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RESEARCH ARTICLE

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Responses of naturalized alien plants to soil heterogeneity and competition vary with the global naturalization success of the native competitors

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Abstract

1. Soil heterogeneity (i.e. the heterogeneous distribution of nutrients, soil types or other soil characteristics) has been found to promote the invasion success of naturalized alien plants (i.e. plants that have been introduced by humans to new ranges, where they have established persistent populations) when competing with native plants. However, native species that compete with the naturalized aliens may themselves be naturalized alien species elsewhere. It has also been found that common species, irrespective of whether they are alien or native, benefit more from high resource availability than rare species. Therefore, it remains unknown how regional commonness of alien plants and the extent of the worldwide naturalized geographical distribution of native species impact the invasion process on heterogeneous soils.
2. We considered the geographical distributions of native and alien species in Germany at two scales: commonness (i.e. grid-cell frequency) in Germany and the global naturalized distribution. Then, to test whether the performance of common ($n=7$) and rare ($n=7$) alien species in Germany depends on soil heterogeneity and on whether the natives they compete with are themselves widely naturalized elsewhere (i.e. outside of Germany; $n=10$) or not ($n=5$), we conducted a large outdoor pot experiment.
3. We found that the growth of the alien plants, irrespective of whether they are relatively rare or common in Germany, was reduced by competition, and particularly if the native competitor is widely naturalized elsewhere. Consequently, the relative biomass of the alien plants (i.e. the ratio of alien to total biomass) was reduced when growing with a native plant that is widely naturalized elsewhere. Soil heterogeneity overall resulted in a reduced growth, but this was not the case for the common aliens when they were competing with a native that is widely naturalized elsewhere.
4. *Synthesis*. Our findings thus show that soil heterogeneity does not always promote alien plants over native plants. Moreover, our findings show that when testing the

effects of native species on naturalized alien species, it is important to consider whether the native species themselves are widely naturalized around the globe or not.

KEYWORDS
competition, environmental heterogeneity, facilitation, geographical commonness, invasibility, invasion ecology, plant–plant interactions

1 | INTRODUCTION

Together with the increasing movement of humans, culture and goods, more and more species have been introduced across geographical barriers into novel regions, leading to floristic homogenization (Kinlock et al., 2022; Yang et al., 2021). A subset of these so-called alien species has formed self-sustaining populations in nature (i.e. are naturalized alien species), and the naturalized species that spread rapidly and frequently have negative impacts on the environment are considered invasive (Blackburn et al., 2011; Richardson et al., 2000). Naturalization, however, is a central stage of the invasion process, and it is of high importance to study and understand the mechanisms underlying the invasion (i.e. establishment) of naturalized alien species into local communities (Richardson & Pyšek, 2012).

Worldwide, at least 13,000 plant species have become naturalized due to human activities during the past centuries, and the pace of biological invasions does not seem to slow down in the foreseeable future (Seebens et al., 2017; Seebens et al., 2021; van Kleunen et al., 2015). Thus, how introduced alien plants interact with the local plant species remains one of the key questions in ecology. Answering this question will be necessary in order to reduce biological invasions and maintain native biodiversity and the functioning of ecosystems under global change (IPBES, 2023; Valladares et al., 2015).

Competition between alien and native plants is commonly thought to play an important role in the invasion process (Gioria & Osborne, 2014; Kuebbing & Nuñez, 2015). A large number of studies have tested whether aliens are more competitive than natives in different aspects, yet no agreement has been reached (Kuebbing & Nuñez, 2016; Vilà & Weiner, 2004; Zhang & van Kleunen, 2019). So, key questions are what determines the competitiveness of alien species, and are they really different from native species. With regard to the latter, it is important to consider that a species that is native to a region may at the same time be a naturalized alien in other regions (van Kleunen et al., 2010). So, when comparing alien to native species, it might be important to consider how successful the native species are as naturalized aliens in other parts of the world.

Similarly, not all naturalized alien species are equally competitive and successful. Some occur in relatively few regions or are relatively rare within their non-native range. So, both among the natives and aliens in a region, we have successful and less successful species both at the regional scale and at the global scale. Frequently, species that are widespread globally grow faster than less widely distributed species (Dawson et al., 2011). A recent study also found that common aliens are more competitive than rare natives but are not necessarily more competitive than common natives due to the high intrinsic growth rates of both groups of common species (Zhang & van Kleunen, 2019). Furthermore, it has been shown that common species, and especially common aliens, may take more advantage of nutrient addition (i.e. eutrophication), resulting in a higher competitiveness (Dawson et al., 2012). However, whether this is a general pattern and how it depends on the spatial distribution of resources remains unclear.

Soil heterogeneity, that is, the heterogeneous distribution of nutrients, soil types and various physical and chemical characteristics of the soil (Xue et al., 2019), is ubiquitous in nature. Heterogeneous soils can impact seed germination (Liu & Hou, 2021), ramet placement of clonal plants (Dong et al., 2015), root foraging (Keser et al., 2014), as well as growth and biomass allocation of plants (Liu, Li, et al., 2021). In addition, heterogeneous soils are thought to create more niche opportunities, and thus could promote species coexistence (Beck & Givnish, 2021; Liu, Bortier, et al., 2021; Stover & Henry, 2019). Indeed, some recent studies found that soil heterogeneity benefited common alien species by alleviating the competitive pressure from native plant communities (Gao et al., 2021; Wei & van Kleunen, 2022). However, whether this is also true for less common alien species, and how it depends on whether the native competitors themselves are widespread as alien species elsewhere, remains unknown.

Here, we conducted an experiment with seven rare and seven common alien species in Germany. We grew these 14 alien species on homogeneous and heterogeneous substrates alone or in pairwise competition with 15 native species, of which 10 are widely naturalized elsewhere (outside of Germany) and 5 are not widely naturalized. With the 210 alien–native competitor pairs on heterogeneous and homogeneous soils, we aimed to answer the following questions: (1) Do the alien species take more advantage of the heterogeneous soil conditions than the native species and is this effect stronger for the common alien species than for the rare ones? (2) Are the alien species, and particularly the rare ones, less competitive when they compete with natives that are widely naturalized elsewhere in the world?

