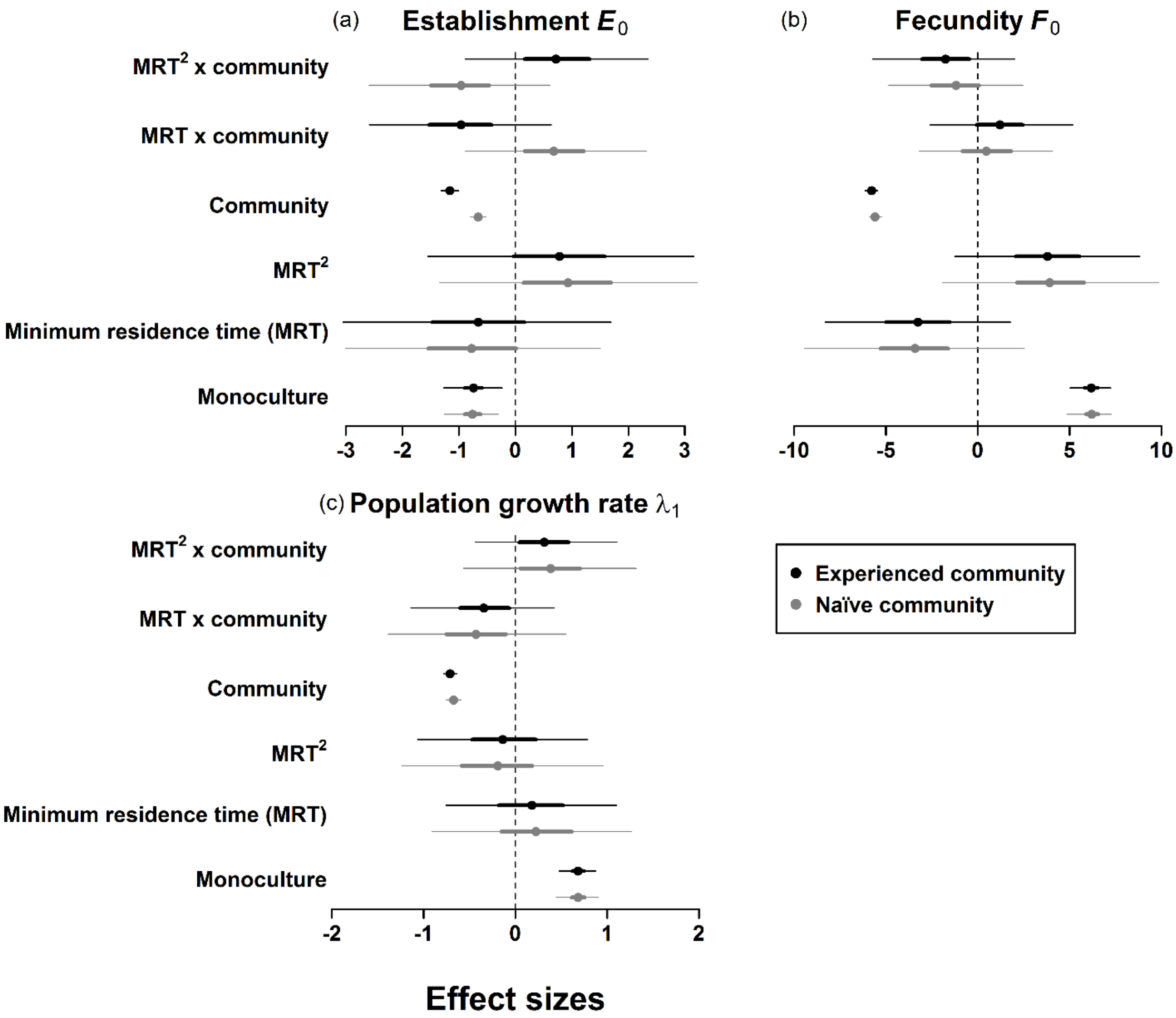

Figure S8: Effects of minimum residence time (linear and quadratic term), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction on (a) establishment (E_0), (b) fecundity (F_0) (in the first year), and (c) population growth rate in the second year (λ_1). Effect sizes of the models contrasting monoculture vs. experienced community are shown in black and effect sizes of the models contrasting monoculture vs. naïve community are shown in grey. Note that monoculture effect sizes refer to the intercept of the respective models and the community effect sizes refer to the contrast of monoculture vs. community. Filled circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals.

