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RESEARCH ARTICLE

Soil heterogeneity tends to promote the growth of naturalized aliens when competing with native plant communities

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Abstract

1. Elton's diversity-invasibility hypothesis predicts that diverse communities are more resistant against alien invaders. However, observational studies frequently find positive relationships between the numbers of alien and native species. It has been suggested, but rarely tested, that environmental heterogeneity may cause such positive relationships.
2. Here, we experimentally tested the effects of soil heterogeneity and diversity (species richness) on the invasibility of native communities. We first filled mesocosm pots with either a heterogeneous soil, consisting of one patch of sand, one patch of peat and one patch of an equal mixture of both substrates, or a homogeneous soil, consisting of the mixture only. Then, we planted those pots with 29 native communities consisting of one, four or eight species, and invaded them with populations of four individuals of one of five alien species.
3. In the heterogeneous soils, individual alien plants benefited more strongly from the resource-rich peat soil than the native communities did. Moreover, in the mixture soil of the heterogeneous treatment, individual alien plant overproportionally produced more biomass than in the mixture soil of the homogeneous treatment. Consequently, the populations of naturalized alien plants in each pot benefited from heterogeneous soil conditions, and this tended to be particularly the case when a native community was present. The native communities did not respond to soil heterogeneity, but they had a negative effect on the naturalized plants, irrespective of their diversity.
4. *Synthesis*. Our results indicate that soil heterogeneity might alleviate the competitive effects of native communities on the alien invaders, as the latter took more advantage of the high resource patches than the natives did. The beneficial effect of heterogeneity on invasion success could thus explain why observational studies usually find positive relationships between the numbers of alien and native species.

KEYWORDS
biodiversity, biological invasion, community, competition, environmental heterogeneity, invasibility, invasion ecology

1 | INTRODUCTION

In the past centuries, the pace of biological invasions has accelerated as a consequence of globalization (Seebens et al., 2017). Currently, more than 13,000 plant species have established outside their native ranges (i.e. have become naturalized; van Kleunen et al., 2015), resulting in floristic homogenization (Yang et al., 2021). Therefore, one of the key questions in ecology is how alien species can invade native communities and can coexist with the natives or even replace them (Valladares et al., 2015). A major hypothesis in this regard is the 'diversity-invasibility hypothesis', one of the classic theories proposed by Elton (1958). It poses that alien species may be more successful in invading a species-poor than a more diverse community. This hypothesis has been tested ever since, but the results of those studies have been variable.

Theoretical and experimental studies that considered small spatial scales frequently find a negative relationship between native diversity and invasibility in different ecosystems (Gazol et al., 2013; Kennedy et al., 2002; Levine, 2000; van Ruijven et al., 2003). For example, diverse native communities were less heavily invaded compared to less diverse native communities, even when the resource availability increased, indicating the robustness of biotic resistance (Li et al., 2021; Maron & Marler, 2007). However, observational field studies found that, particularly at larger spatial scales, habitats of high native diversity were more heavily invaded than habitats of low native diversity, suggesting a so-called 'the rich get richer pattern' (Jauni & Hyvonen, 2012; Peng et al., 2019; Stohlgren et al., 2003). This invasion paradox—the spatial scale-dependent diversity-invasibility relationship—is frequently attributed to spatial heterogeneity, as this would increase both the richness of natives and aliens (Chen et al., 2010; Davies et al., 2005; Fridley et al., 2007). However, to the best of our knowledge, the importance of environmental heterogeneity in this regard has not been explicitly tested yet.