2 | MATERIALS AND METHODS

2.1 | Study species

To increase the generality of our findings (van Kleunen et al., 2014), we selected 14 herbaceous species that are naturalized aliens in Germany as target plants and 15 native species as competitors (Table S1). To determine whether a species is relatively common or rare in Germany, we used grid-cell occupancy data from the FloraWeb database (https://www.floraweb.de/). Germany has a total of 3000 grid cells, each with an area of c. 133 km^2. The naturalized alien species differ in their occurrence frequencies within Germany, and the seven species that occur in fewer than 25% (<750 grid cells) of the 3000 grid cells in Germany were categorized as rare (ranging from 23 to 715 grid cells), and the seven species that occur in more than 36% (>1100 grid cells) were categorized as common (ranging from 1168 to 2863 grid cells; Figure 1a). These cut-offs for rare and common are arbitrary, but there was a clear difference between both groups in occupied grid-cell numbers in Germany. How widely naturalized a species is globally was assessed using the number of regions (predominantly administrative regions such as countries, states and provinces) in which the species is known to be naturalized. This was obtained from the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al., 2019), which provides such data for 947 non-overlapping regions. We defined a species as widely naturalized when it has naturalized in at least 45 regions (is within the top 10% of the most widely naturalized species, Figure S1). The common alien species are widespread (i.e. occur in many grid cells) in Germany and are also widely naturalized globally (ranging from 89 to 302 regions), whereas the rare alien species are overall less widespread in Germany and less widely naturalized (ranging from 17 to 162 regions; Figure 1b). To increase the likelihood that the alien species encounter all native study species in Germany, we only selected native species that are common in Germany (i.e. occur in many grid cells). However, to study the effect of global naturalization success of native species on competition, we also wanted the native species to differ in how widely naturalized they are in other parts of

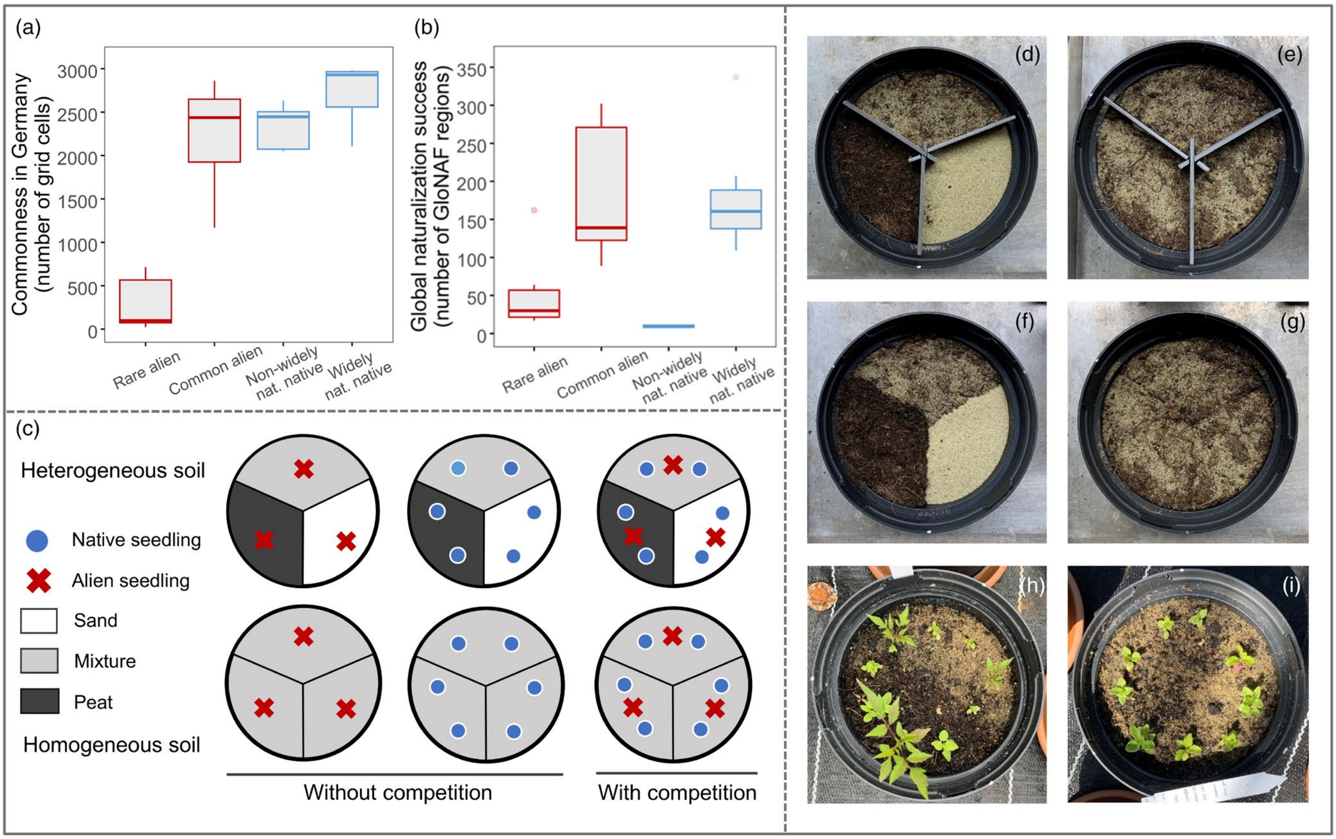

FIGURE 1 Overview of the experiment. (a) Number of grid cells (out of 3000) in which the two groups of alien target species (in red; rare, common) and the two groups of native competitor species (in blue; non-widely naturalized, widely naturalized elsewhere) occur in Germany according to the FloraWeb database (www.floraweb.de). (b) Number of regions around the world in which the two groups of alien species (in red; rare, common) and the two groups of native competitor species (in blue; non-widely naturalized, widely naturalized elsewhere) are naturalized according to the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al., 2019). (c) Illustrations of soil heterogeneity treatments, planting positions of the alien plants (red crosses), planting positions of the native competitor plants (blue dots) in the treatments without and with competition. (d–i) Photos of the soil heterogeneity treatments. A 3-L pot with the divider used to create three equally sized patches in the heterogeneous soil treatment (d) and the homogeneous soil treatment (e). Photos of the heterogeneous soil treatment (f) and homogeneous soil treatment (g) after removing the divider from the pot. Plants after one week of growth in the heterogeneous soil treatment (h) and in the homogeneous soil treatment (i).

the world. Therefore, we selected 15 native species that are common in Germany (ranging from 2050 to 2981 grid cells; Figure 1a), but differ in how widely they are naturalized elsewhere in the world. Ten of the native species are naturalized in more than 100 regions (ranging from 109 to 337 regions), and are classified as globally widely naturalized native species, whereas the remaining five native species are classified as globally non-widely naturalized native species (ranging from 7 to 12 regions; Figure 1b). So, we had four groups of species: common and rare alien species, and widely and non-widely naturalized natives. Seeds of the 29 study species came from the seed collection of the Botanical Garden of the University of Konstanz and the commercial seed supplier Rieger-Hofmann GmbH, Germany (Table S1).

2.2 | Plant materials, experimental setup and measurements

The experiment was conducted in the Botanical Garden of the University of Konstanz, Germany (47°69′19.56″N, 9°17′78.42″E). We started the seed germination of the 14 alien and 15 native plant species between the 17 and 25 May 2021 in a greenhouse of the botanical garden. From previous experiments, we knew that the germination speed varies among the species. Therefore, to assure that the seedlings of the different species would be at a similar developmental stage at the start of the experiment, we sowed the seeds on different dates (Table S1). Seeds of each species were sown separately in plastic trays (18.5 cm × 14 cm × 5 cm, length × width × height) filled with a peat-based potting soil (Pikiererde®, Einheitserdewerke Patzer PATZER ERDEN GmbH, Sinntal-Altengronau, Germany; pH 5.8; 1.5 g/L KCl; 180 mg/L N; 200 mg/L P_2O_5; 240 mg/L K_2O; 130 mg/L S and 150 mg/L Mg).