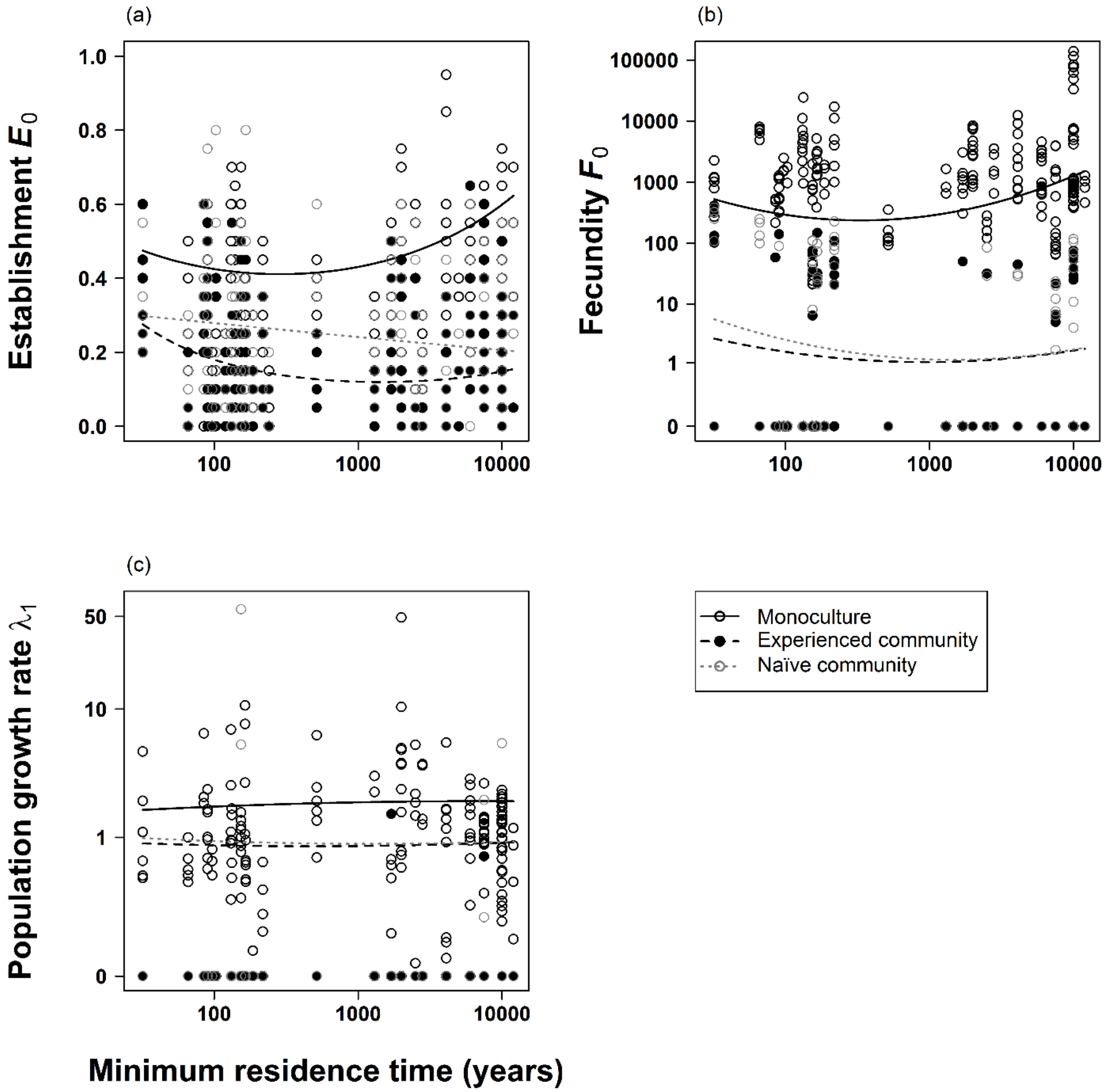

Figure S9: Predictions of the models relating (a) establishment (E_0), (b) fecundity (F_0) (in the first year), and (c) population growth rate in the second year (λ_1) to minimum residence time, competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction. Predictions of the models contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). The predictions of competition by the naïve community (based on the models contrasting monoculture vs. naïve community) are shown as grey dotted line. For each demographic performance measure, both models have identical effect sizes for monoculture (see Fig. S8), thus only one prediction is shown. All axes (except for E_0) are shown on log-scale.

Control analyses for effects of functional traits, competition treatment, and residence time on fitness

Table S5: Properties of the models for control analyses (only including wild populations) relating finite rate of increase (λ_0) to three functional traits (linear and quadratic effect of log-transformed seed mass, maximum height and specific leaf area), competition treatment, and their interaction (top row); and to minimum residence time (MRT), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction (bottom row).

		Mean R^2 (95% credible interval)		**Mean phylogenetic signal (95% credible interval)**	
Model	**Competition treatment**	**marginal**	**conditional**	**Pagel's lambda**	**Sample size (species, populations, mesocosms)**
Functional traits	monoculture vs. experienced community	0.70 (0.62, 0.77)	0.83 (0.79, 0.87)	0.32 (0.002, 0.53)	24, 67, 277
	monoculture vs. naïve community	0.67 (0.59, 0.75)	0.83 (0.78, 0.86)	0.35 (0.11, 0.61)	24, 67, 275
Minimum residence time	monoculture vs. experienced community	0.63 (0.55, 0.70)	0.77 (0.73, 0.82)	0.29 (0.001, 0.51)	24, 67, 277
	monoculture vs. naïve community	0.61 (0.52, 0.69)	0.78 (0.74, 0.83)	0.31 (0.001, 0.53)	24, 67, 275