Soil heterogeneity, one type of spatial environmental heterogeneity, is thought to promote species coexistence and richness for several reasons (Stein et al., 2014). First, highly heterogeneous soils (e.g. patchy soil types and fluctuating soil nutrients) could provide different resources in different patches, thereby creating more niche opportunities for various species, and thus promote species coexistence and species richness (Beck & Givnish, 2021; Levine & HilleRisLambers, 2009). Second, heterogeneous soils are usually more likely to provide shelter and refuges under stressful conditions, which also promotes species coexistence and species richness (Hutchings et al., 2003; Liu et al., 2021; Stover & Henry, 2019). Such heterogeneity–species richness relationships are more pronounced at large spatial scales, while at small spatial scales the pattern still remains unclear (Stein et al., 2014). Despite the potential benefits that soil heterogeneity might cast on the individual plant, evidence for the positive relationship between heterogeneity and diversity have rarely been found at small spatial scales (Lundholm, 2009). Moreover, neutral or even negative effects of soil heterogeneity have more frequently been found in experimental studies regarding the total species richness it sustained (Gazol et al., 2013; Tamme et al., 2010). Therefore, more fine-scale studies are needed to disentangle the mechanisms underlying the heterogeneity–species richness relationships across spatial scales (Stein et al., 2014).

Many experimental studies on the ecological importance of soil heterogeneity have been carried out in the last decades (Hutchings & John, 2004; Wacker et al., 2008; Xue et al., 2021). Soil heterogeneity was found to affect growth, foraging behaviour and biomass allocation of plants (Dong et al., 2015). In recent years, more and more studies on soil heterogeneity focused on its importance for species coexistence (Gazol et al., 2013; Reynolds et al., 2007; Xue et al., 2019). Other recent studies addressed the role of soil heterogeneity in plant invasions, as soil heterogeneity might increase resource availability, and thereby increase the invasibility of communities to alien species (Davis et al., 2000). For example, pot experiments showed that clonal invasive alien species exerted greater root-foraging plasticity and benefited more in terms of biomass production from heterogeneous soils than native species did (Keser et al., 2014; Wang et al., 2017). This might further increase the establishment and growth of alien species in heterogeneous habitats with a native community. On the other hand, a recent study found that heterogeneity in soil nutrients positively affected the growth of invasive plants, but did not necessarily promote invasion success in the presence of native communities (Gao et al., 2021). Although experimental studies frequently find that environmental heterogeneity is beneficial to plant growth of alien plants, still little is known about how fine-scale environmental heterogeneity affects the native–alien richness relationship and the invasion process.

Here, by modifying the classic 'checkerboard' patterned experimental design on soil heterogeneity (Fransen et al., 2001; Gazol et al., 2013; Xue et al., 2019), we experimentally tested the potential effect of soil heterogeneity on the native–alien richness relationship. By conducting a multispecies mesocosm experiment of small populations of five naturalized alien species in 29 native communities of different species richness under uniform homogeneous and patchy heterogeneous soil conditions, we tested the following hypotheses: (a) individual alien plants benefit more from the high resource patches than the native communities do; (b) individual alien plants benefit more from being surrounded by heterogeneous soil than the native communities do; (c) soil heterogeneity increases the growth and relative abundance of populations of the alien plants; (d) the performance of individual alien plants and populations decreases with increasing diversity (species richness) of the native community; (e) soil heterogeneity increase the relative abundance of populations of alien plants when grown in diverse native communities.

2 | MATERIALS AND METHODS

2.1 | Study species

To create communities of different species richness, we selected 10 native species that are common in mesotrophic grasslands in Central Europe (Table S1). As we wanted to simulate grassland communities, which are usually dominated by Poaceae (Gibson, 2009), we included a relatively large number of Poaceae species in the pool of native species. As invaders, we selected five alien herbaceous species that are widely naturalized in Germany according to the FloraWeb database of the German flora (www.floraweb.de; Table S1). To increase the generality of our findings, we used multiple alien species, and we chose them from four different families (van Kleunen et al., 2014). We included two species of Asteraceae, as this is one of the largest families and includes many naturalized species (Pysek et al., 2017). We included only one grass species as relatively few of the alien species in Germany are Poaceae. According to the FloraWeb database, distributions of all 15 species are highly overlapping in Germany. Thus, all the species are likely to co-occur and interact in grassland communities.