To test the effect of soil heterogeneity and competition by native plant species that are globally widely or non-widely naturalized on the growth of the rare and common alien species, we set up a factorial experiment (Figure 1c). Firstly, we created spatially homogeneous and spatially heterogeneous soils in 3-L pots (top Ø: 19 cm, bottom Ø: 14 cm, height: 15 cm). By using a specially designed plastic divider, we divided each pot into three thirds. In pots with heterogeneous soil, we filled one third with sand (commercial river sand), one third with potting substrate that contains 55% white peat (Cyclamen®, HAWITA GRUPPE GmbH, Vechta, Germany; pH 6.0; 150 mg/L N; 150 mg/L P_2O_5; 250 mg/L K_2O and 130 mg/L Mg), further referred to as peat, and one third with a 1:1 (v:v) mixture of sand and peat, whereas in pots with homogeneous soil, all three thirds were filled with the 1:1 mixture of sand and peat (Figure 1d,e). Thus, the total amounts of peat and sand were the same in both heterogeneous and homogeneous pots (i.e. they only differed in soil heterogeneity). The divider was removed from each pot after filling in the soil (Figure 1f,g). Although the pots in the homogeneous treatment had no patches of different substrate, we still marked the three thirds as patches for comparative purposes.

On the 31 May 2021, we started to transplant seedlings of the different plant species into each pot. For pots without interspecific competition, we planted one seedling of the alien species in each of the three patches per pot, with five replicate pots per alien species per heterogeneity treatment (Figure 1c). For the treatment with interspecific competition, we additionally planted two seedlings of one of the native species into each of the three patches per pot, with one native seedling on each side of the alien seedling in the patch (Figure 1c). Each of the 14 alien species was grown in pairwise competition with each of the 15 native species, resulting in 210 species combinations. We chose to have more native plant seedlings than alien seedlings to better mimic the natural condition of introducing an alien species into a site already occupied by a native species. To also be able to assess the effect of the alien target species on the native competitors, we also had pots with only the native species (two plants per patch) (Figure 1c), with five replicate pots per native species per heterogeneity treatment. In total, we had 2 soil heterogeneity treatments × (210 pairwise alien-native species combinations + [14 alien + 15 native single species] × 5 replicates) = 710 pots. We transplanted 1680 alien plant seedlings and 3420 native plant seedlings, totalling 5100 seedlings ([(14 Alien × 3 seedlings + 15 Native × 6 seedlings) × 5 replicates + (14 Alien × 15 Native) competition combinations × 9 seedlings] × 2 soil heterogeneity treatments).

In the week after transplanting, we replaced any seedlings that had died, and we measured the initial sizes of all transplanted alien seedlings to be able to account for initial size differences. Firstly, we counted the number of cotyledons and true leaves, and measured the length and width of the largest cotyledon and true leaf of all alien seedlings. For grasses, we did not differentiate between the cotyledon and true leaves as they were very similar. Secondly, we randomly selected 20 left-over seedlings of each of the 14 alien species from the germination trays and did the same initial size measurements as for the transplanted seedlings in the pots. Then, we scanned the leaves and calculated the leaf area using the software ImageJ (Schneider et al., 2012). For the 14 alien species, we then did for each species a regression of the total leaf area on the number of leaves, and the length and width of the largest leaf. The resulting regression equations were then used to estimate the total initial leaf area of each alien seedling in the pots (Table S2).

We started the experiment on the 14 June 2021, and ran the experiment for 10 weeks. The air temperature in the botanical garden during the experiment was between 7.6°C and 33.4°C. We watered each pot depending on the precipitation to maintain the soil moist, and we fertilized each pot after 4 and 8 weeks by applying 500 mL of nutrient solution (1 g/L Universol® Blue; ICL Deutschland, Nordhorn, Germany) to maintain soil fertility. On the 23 August 2021, we harvested the aboveground parts by species in each of the three patches per pot. All the plant materials were air-dried in an oven at 70°C for at least 72 h before weighing.

2.3 | Statistical analyses

Linear mixed effects models estimated by restricted maximum likelihood were fitted to test whether the responses of the alien plants were related to their commonness, soil heterogeneity, interspecific competition (without competition, with a globally widely naturalized native, with a globally non-widely naturalized native) and their interactions. All analyses were conducted using the *lmer* function of the *lme4* package (Bates et al., 2015), and figures were made using the *ggplot* function of the *ggplot2* package (Wickham, 2016) in R 4.4.1 (R Core Team, 2024). We graphically checked for all models whether the residuals were normally distributed using histograms and quantile-quantile plots. Homoscedasticity was checked by plotting the residuals against the fitted values and against each explanatory variable. If the data violated the assumptions of normality or homoscedasticity, we tried different transformations and chose the one that improved normality and homoscedasticity of the residuals the most (Table S3).

As we had collected the aboveground biomass data of plants in each pot by patch and by species, we had biomass data at the individual-plant level for the alien species, and at the patch level for the native species (2 individuals per patch). From the patch-level data, we also calculated the pot-level aboveground biomass data, which reflects the performance of the small experimental populations of alien ($n=3$) and native ($n=6$) plants in each pot. Therefore, by selecting specific subsets of our entire dataset, we were able to test our different research questions at the level of individuals/patches or populations/pots. In the main text, we focus on the responses of the alien plant species, but we also analysed the biomass of the native plant species as well as the biomass of the alien and native plants combined (see Tables S4–S9).

Firstly, we tested whether the different soil-patch types in the heterogeneous treatment, the commonness of the alien species, interspecific competition, and their interactions affected the aboveground biomass production of the alien plants in different soil patches. Therefore, we analysed the subset of data collected from pots in the heterogeneous treatment. We included patch type (sand, mixture and peat), interspecific competition (without competition, with a globally widely naturalized native, with a globally non-widely naturalized native), the commonness of the alien species (rare species or common species), and their interactions as fixed effects in the model. To further partition the effect of interspecific competition (if it was at least marginally significant), we ran orthogonal hierarchical contrasts to test the effect of competition per se ($\text{Competition}_{\text{without:with}}$: without competition vs competition with native species), and the effect of the global naturalization success of the native competitor ($\text{Competition}_{\text{non-widely:widely}}$, competition with a native species that is globally widely naturalized vs competition with a native species that is globally non-widely naturalized). For the subset of plants grown with competition, we also analysed the relative aboveground biomass (aboveground biomass of alien plant divided by aboveground biomass of alien and native plants combined in each soil patch).