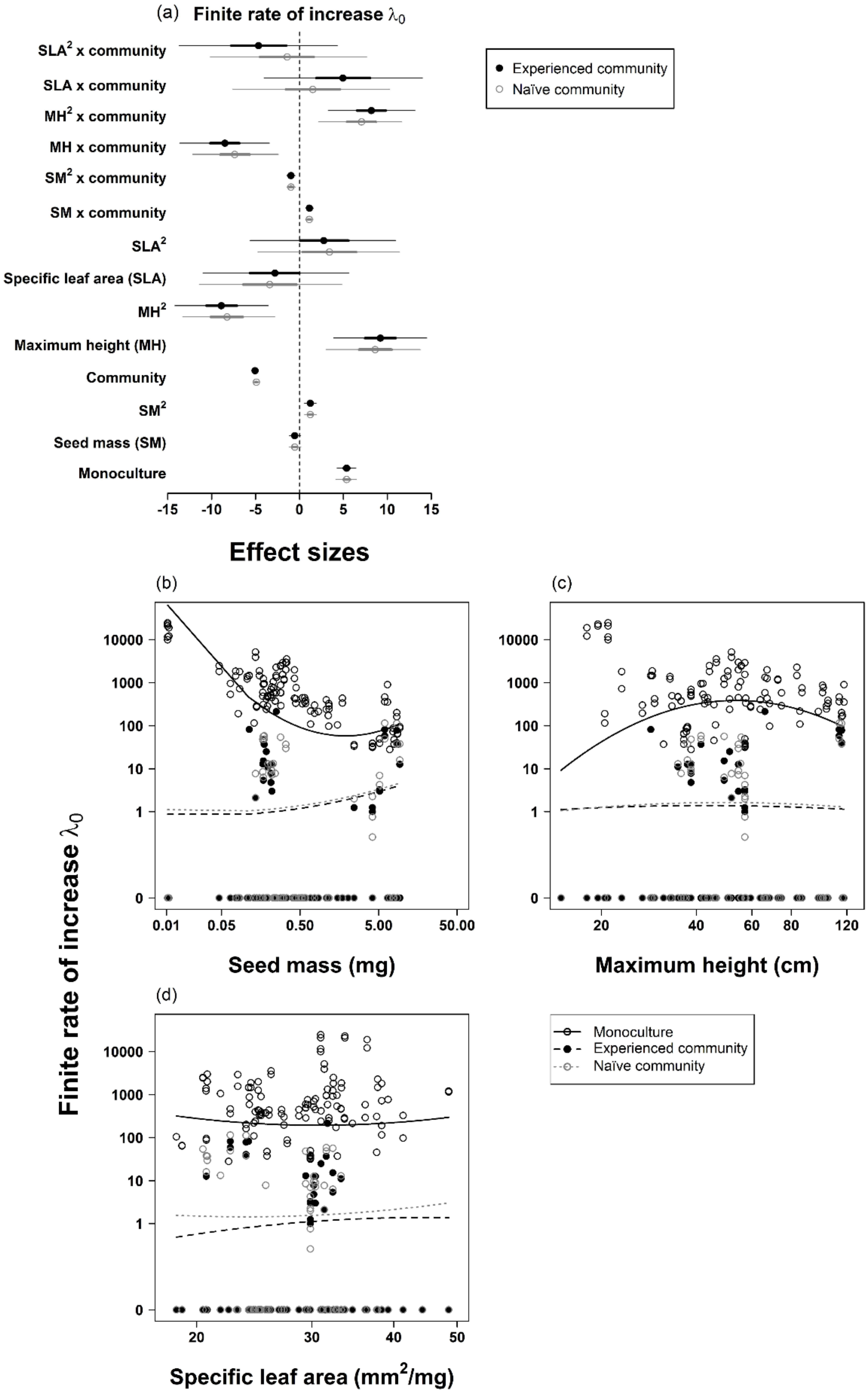

Figure S10: Effects of functional traits (linear and quadratic term of seed mass, maximum height, and specific leaf area), competition treatment (contrasting monoculture vs. experienced/naïve community), and their interaction on the finite rate of increase (λ_0) only including wild populations (<u>control analyses</u>).

Figure S10: (Continued) (a) Effect sizes of the model contrasting monoculture vs. experienced community are shown in black and effect sizes of the model contrasting monoculture vs. naïve community are shown in grey. Note that the monoculture effect sizes refer to the intercept of the respective model and the community effect sizes refer to the contrast of monoculture vs. community. Circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals. (b-d) Relationships between functional traits and the finite rate of increase (λ_0) in monoculture and the two community types (experienced and naïve community). Predictions of the model contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). Predictions for the naïve community (based on the model contrasting monoculture vs. naïve community) are shown as grey dotted line. Both models have identical effect sizes for monoculture, thus only one prediction is shown. Predictions are based on the full model with the other explanatory variables set to their mean value (i.e., zero, since the functional traits were scaled and centred, allowing the response of λ_0 to any given trait to be interpreted independently of the other trait variables in the respective model). Note that only interactions between functional traits and competition treatment (monoculture vs. community) in (b) and (c) are significant. All axes are shown on log-scale.