2.2 | Plant materials and experimental design

We obtained the seeds of four alien species from the Botanical Garden of the University of Konstanz, Germany, and of one alien species as well as of the 10 native species from Rieger-Hofmann GmbH, Germany (Table S1). Seed germination and pre-cultivation of the seedlings were conducted inside a greenhouse, and the experiment was conducted outside in the Botanical Garden of the University of Konstanz, Germany (47°69′19.56″N, 9°17′78.42″E). We sowed the seeds of the species on different dates in the period from 25 May to 3 June 2020 (Table S1), according to prior information on germination speeds of the species (Liu et al., 2018). Seeds of the alien species were sown in plastic trays (18.5 cm × 14 cm × 5 cm, length × width × height) filled with 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). Seeds of the native species were sown in larger plastic trays (48 cm × 33 cm × 6.5 cm, length × width × height), as we required more seedlings of native species than of alien species.

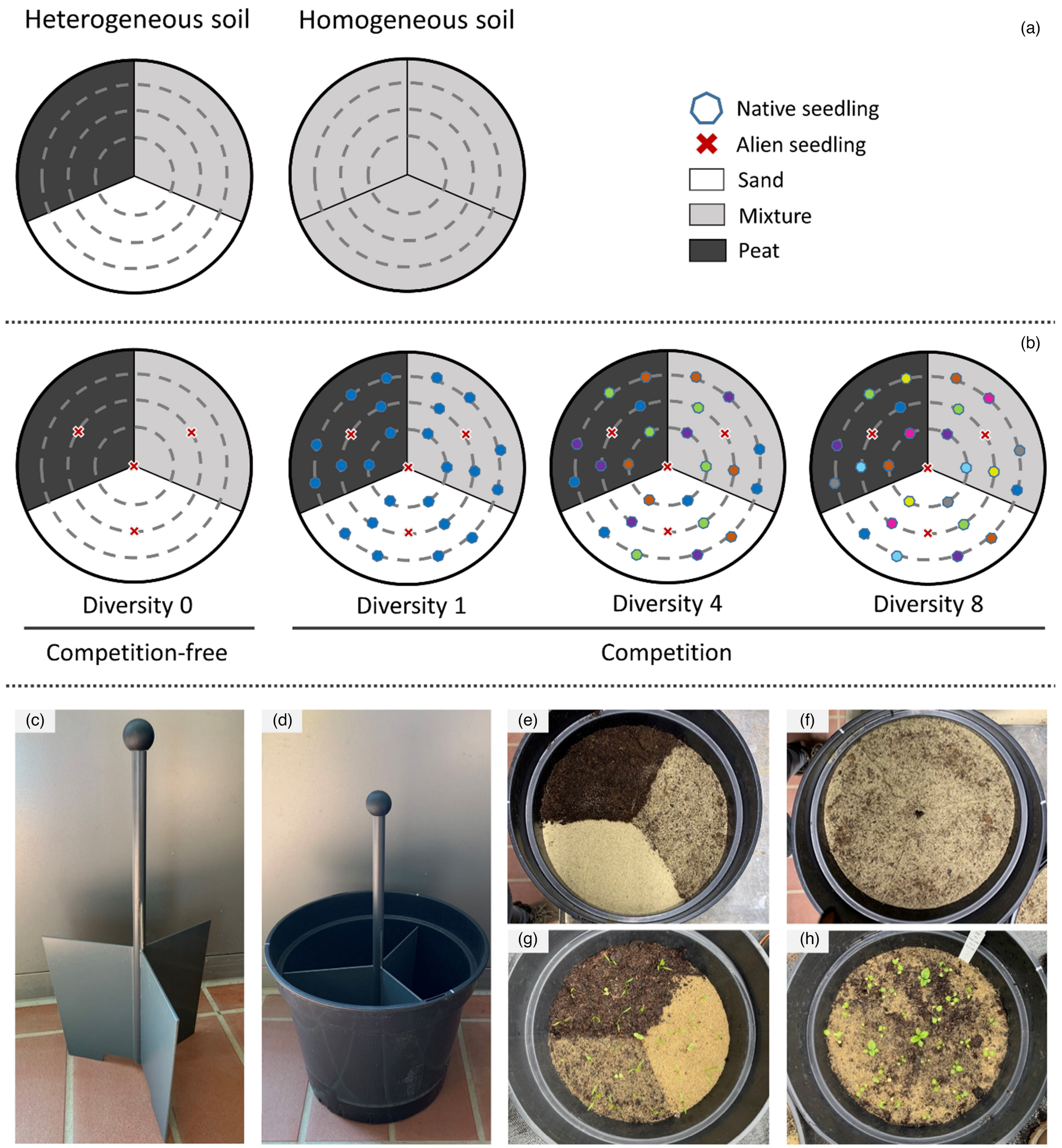
To test the effects of soil heterogeneity and native species richness on performance of the invader, we set up a factorial experiment consisting of two levels of soil heterogeneity (spatially homogeneous and spatially heterogeneous) and four diversity levels of native communities (Diversity 0 – no native community, Diversity 1 – native monoculture, Diversity 4 – native community consisting of four species and Diversity 8 – native community consisting of eight species). Therefore, Diversity 0 refers to a competition-free treatment with alien plants only. Diversity 1, Diversity 4 and Diversity 8 refer to competition treatments with alien plants and native communities.