Secondly, we tested whether soil heterogeneity, commonness of the alien species, interspecific competition, and their interactions affected the joint aboveground biomass of the three alien plants in a pot (i.e. whether they affected the performance of the small population of alien plants in a pot). In these models, we included soil heterogeneity (heterogeneous and homogeneous), commonness of the alien species (rare species and common species), interspecific competition (without competition, with a globally widely naturalized native and with a globally non-widely naturalized native) and their interactions as fixed effects. To further partition the effect of competition (if it was at least marginally significant), we again ran orthogonal hierarchical contrasts to test the effect of competition per se ($\text{Competition}_{\text{without:with}}$) and the effect of the global naturalization success of the native competitor ($\text{Competition}_{\text{non-widely:widely}}$). When testing the effects on the relative aboveground biomass of the alien plants (aboveground biomass of three alien plants divided by aboveground biomass of three alien and six native plants combined in each pot), we used the subset of data from pots with interspecific competition.

To account for non-independence of plants in the three patches within the same pot (i.e. to account for pseudoreplication), we included pot identity as a random effect when analysing the effect of soil-patch types in the heterogeneous pots at the individual level. As we were interested in how a group of species that differ in commonness responds to soil heterogeneity and competition rather than species-specific response differences, we included species identity of both the alien target plant and the native competitor plant as random terms in the statistical models described above to account for variation within each commonness species group. Therefore, for each of the interactions associated with commonness in the fixed terms of the model, the corresponding interaction associated with species identity was also included in the random terms of the same model to account for different responses of each plant species within the commonness groups to the treatments. When the response variable was aboveground biomass of the alien plant, we accounted for initial variation in alien plant size by including its initial leaf area as a covariate in the model.

The significance of fixed effects of the models was assessed with type I ANOVA using the Kenward–Roger method. The *F* values are reported together with the numerator degrees of freedom and denominator degrees of freedom. The results were qualitatively the same when we used type III ANOVA. However, we chose type I ANOVA (i.e. we used sequential sum of squares) because we were interested in partitioning the effects of the three competition treatments. Therefore, we ran orthogonal hierarchical contrasts to test the effect of competition per se ($\text{Competition}_{\text{without:with}}$) and, among the plants with competition, the effect of competition with a globally widely naturalized species versus competition with a globally non-widely naturalized species ($\text{Competition}_{\text{non-widely:widely}}$).

Due to mortality, we had two missing values out of 710 total observations at the population/pot level. At the individual/patch level, there were slightly more missing values: 33 out of a total of 1674 observations for alien individuals and 93 out of a total of 1704 observations for native individuals.

In addition to the analyses described above, we also calculated the relative interaction intensity (RII; Armas et al., 2004). However, as the results of both analyses were similar, we focused on the aboveground growth responses in the main text. The methods and results of the RII analysis are included in the Supporting Information (Tables S10–S12; Figures S8–S10).

3 | RESULTS

3.1 | Biomass of alien plant individuals in patches of the heterogeneous pots

Aboveground biomass of individual alien plants increased significantly from sand (mean ± SE: 1.07 ± 0.06 g) via the sand-peat mixture (mean ± SE: 1.58 ± 0.11 g) to peat (mean ± SE: 2.56 ± 0.16 g) patches (Table 1, $F_{\text{numerator-df,denominator-df}} = F_{2,24.4} = 22.19$, $p < 0.001$). Aboveground biomass production of alien individuals in the different patches tended to depend on the global naturalization success of their native competitors (marginally significant patch type × competition$_{\text{non-widely:widely}}$ interaction in Table 1, $F_{2,44.5} = 2.60$, $p = 0.085$; Figure 2a). When planted in sand or the mixture, the aboveground biomass of alien individuals was on average reduced by 25% and 15%, respectively, when competing with a globally widely naturalized native plant instead of a non-widely naturalized native plant. However, when planted in the peat patch, the aboveground biomass of alien individuals increased by 5% when competing with a globally widely naturalized native plant instead of a non-widely naturalized native plant (Figure 2a). Besides, aboveground biomass of rare alien individuals tended to be more negatively affected by competition with native plants (45.4% mean biomass reduction) than aboveground biomass of common alien individuals (7.6% mean biomass reduction), especially in the peat patch (marginally significant patch type × commonness × competition$_{\text{without:with}}$ interaction in Table 1, $F_{2,54.7} = 2.87$, $p = 0.065$; Figure 2a).

Although aboveground biomass of alien plants, native plants and both combined were significantly affected by the three types of soil patches in the heterogeneous pots, the relative aboveground biomass of alien plants did not significantly differ between the three patch types (Table 1; Tables S4 and S5; Figure 2a,b; Figures S2 and S3). Relative aboveground biomass of alien plants did, on average, not depend on the commonness of the alien plant, but it tended to be higher (on average by 47.6%) when competing with a globally non-widely naturalized native plant instead of with a widely naturalized native plant (marginally significant $C_{\text{non-widely}}$:C_{widely} effect in Table 1, $F_{1,13} = 3.25$, $p = 0.095$; Figure 2b). However, this effect of naturalization status of the native competitor also tended to depend on the commonness of the alien plant and soil patch type (marginally significant patch type × commonness × competition$_{\text{non-widely:widely}}$ interaction in Table 1, $F_{2,358.4} = 2.45$, $p = 0.088$; Figure 2b). While the negative effect of naturalization success of the native competitors for rare aliens was the weakest in the patches with a sand-peat mixture (on average, a 26.6% reduction of the aboveground relative abundance, followed by a 33.3% reduction on peat and a 34.8% reduction on sand), the reverse was true for common aliens (on average, a 39.7% reduction of the aboveground relative abundance on the sand-peat mixture, followed by a 36.8% reduction on sand and a 25.5% reduction on peat).

3.2 | Biomass of alien plant populations in the heterogeneous and homogeneous pots

The combined aboveground biomass of the population of three alien individual plants in each pot was on average 22.2% less on the heterogeneous soils than on homogeneous soils (Table 2, $F_{1,14.8} = 29.50$, $p < 0.001$; Figure 3a). This negative effect of soil heterogeneity was on average stronger (−25.9%) when the alien plants were growing without competition than when competing with native plants (−20.4%; significant soil heterogeneity × competition$_{\text{without:with}}$ interaction in Table 2, $F_{1,30.2} = 5.56$, $p = 0.025$; Figure 3a). However, when grown with competition, the negative effect of soil heterogeneity was on average stronger when the competitor was a non-widely naturalized native plant (−27.1%) than when it was a widely naturalized native plant (−16.2%; significant soil heterogeneity × competition$_{\text{non-widely:widely}}$ interaction in Table 2, $F_{1,23.4} = 11.71$, $p = 0.002$; Figure 3a). Furthermore, whereas the negative soil-heterogeneity effect on total biomass of the rare aliens was hardly affected by competition (Figure 3a), the soil-heterogeneity response of common alien plants declined with competition, and even disappeared when the competitors were widely naturalized native plants (significant soil heterogeneity × competition$_{\text{without:with}}$ × commonness interaction in Table 2, $F_{1,30.3} = 8.35$, $p = 0.007$, and significant soil heterogeneity × competition$_{\text{non-widely:widely}}$ × commonness interaction in Table 2, $F_{1,23.4} = 9.02$, $p = 0.006$; Figure 3a).