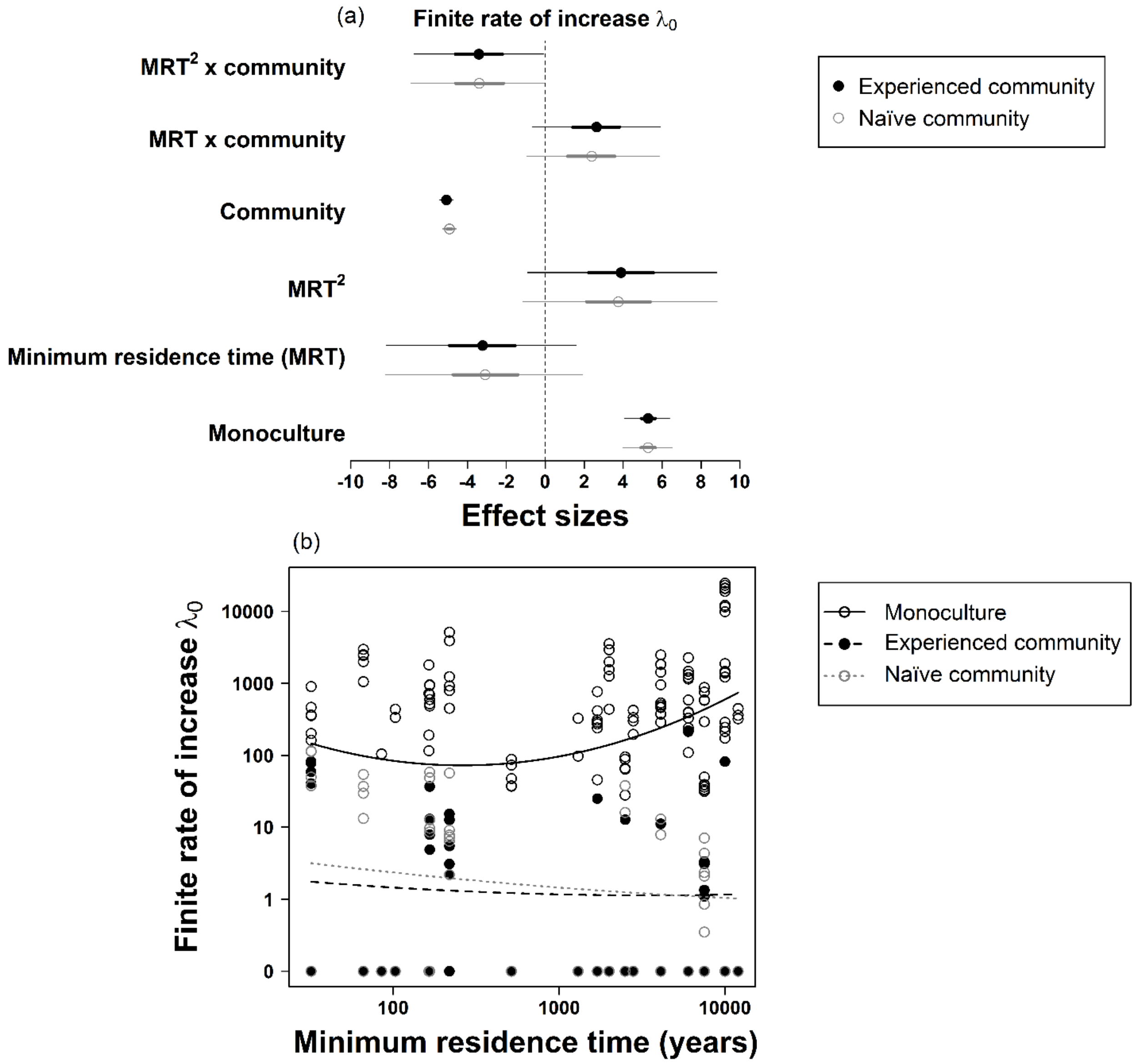

Figure S11: Effects of minimum residence time (MRT, linear and quadratic term), competition treatment (monoculture vs. experienced/naïve community), and their interaction on the finite rate of increase (λ_0) only including wild populations (control analyses). (a) Effect sizes of the model contrasting monoculture vs. experienced community are shown in black and effect sizes of the model contrasting monoculture vs. naïve community are shown in grey. Note that monoculture effect sizes represent the intercept of the respective model and the community effect sizes refer to the contrast of monoculture vs. community. Circles show the posterior mean effects. Thick lines represent the 68% inner credible intervals and thin lines the 95% outer credible intervals. (b) Predictions of the model contrasting monoculture vs. experienced community are shown in black (solid line: monoculture; dashed line: experienced community). The prediction of competition by the naïve community (based on the model contrasting monoculture vs. naïve community) is shown as dotted grey line. Both models have identical effect sizes for monoculture, thus only one prediction is shown. All axes are shown on log-scale.

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Supporting Information Chapter 3

Competitive ability of native and alien plants: effects of residence time and invasion status

Alien-native species continuum

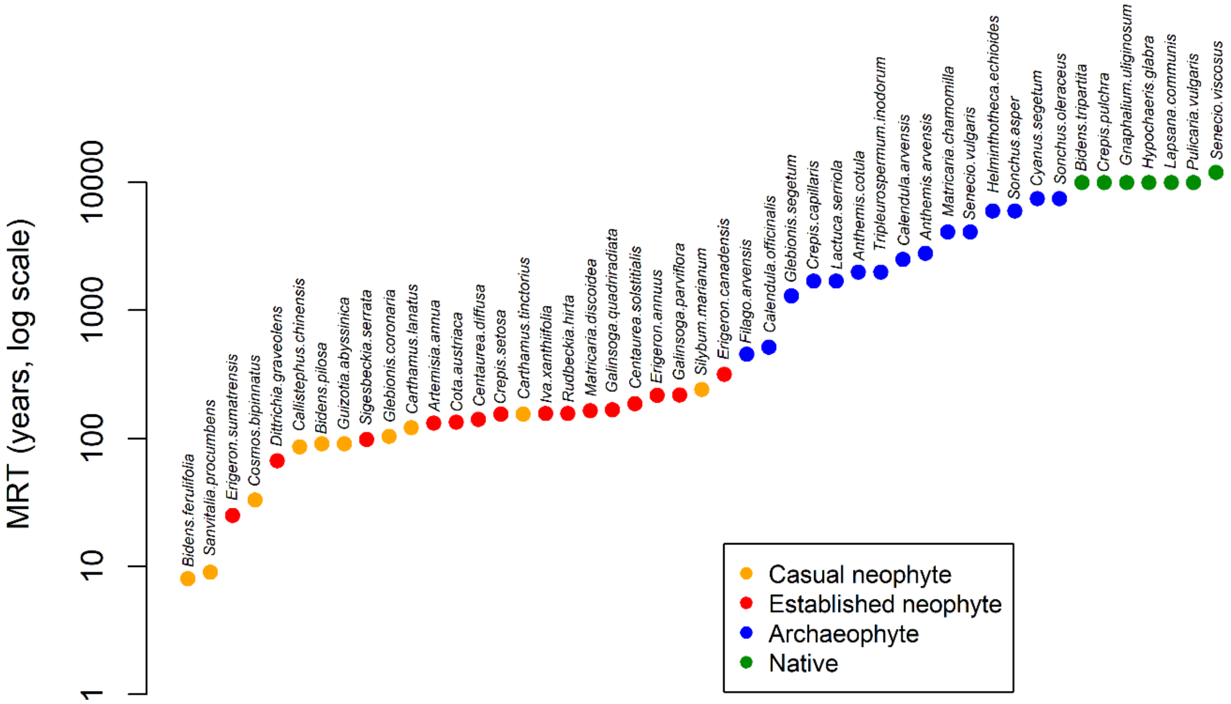

Figure S1: Alien-native continuum of 47 Asteraceae species, with their minimum residence times (MRT) and invasion status in Germany. Information on MRT was extracted from various databases (Sheppard & Schurr 2019). Note that for native species, MRT was usually assigned as 10,000 years (12,000 if there were pollen records from the late glacial) because the selected species likely re-immigrated at some point before the end of the last glacial period (Sheppard & Schurr 2019; Brendel *et al.* 2021).