The aboveground biomass of the population of alien plants as a proportion of the total aboveground biomass per pot was on average not affected by soil heterogeneity nor by their own commonness (Table 2; Figure 3b). However, the relative biomass of the alien plants on average tended to decrease from 63.5% when competing with non-widely naturalized native plants to 42.4% when competing with widely naturalized plants (marginally significant effect in Table 2, $F_{1,13} = 3.91$, $p = 0.070$; Figure 3b). This effect, however, was mainly driven by the common alien plants in the homogeneous treatment (significant soil heterogeneity × competition$_{\text{non-widely:widely}}$ × commonness interaction in Table 2, $F_{1,179.7} = 7.14$, $p = 0.008$). When competing with non-widely naturalized natives, the relative aboveground biomass of common alien plants was on average reduced by 5.1% in heterogeneous soils compared to homogeneous soils, whereas it was increased by 3.2% when competing with widely naturalized natives (Figure 3b).

4 | DISCUSSION

Our study showed that plants grew best on the peat patches and worst on the sand patches, and that soil heterogeneity decreased the growth of both alien and native plants. However, the growth of

TABLE 1 Results of linear mixed models at the individual plant or patch level testing the effects of patch type (P: Sand, mixture and peat), commonness of the alien plant in Germany (Commonness: Common and rare aliens), competition with a native competitor (Competition: Without competition, competition with a globally non-widely naturalized native plant species, competition with a globally widely naturalized native plant species), and their interactions on aboveground biomass of the alien plant and relative aboveground biomass of the alien plant in the different patches of the heterogeneous pots.

Model terms	Aboveground biomass of alien plant				Relative aboveground biomass of alien plant			
Fixed effects	**ndf**	**ddf**	***F***	***p***	**ndf**	**ddf**	***F***	***p***
Initial leaf area	1	118.2	48.62	**<0.001**	—	—	—	—
Patch type (P)	2	24.4	22.19	**<0.001**	2	18.7	0.558	0.581
Commonness	1	12.0	0.108	0.748	1	12.0	1.020	0.332
Competition	2	12.6	1.534	0.253	—		—	—
$C_{without}$:C_{with} ($Comp_1$)	1	11.3	1.989	0.185	—		—	—
$C_{non\text{-}widely}$:C_{widely} ($Comp_2$)	1	14.1	1.084	0.315	1	13.0	3.251	*0.095*
P × Commonness	2	24.0	0.301	0.743	2	24.0	0.290	0.751
P × Competition	4	49.3	2.254	*0.077*	—		—	—
P × $Comp_1$	2	54.8	1.750	0.183	—		—	—
P × $Comp_2$	2	44.5	2.602	*0.085*	2	25.8	0.605	0.554
Commonness × Competition	2	24.1	1.249	0.305	—		—	—
Commonness × $Comp_1$	1	26.3	1.511	0.230	—		—	—
Commonness × $Comp_2$	1	22.1	1.133	0.299	1	179.0	0.111	0.740
P × Commonness × Competition	4	49.2	1.567	0.198	—		—	—
P × Commonness × $Comp_1$	2	54.7	2.867	*0.065*	—		—	—
P × Commonness × $Comp_2$	2	44.5	0.327	0.723	2	358.4	2.448	*0.088*
Random effects				**SD**				**SD**
Pot				0.082				0.089
Alien species identity (ID_{Alien})				0.324				0.173
Native species identity (ID_{Native})				0.111				0.200
ID_{Alien} × P				0.098				0.028
ID_{Native} × P				—				0.019
ID_{Alien} × ID_{Native}				—				0.090
ID_{Alien} × Competition				0.031				—
ID_{Alien} × P × Competition				0.037				—
Residual				0.188				0.161

Note: The effect of competition per se is indicated as $C_{without}$:C_{with} ($Comp_1$), and the competition between non-widely naturalized and widely naturalized native plants is indicated as $C_{non\text{-}widely}$:C_{widely} ($Comp_2$) in the table. Shown are the *F* values, numerator and denominator degrees of freedom (ndf, ddf) and *p* values for the fixed effects, and standard deviations (SD) for the random effects. Significant effects ($p < 0.05$) are shown in bold and marginally significant effects ($0.05 \leq p < 0.1$) are shown in italics.

common aliens was less negatively affected by heterogeneity when they competed with a widely naturalized native. Moreover, the relative biomass of alien plants grown with competition was more strongly related to the global naturalization success of their native competitors than to their own commonness. While previous studies showed that soil heterogeneity increased the growth of alien species (Gao et al., 2021; Wang et al., 2021; Wei & van Kleunen, 2022), our results suggest that this is not always the case, and that it might depend on the commonness of the alien plant and the naturalization success of the native competitor elsewhere. It is thus important to consider the naturalization success of native species when studying competition between naturalized alien and native plants.

4.1 | Global naturalization success of the native competitors mattered more to the aliens than their own commonness

In terms of aboveground biomass production and relative aboveground biomass production, rare alien species were not significantly different from common alien species. However, we found that the relative aboveground biomass of alien plants was more negatively affected when competing with native plants widely naturalized elsewhere than with non-widely naturalized native plants. This indicates that the widely naturalized natives were stronger competitors than the non-widely naturalized

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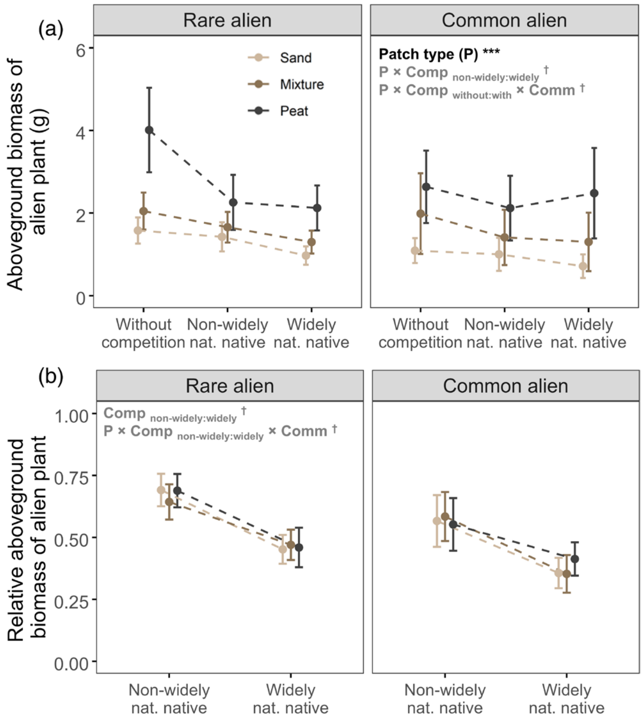