Table S1: The 47 Asteraceae species (nomenclature according to the Plant List, http://www.theplantlist.org, Kalwij 2012) and their seed source (F1: seed material collected from wild populations or obtained from botanical gardens in 2015; F2: seeds initially originated from wild populations or botanical gardens and collected from mother plants that were grown for one generation in monoculture pots during 2016), the number of pots per species (only interspecific competition with target species shown; for the nutrient-poor and nutrient-rich soil), the average biomass (dry mass in g) per individual (n = number of individual plants used to calculate the average), the number of individuals needed to reach the reference neighbour biomass (21.38 g; for species with higher individual biomass than the reference biomass, the number of individuals was fixed at 2), the average establishment rate (n = number of pots used to calculate the average), and the number of seeds, after accounting for the average establishment rate, that entered the pots to initiate interspecific competition.

Species (seed source)	**Pots (nutrient-poor, nutrient-rich soil)**	**Average biomass per individual**	**Number of individuals**	**Average establishment rate**	**Number of seeds per pot**
Anthemis arvensis L. (F2)	11, 4	7.04 (n = 4)	3	0.40 (n = 2)	8
Anthemis cotula L. (F2)	15, 4	2.13 (n = 3)	10	0.50 (n = 2)	20
Artemisia annua L. (F2)	16, 3	6.57 (n = 4)	3	0.50 (n = 2)	6
Bidens ferulifolia (Jacq.) Sweet (F2)	17, 3	4.62 (n = 6)	5	0.50 (n = 2)	10
Bidens pilosa L. (F2)	14, 6	11.32 (n = 4)	2	0.53 (n = 2)	4
Bidens tripartita L. (F2)	15, 4	1.92 (n = 12)	10	0.15 (n = 100) †	67
Calendula arvensis M.Bieb. (F2)	17, 3	4.65 (n = 4)	5	0.58 (n = 2)	9
Calendula officinalis L. (F2)	17, 3	5.75 (n = 4)	4	0.35 (n = 2)	11
Callistephus chinensis (L.) Nees (F2)	13, 6	3.23 (n = 4)	7	0.10 (n = 2)	70
Carthamus lanatus L. (F2)	10, 3	41.16 (n = 4)	2	0.23 (n = 4)	9
Carthamus tinctorius L. (F2)	0, 5	1.99 (n = 4)	10	0.19 (n = 4)	52
Centaurea diffusa Lam. ($F1_{wild}$)	15, 5	6.78 (n = 4)	3	0.45 (n = 2)	7
Centaurea solstitialis L. (F2)	14, 5	12.95 (n = 4)	2	0.16 (n = 4)	13
Cosmos bipinnatus Cav. (F2)	14, 3	13.80 (n = 6)	2	0.38 (n = 2)	5
Cota austriaca (Jacq.) Sch.Bip. (F2)	16, 3	3.53 (n = 8)	6	0.57 (n = 3)	11
Crepis capillaris (L.) Wallr. (F2)	12, 6	4.26 (n = 4)	5	0.60 (n = 2)	8
Crepis pulchra L. (F2)	11, 4	3.79 (n = 6)	6	0.48 (n = 4)	13
Crepis setosa Haller f. (F2)	16, 4	2.38 (n = 6)	9	0.54 (n = 6)	17
Cyanus segetum Hill. (F2)	14, 6	4.28 (n = 10)	5	0.45 (n = 4)	11
Dittrichia graveolens (L.) Greuter (F2)	10, 1	11.08 (n = 4)	2	0.48 (n = 2)	4
Erigeron annuus (L.) Pers. ($F1_{wild}$)	13, 2	3.71 (n = 12)	6	0.23 (n = 2)	27
Erigeron canadensis L. ($F1_{wild}$)	15, 3	6.93 (n = 4)	3	0.43 (n = 2)	7

Table S1: (Continued).

Species (seed source)	Pots (nutrient-poor, nutrient-rich soil)	Average biomass per individual	Number of individuals	Average establishment rate	Number of seeds per pot
Erigeron sumatrensis Retz. (F1_{wild})	5, 5	9.11 (n = 12)	2	0.42 (n = 6)	5
Filago arvensis L. (F2)	5, 2	8.66 (n = 6)	3	0.50 (n = 2)	6
Galinsoga parviflora Cav. (F2)	15, 5	6.97 (n = 6)	3	0.48 (n = 2)	6
Galinsoga quadriradiata Ruiz & Pav. (F2)	14, 4	2.84 (n = 4)	8	0.75 (n = 2)	11
Glebionis coronaria (L.) Cass. ex Spach (F2)	17, 2	2.35 (n = 6)	9	0.30 (n = 2)	30
Glebionis segetum (L.) Fourr. (F2)	6, 1	12.88 (n = 4)	2	0.33 (n = 2)	6
Gnaphalium uliginosum L. (F2)	4, 0	4.65 (n = 6)	5	0.35 (n = 4)	14
Guizotia abyssinica (L.f.) Cass. (F2)	17, 3	8.34 (n = 6)	3	0.30 (n = 2)	10
Helminthotheca echioides (L.) Holub (F2)	15, 4	7.97 (n = 4)	3	0.70 (n = 2)	4
Hypochaeris glabra L. (F2)	14, 2	2.07 (n = 6)	10	0.56 (n = 6)	18
Iva xanthiifolia Nutt. (F2)	14, 3	2.73 (n = 2)	8	0.10 (n = 2)	80
Lactuca serriola L. (F1_{wild})	16, 4	24.86 (n = 4)	2	0.40 (n = 2)	5
Lapsana communis L. (F2)	11, 5	3.86 (n = 4)	6	0.50 (n = 2)	12
Matricaria chamomilla L. (F2)	11, 2	4.96 (n = 4)	4	0.50 (n = 2)	8
Matricaria discoidea DC. (F2)	16, 1	3.49 (n = 4)	6	0.45 (n = 2)	14
Pulicaria vulgaris Gaertn. (F2)	13, 3	6.05 (n = 4)	4	0.33 (n = 2)	12
Rudbeckia hirta L. ($\text{F1}_{\text{Dresden}}$)	13, 6	7.54 (n = 6)	3	0.40 (n = 2)	8
Sanvitalia procumbens Lam. (F2)	15, 3	4.59 (n = 4)	5	0.48 (n = 2)	11
Senecio viscosus L. (F2)	14, 1	4.28 (n = 4)	5	0.70 (n = 2)	7
Senecio vulgaris L. (F2)	11, 4	2.28 (n = 4)	9	0.50 (n = 2)	18
Sigesbeckia serrata DC. (F2)	12, 6	6.01 (n = 12)	4	0.10 (n = 6)	40
Silybum marianum (L.) Gaertn. (F2)	14, 6	4.08 (n = 12)	5	0.15 (n = 4) ‡	33
Sonchus asper (L.) Hill (F2)	15, 5	2.39 (n = 4)	9	0.48 (n = 2)	19
Sonchus oleraceus (L.) L. (F2)	16, 2	4.00 (n = 4)	5	0.35 (n = 2)	14
Tripleurospermum inodorum (L.) Sch.Bip. (F2)	17, 3	14.19 (n = 4)	2	0.35 n = 2)	6

† germination rate (of 100 seeds) measured under greenhouse conditions in 2015

‡ average establishment rate taken from different populations of the same species

Appendix S1: Establishment of targets and neighbours

To establish target individuals, three seeds for *Crepis pulchra*, *Hypochaeris glabra*, *Lapsana communis*, and *Senecio viscosus,* and five seeds for *Pulicaria vulgaris* were added to the centre of each pot. A species-specific number of neighbour seeds was sown around the target seeds. To determine the required number of seeds to be sown for each neighbour species, we used data on the average biomass production (in low intraspecific competition: 6 individuals were transplanted in 50L-pots) and establishment rates of the same species (and populations) from a previous experiment in 2016 (Brendel *et al.* 2021). Given the size of our pots, we aimed for the number of neighbour individuals to range between two and ten. Using this basis, we calculated a reference value for the neighbour biomass: the median of the average biomass at population-level across all Asteraceae species multiplied with half of the maximum number of neighbour individuals per pot we aimed for (i.e., five). In this way, we guaranteed that for each Asteraceae species, no more than ten individuals were needed to reach this reference biomass. Since competition was initiated from seeds, we multiplied the number of individuals per population with the respective establishment rate, which resulted in a species-specific amount of seeds for the neighbours that entered the pots (see Table S1).

If a target did not germinate, we transplanted a back-up seedling from additional germination trays established in the greenhouse. Because we aimed to have similar starting sizes compared to the seedlings sown from seed in case transplanting was necessary, these additional germination trays were established two weeks after sowing into pots due to the faster germination and growth rates in the greenhouse. If a neighbour did not germinate, neighbour seeds were re-sown. In the nutrient-poor soil type, 204 of a total of 615 pots thus had either transplanted targets (101 pots) or re-sown neighbours (88 pots) or both (15 pots); for the nutrient-rich soil type it was 44 of 168 pots respectively (28 transplanted targets, 12 re-sown neighbours, 4 both).

Competitive effect of each neighbour species on the target species

Table S2: Linear regressions of species-specific competitive effects of neighbours on the five native target species. Slope (indicating competitive effect), standard error of the slope (used for weighing), R^2 and results of F-test (F-test statistic, degrees of freedom [whereby sample sizes are df+2] and *P*-values) are shown.

Species	Slope	Standard error	R^2	F	df	*P*-value
Anthemis arvensis	-0.700	0.118	79.7	35.3	9	<0.001
Anthemis cotula	-0.849	0.235	50.2	13.1	13	0.003
Artemisia annua	-0.777	0.096	82.5	65.9	14	<0.001
Bidens ferulifolia	0.325	0.124	31.4	6.9	15	0.019
Bidens pilosa	-0.318	0.176	21.3	3.3	12	0.096
Bidens tripartita	-1.048	0.316	45.8	11.0	13	0.006
Calendula arvensis	-0.799	0.315	30	6.4	15	0.023
Calendula officinalis	-0.683	0.167	52.7	16.7	15	0.001
Callistephus chinensis	0.043	0.178	0.5	0.1	11	0.813
Carthamus lanatus	-0.581	0.194	52.9	9.0	8	0.017
Centaurea diffusa	-1.033	0.420	31.8	6.1	13	0.029
Centaurea solstitialis	-0.461	0.224	26.1	4.2	12	0.062
Cosmos bipinnatus	-0.293	0.113	35.9	6.7	12	0.024
Cota austriaca	-0.354	0.361	6.4	1.0	14	0.343
Crepis capillaris	-1.656	0.874	26.4	3.6	10	0.087
Crepis pulchra	-0.296	1.169	0.7	0.1	9	0.806
Crepis setosa	-0.861	0.160	67.3	28.8	14	<0.001
Cyanus segetum	-0.881	0.236	53.8	14.0	12	0.003
Dittrichia graveolens	-0.513	0.192	47.2	7.1	8	0.028
Erigeron annuus	-0.864	0.231	56.1	14.1	11	0.003
Erigeron canadensis	-1.132	0.268	57.8	17.8	13	0.001
Erigeron sumatrensis	-1.158	0.254	87.4	20.8	3	0.02
Filago arvensis	-0.146	0.499	2.8	0.1	3	0.788
Galinsoga parviflora	-0.904	0.205	59.9	19.4	13	0.001
Galinsoga quadriradiata	-1.207	0.338	51.6	12.8	12	0.004

Table S2: (Continued).