FIGURE 2 (a) Aboveground and (b) relative biomass of individual alien plants in the subset of pots from the heterogeneous soil treatment. Shown are individual-plant or patch-level effects of patch type (P: Sand, mixture and peat), commonness of the alien plant in Germany (Comm: Common and rare aliens), and competition with the native competitor (Comp: Without competition, competition with a globally non-widely naturalized native plant species, competition with a globally widely naturalized native plant species). Data shown are mean species-group values (±SEs) calculated from the means of the individual alien species in each group. Significant and marginally significant effects (see Table 1) are indicated in the figures. $^{\dagger}p<0.1$, $^{***}p<0.001$.

natives (Tables 1 and 2; Figures 2b and 3b). Indeed, the widely naturalized natives tended to produce more biomass than the non-widely naturalized natives (Tables S4 and S8; Figures S2a and S6a). This is in line with previous findings that plants with higher growth rates are more widespread globally, and that common species usually have higher growth rates than rare ones (Dawson et al., 2011; Zhang & van Kleunen, 2019). Notably, native plants that are widely naturalized elsewhere grew better than the native plants that are not widely naturalized on each of the patches in the heterogeneous soil treatment (Figure S2). This indicates that widely naturalized plants have a greater ecological breadth (i.e. are Jack-and-masters in the framework of Richards et al., 2006). Thus, assessing the global naturalization success of native species can indeed provide us with important information on their competitiveness. Moreover, native species that are widely naturalized elsewhere can be strong competitors that inhibit the growth of alien plants (mean relative biomass of alien plants <50%, Figures 2b and 3b), and thus can slow down the invasion process.

Interestingly, although the common and rare aliens also differed widely in their global naturalization success (Figure 1), they did not differ in biomass production. In contrast to the invaders of European origin (such as our native competitors), which have been translocated early on within the colonial networks of the previous European empires (Lenzner et al., 2022), many of the invaders from other continents were introduced later to non-native regions and probably less frequently. It has been reported that time since introduction influences naturalization success and invasiveness (Harris et al., 2007; Pyšek et al., 2015). As the actual year of introduction is unknown for the vast majority of alien species, we assessed the time effect using the first wild record of the studied alien species in Europe (Alien Species First Records Database (v3.1, https://zenodo.org/records/10039630; Seebens et al., 2017)). The common alien species were on average recorded for the first time as naturalized in the wild around the year 1749 (range: 1597–1814), and the first observations of the rare aliens in the wild were on average recorded about 25 years later from 1589 to 1865. As all alien species included in our study were recorded for the first time more than 150 years ago, we believe that this should have given the species sufficient time to spread. However, our findings might suggest that we have underestimated the time effect on the distribution and naturalization success of the alien species. In other words, the rare alien species in our study may not yet have had enough time to reach their full naturalization potential in Germany. Hence, the current geographical distribution of alien species might not yet reflect their full invasion potential.

4.2 | Soil heterogeneity reduced plant growth

In general, aboveground biomass of the populations of the alien plants as well as of the native plants on heterogeneous soils was lower than on homogeneous soils. Contrary to previous studies, which found that soil heterogeneity promoted plant growth (Gao et al., 2021; Wang et al., 2022; Wei & van Kleunen, 2022), our findings showed an overall negative soil heterogeneity effect. In the heterogeneous treatment of our study, we found that individual alien plants produced most biomass on the peat patches and the least on the sand patches, and intermediate biomass on the mixture patches. This most likely reflects that peat soil contains more nutrients than sand, and therefore benefits plant growth (Kitir et al., 2018). To our surprise, aboveground biomass of alien plants on the mixture patches of the homogeneous treatment was much higher than the biomass on the mixture patches and almost as high as on the peat patches of the heterogeneous treatment (compare Figure 2a with Figure S4a). This would suggest that additional factors might impact plant growth together with nutrient differences between the patches.

What factor could have reversed the effect of soil heterogeneity on plant growth? We can only speculate on this, but as the experiment was done outside, the extreme weather conditions during the experiment were likely responsible. In the summer of 2021, heavy precipitation frequently happened in southern Germany (Figure S11). During a rainfall event which lasted for a few days,

TABLE 2 Results of linear mixed models at the population or pot level testing the effects of soil heterogeneity (H: Heterogeneous and homogeneous), commonness of the alien plants in Germany (Commonness: Common and rare aliens), competition with a native competitor (Competition: Without competition, competition with a globally non-widely naturalized native plant species or competition with a globally widely naturalized native plant species), and their interactions on total aboveground biomass of the alien plants and relative aboveground biomass of the alien plants in the heterogeneous pots and homogeneous pots.

Model terms	Total aboveground biomass of alien plants				Relative aboveground biomass of alien plants			
Fixed effects	ndf	ddf	*F*	*p*	ndf	ddf	*F*	*p*
Initial leaf area	1	90.6	6.619	**0.012**	–	–	–	–
Soil heterogeneity (H)	1	14.8	29.50	**<0.001**	1	11.8	1.424	0.256
Commonness	1	12.0	0.248	0.628	1	12.0	0.507	0.490
Competition	2	13.4	2.056	0.167	–		–	–
$C_{without}$:C_{with} (Comp$_1$)	1	12.5	2.147	0.168	–		–	–
$C_{non\text{-}widely}$:C_{widely} (Comp$_2$)	1	14.3	1.980	0.181	1	13.0	3.910	*0.070*
H × Commonness	1	11.9	1.982	0.185	1	12.0	1.159	0.303
H × Competition	2	26.0	8.571	**0.001**	–		–	–
H × Comp$_1$	1	30.2	5.558	**0.025**	–		–	–
H × Comp$_2$	1	23.4	11.71	**0.002**	1	12.9	3.265	*0.094*
Commonness × Competition	2	24.1	0.256	0.776	–		–	–
Commonness × Comp$_1$	1	25.3	0.429	0.518	–		–	–
Commonness × Comp$_2$	1	22.4	0.125	0.727	1	180.4	0.328	0.567
H × Commonness × Competition	2	26.0	8.614	**0.001**	–		–	–
H × Commonness × Comp$_1$	1	30.3	8.347	**0.007**	–		–	–
H × Commonness × Comp$_2$	1	23.4	9.016	**0.006**	1	179.7	7.137	**0.008**
Random effects				SD				SD
Alien species identity (ID_{Alien})				0.514				0.711
Native species identity (ID_{Native})				0.192				0.589
ID_{Alien} × H				0.047				0.108
ID_{Native} × H				–				0.095
ID_{Alien} × ID_{Native}				–				0.337
ID_{Alien} × Competition				0.064				–
ID_{Alien} × H × Competition				0.016				–
Residual				0.211				0.485