Species	Slope	Standard error	R^2	F	df	*P*-value
Glebionis coronaria	-0.497	0.137	46.6	13.1	15	0.003
Glebionis segetum	-0.344	0.309	23.7	1.2	4	0.327
Gnaphalium uliginosum	-0.54	0.669	24.6	0.7	2	0.504
Guizotia abyssinica	-0.412	0.175	26.9	5.5	15	0.033
Helminthotheca echioides	-0.83	0.169	65.1	24.3	13	<0.001
Hypochaeris glabra	-0.899	0.383	31.4	5.5	12	0.037
Iva xanthiifolia	-0.963	0.104	87.7	85.8	12	<0.001
Lactuca serriola	-0.535	0.220	29.6	5.9	14	0.029
Lapsana communis	-1.024	0.171	80	35.9	9	<0.001
Matricaria chamomilla	0.221	0.380	3.6	0.3	9	0.575
Matricaria discoidea	-0.63	0.238	33.3	7.0	14	0.019
Pulicaria vulgaris	-0.818	0.244	50.6	11.3	11	0.006
Rudbeckia hirta	-0.854	0.166	70.7	26.5	11	<0.001
Sanvitalia procumbens	-0.528	0.134	54.4	15.5	13	0.002
Senecio viscosus	-0.442	0.308	14.7	2.1	12	0.177
Senecio vulgaris	-0.848	0.474	26.2	3.2	9	0.107
Sigesbeckia serrata	-0.381	0.122	49.6	9.8	10	0.011
Silybum marianum	-0.916	0.320	40.6	8.2	12	0.014
Sonchus asper	-0.847	0.299	38.1	8.0	13	0.014
Sonchus oleraceus	-0.459	0.285	15.6	2.6	14	0.129
Tripleurospermum inodorum	-0.334	0.099	43.2	11.4	15	0.004