Note: The effect of competition per se is indicated as $C_{without}$:C_{with} (Comp$_1$), and the competition between non-widely naturalized and widely naturalized native plants is indicated as $C_{non\text{-}widely}$:C_{widely} (Comp$_2$) in the table. Shown are the *F* values, numerator and denominator degrees of freedom (ndf, ddf) and *p* values for the fixed effects, and standard deviations (SD) for the random effects. Significant effects ($p < 0.05$) are shown in bold and marginally significant effects ($0.05 \le p < 0.1$) are shown in italics.

large amounts of rainwater ran through the pots in our experiment. This excess water flow may have flushed out many of the soluble nutrients. Because pure sand has a poor water-holding capacity, the heterogeneous pots may have lost more nutrients than the homogeneous pots, resulting in reduced plant growth in the heterogeneous pots of our current experiment. Even though we poured out excess water that remained in the trays below the pots after a heavy rainstorm, we could not prevent stagnant water in the pots causing flooding-like conditions. Due to the high water-holding capacity of peat, the peat patches remained waterlogged for a longer time after the rainstorms. During drier conditions, the high water-holding capacity of peat in the heterogeneous soils may have alleviated drought stress and benefited plant growth more than the homogeneous soils (Liu, Bortier, et al., 2021). Waterlogging in the heterogeneous soils may have resulted in oxygen deficiency and accumulation of toxic metabolites, which inhibit plant growth (Habibi et al., 2023; Pan et al., 2021). Additionally, biomass allocation might also have changed under waterlogging, as more energy will be invested to develop aerenchyma or adventitious roots to improve aeration (Manghwar et al., 2024; Voesenek & Bailey-Serres, 2015). However, as belowground productivity as well as root traits were not our main focus in this study, we did not collect or measure any root-related traits. Therefore, to find out what caused the opposing effects of soil heterogeneity on plant growth between this study and the one by Wei and van Kleunen (2022), more research is needed, especially from the belowground perspective.

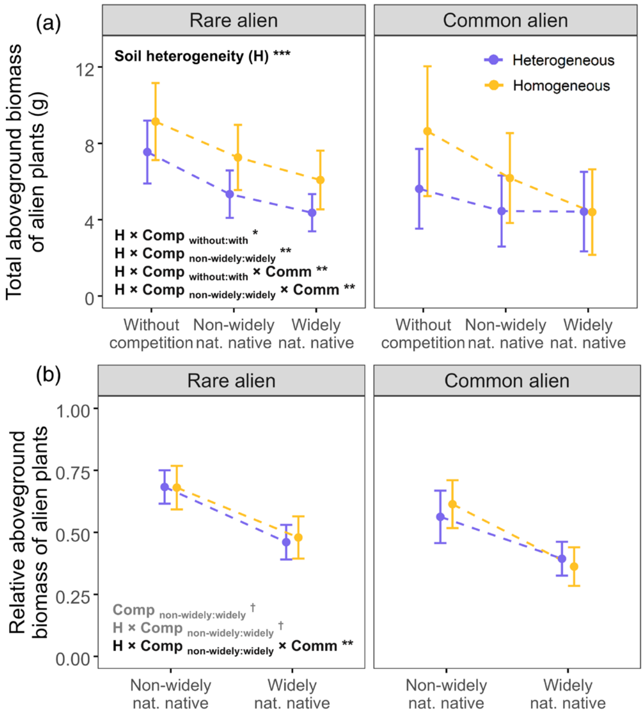

FIGURE 3 (a) Aboveground and (b) relative biomass of the small populations of alien plants per pot. Shown are population- or pot-level effects of soil heterogeneity (H: Heterogeneous, homogeneous), commonness of the alien plants in Germany (Comm: Common and rare aliens), and competition with the native competitor (Comp: Without competition, competition with a globally non-widely naturalized native plant species, competition with a globally widely naturalized native plant species). Data shown are mean species-group values (±SEs) calculated from the means of the individual alien species in each group. Significant and marginally significant effects (see Table 1) are indicated in the figures. †$p<0.1$, *$p<0.05$, **$p<0.01$, ***$p<0.001$.

While soil heterogeneity reduced biomass of the alien populations, the relative abundance of the alien plants in the pots did not change greatly in response to soil heterogeneity. Similarly, the relative biomass of the individual alien plants in the different soil-patch types of the heterogeneous pots did not vary greatly. In other words, the reduced growth responses to soil heterogeneity were similar for the alien and native plants. This indicates that the alien plants in our experiment were neither more stress-resistant nor more stress-sensitive than the native plants.

4.3 | Common aliens were less negatively affected by soil heterogeneity when competing with widely naturalized natives

As mentioned above, soil heterogeneity decreased the aboveground biomass production of alien and native plants. However, the negative effect of soil heterogeneity on the growth of the common alien plant populations disappeared when they were competing with widely naturalized native plants (Figure 3a). Our supplemental results on the relative interaction intensity (RII) accordingly also indicated that on average there was a weaker interaction for common alien plants competing with widely naturalized natives when grown in the heterogeneous pots instead of the homogeneous ones (Table S12; Figure S10). On the one hand, a reduced competition intensity in heterogeneous soils compared to homogeneous soils might simply indicate that competition was less intense due to decreased growth in the heterogeneous soils, which appeared overall to be more stressful. However, this is unlikely to explain our finding. The average aboveground biomass of the common alien plants was similar between homogeneous and heterogeneous soils, and so was the aboveground biomass of the widely naturalized native competitors (Figure 3a; Figure S6a). Therefore, regarding plant growth, the competition intensity between common alien plants and widely naturalized native plants should not greatly differ between homogeneous and heterogeneous soils.

On the other hand, as shown in the density plots of the RII values, the change in the average RII value is mostly because there were more positive RII values for individual pots, indicating facilitation (Figure S10b). So, in the homogeneous treatment, the aliens suffered from stronger competitive interactions by the globally widely naturalized native plants—probably due to their larger sizes—than from the non-widely naturalized ones (Figure S5). However, facilitative interactions became more important in the heterogeneous treatment, which was more stressful, possibly due to prolonged hypoxic conditions after heavy rains. This would be in line with previous findings that competitive interactions are in general more intense under benign environmental conditions, whereas facilitative interactions are more frequent under more stressful conditions (Callaway et al., 2002; Cavieres, 2021; Cavieres et al., 2014; He et al., 2013). It remains, however, unclear why this pattern only emerged for the common alien plants and not for the rare ones. Nevertheless, our results suggest that facilitative interactions between globally widely naturalized native plant species and common alien plant species under stressful conditions could further promote the spread of the common alien plant species.