Biomass production of the target species

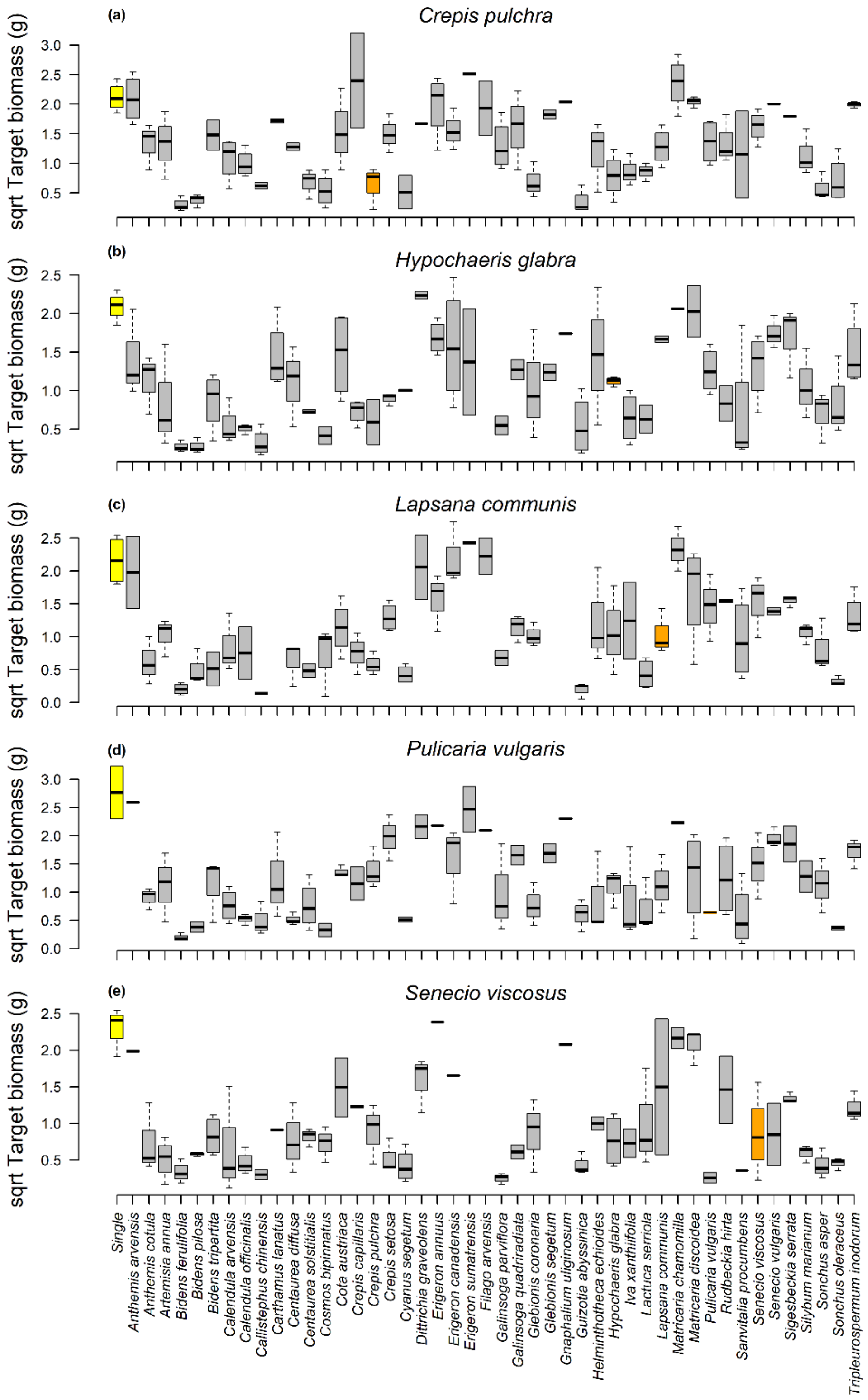

Figure S2: Square-root-transformed target biomass depending on neighbour species in the nutrient-poor soil. (a) *Crepis pulchra* (n = 137), (b) *Hypochaeris glabra* (n = 136), (c) *Lapsana communis* (n = 131), (d) *Pulicaria vulgaris* (n = 126), and (e) *Senecio viscosus* (n = 117). Single target plants are highlighted in yellow, conspecific neighbours (intraspecific competition) in orange.

Results of control analyses for effects of neighbour biomass on target performance

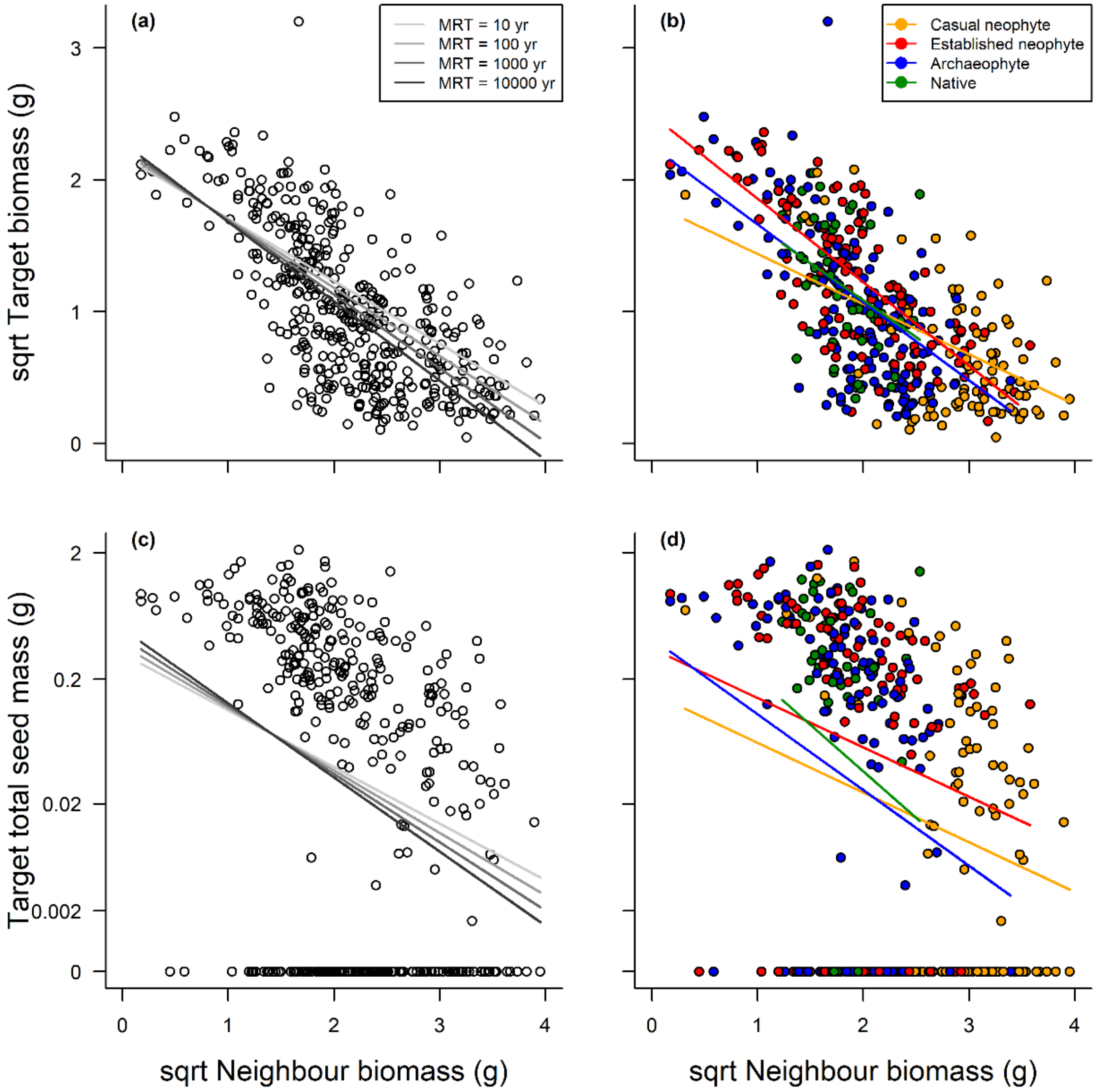

Figure S3: Effects of square-root-transformed neighbour biomass on target performance: (a,b) square-root-transformed aboveground biomass (n = 411), and (c,d) total seed mass (shown on log-scale, n = 411), depending on (a,c) minimum residence time (MRT) or (b,d) invasion status in the control analysis (without transplanted targets and/or re-sown neighbours) for the nutrient-poor soil. To illustrate the interaction between continuous MRT and neighbour biomass in (a,c), a few representative values were chosen.

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