Experiments like ours provide important insights into potential drivers of invasion success that can inform the management of biological invasions (IPBES, 2023). Our results show that the coexistence between alien and native species may not only depend on environmental heterogeneity, but also on whether the native species are themselves widely naturalized elsewhere or not. This suggests that to prevent plant invasions during vegetation restoration, one could plant or sow the area with native species that themselves are widely naturalized elsewhere. Their higher competitive ability might reduce the establishment chances of alien species. While the negative effect of soil heterogeneity on the alien plants in the current study suggests that managers could manipulate heterogeneity to reduce the establishment of alien plants, results of previous studies would suggest the opposite (Wei & van Kleunen, 2022). Therefore, more studies are needed to find out under which conditions soil heterogeneity is advantageous or disadvantageous for alien plants.

5 | CONCLUSIONS

Overall, our study suggests that soil heterogeneity under certain conditions could decrease the growth of plants, and therefore is not always beneficial. However, we also found that common aliens were less negatively affected when competing with natives that are globally widely naturalized. The growth of alien plants in competition was more strongly related to the global naturalization success of their native competitors than to their own commonness as aliens in Germany and worldwide. Although we considered both grid-cell frequency in Germany and global naturalization success of the study species, we did not consider other dimensions of commonness (Rabinowitz, 1981) or invasiveness (Catford et al., 2016; Fristoe et al., 2021), such as local population size and habitat generalism. Future studies should therefore aim to include more aspects of commonness and invasiveness to better understand how groups of species varying in their success respond to environmental heterogeneity and competition with species that also vary in their success. Furthermore, although we suggest that the unexpected negative effect of soil heterogeneity is related to the extreme rainfall during the experiment, this remains speculation. Therefore, experimental tests are needed to assess how the effects of soil heterogeneity depend on temporal heterogeneity in precipitation and other climatic factors.

AUTHOR CONTRIBUTIONS

Guan-Wen Wei and Mark van Kleunen conceived the idea and designed the experiment; Guan-Wen Wei performed the experiment; Guan-Wen Wei and Mark van Kleunen conducted the data analyses; Guan-Wen Wei wrote the first draft of the manuscript; Guan-Wen Wei and Mark van Kleunen revised the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code related to this paper can be accessed through the figshare repository: https://doi.org/10.6084/m9.figshare.28608113.v1 (Wei & van Kleunen, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Information about the study species.

Table S2: Regressions for calculating the initial leaf area of true leaf and cotyledon of alien plant species.

Table S3: Data transformations used for different response variables in the linear mixed effects models.

Table S4: Results of linear mixed models at the individual plant or patch level testing the effects of patch type (P: sand, mixture and peat), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), competition with an alien competitor in Germany (Competition: without competition, competition with a rare alien plant species, competition with a common alien plant species), and their interactions on aboveground biomass of the native plants in the different patches of the heterogeneous pots.

Table S5: Results of linear mixed models at the individual plant or patch level testing the effects of patch type (P: sand, mixture and peat), commonness of the alien plant in Germany (Commonness: common and rare aliens), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), and their interactions on total aboveground biomass of the alien and native plants combined in the different patches of the heterogeneous pots.

Table S6: Results of linear mixed models at the individual plant or patch level testing the effects of soil heterogeneity (H: heterogeneous, homogeneous), commonness of the alien plant in Germany (Commonness: common and rare aliens), competition with a native competitor (Competition: without competition, competition with a globally non-widely naturalized native plant species, competition with a globally widely naturalized native plant species), and their interactions on aboveground biomass of the alien plant, total aboveground biomass of the alien and native plants combined, and relative aboveground biomass of the alien plant in the mixture patch of the heterogeneous pots and homogeneous pots.

Table S7: Results of linear mixed models at the individual plant or patch level testing the effects of soil heterogeneity (H: heterogeneous and homogeneous), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), competition with an alien competitor in Germany (Competition: without competition, competition with a rare alien plant species, competition with a common alien plant species), and their interactions on aboveground biomass of the native plants in the mixture patch of the heterogeneous pots and homogeneous pots.

Table S8: Results of linear mixed models at the population or pot level testing the effects of soil heterogeneity (H: heterogeneous and homogeneous), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), competition with an alien competitor in Germany (Competition: without competition, competition with a rare alien plant species, competition with a common alien plant species), and their interactions on total aboveground biomass of the native plants in the heterogeneous pots and homogeneous pots.

Table S9: Results of linear mixed models at the population or pot level testing the effects of soil heterogeneity (H: heterogeneous and homogeneous), commonness of the alien plants in Germany (Commonness: common and rare aliens), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), and their interactions on total aboveground biomass of the alien and native plants combined in the heterogeneous pots and homogeneous pots.

Table S10: Results of linear mixed models at the individual plant or patch level testing the effects of patch type (P: sand, mixture and peat), commonness of the alien plant in Germany (Commonness: common and rare aliens), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), and their interactions on relative interaction intensity of the alien plant and relative interaction intensity of the native plants in the different patches of the heterogeneous pots.

Table S11: Results of linear mixed models at the individual plant or patch level testing the effects of soil heterogeneity (H: heterogeneous and homogeneous), commonness of the alien plants in Germany (Commonness: common and rare aliens), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), and their interactions on relative interaction intensity of the alien plant and relative interaction intensity of the native plants in the mixture patch of the heterogeneous and homogeneous pots.

Table S12: Results of linear mixed models at the population or pot level testing the effects of soil heterogeneity (H: heterogeneous and homogeneous), commonness of the alien plants in Germany (Commonness: common and rare aliens), naturalization success of the native plants (N: non-widely naturalized and widely naturalized natives), and their interactions on relative interaction intensity of the alien plant and relative interaction intensity of the native plants in the heterogeneous pots and homogeneous pots.

Figure S1: Histogram of the global naturalization success (assessed as the number of GloNAF regions per species).

Figure S2: Aboveground biomass of the native plants (a) in the subset of pots from the heterogeneous soil treatment.

Figure S3: Total aboveground biomass of the alien and native plants combined (a) in the subset of pots from the heterogeneous soil treatment.

Figure S4: Aboveground biomass of the alien plant (a), total aboveground biomass of the alien and native plants combined (b), and relative aboveground biomass of the alien plant (c) in the subset of the mixture patches from both heterogeneous and homogeneous soil treatments.
Figure S5: Aboveground biomass of the native plants (a) in the subset of the mixture patches from both heterogeneous and homogeneous soil treatments.
Figure S6: Total aboveground biomass of the native plants (a) per pot.
Figure S7: Total aboveground biomass of the alien and native plants combined (a) per pot.
Figure S8: Relative interaction intensity (a) and density plots of the relative interaction intensity of the alien plant (b) in the subset of pots from the heterogeneous soil treatment with competition.
Figure S9: Relative interaction intensity (a) and density plots of the relative interaction intensity of the alien plant (b) in the subset of the mixture patches from both heterogeneous and homogeneous soil treatments with competition.
Figure S10: Relative interaction intensity (a) and density plots of the relative interaction intensity of alien plants (b) per pot with competition.
Figure S11: Average monthly precipitation in Konstanz during the summer months (June, July, August and September) in the past 5 years (2018–2022).

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