We used 340 circular 12-L pots (Ø 30.7 cm × Ø 24.5 cm × 24.5 cm, upper × bottom × height), which we divided into three equally sized patches using a specially designed plastic divider (Figure 1). In pots with homogeneous soil, all three patches were filled with a 1:1 (v:v) mixture of peat (Cyclamen®, HAWITA GRUPPE GmbH, Vechta, Germany; pH 5.9; 150 mg/L N; 150 mg/L P_2O_5; 250 mg/L K_2O; and 130 mg/L Mg) and sand (Figure 1). In pots with heterogeneous soil, the three patches were filled, respectively, with only peat, only sand, and the same soil mixture as used in the homogeneous soil treatment (Figure 1). The divider was removed from the pot after filling each of the three patches (Figure 1), so that plants would be able to grow their roots into the adjacent patches. As we filled both the homogeneous and heterogeneous pots with the same amounts of peat and sand, the total amounts of nutrients were the same in all pots (i.e. they only differed in soil heterogeneity). In the homogeneous pots, there were no different soil patches, but, for comparative purposes, we still had three patches marked.

In the community diversity treatments, we had 10 monocultures (i.e. one for each native species) for Diversity 1 and 10 different species mixtures for Diversity 4 and Diversity 8. These species mixtures were randomly chosen from the pool of 10 native species, with the restriction that each native species was equally represented in each diversity level (Table S2). However, due to insufficient seedlings of *Bromus hordeaceus*, we used *Leucanthemum ircutianum*, *Lolium perenne* and *Anthoxanthum odoratum* to replace *Bromus hordeaceus* in three compositions of Diversity 4 respectively. Each monoculture and species mixture were considered as one replicate of the diversity level, and thus in total we had 10 replicates for Diversity 1, Diversity 4 and Diversity 8. However, by accident two of the replicates of Diversity 8 happened to have the same species composition (Table S2), effectively resulting in nine replicates of Diversity 8. For the Diversity 0 treatment (no native community), we replicated each of the two soil-heterogeneity treatments for each of the five alien species four times. The treatments of soil heterogeneity and diversity were applied to five different alien species. In total, the factorial experiment consisted of 340 pots (4 Diversity 0 + 10 Diversity 1 + 10 Diversity 4 + 10 Diversity 8 replicates × 2 soil heterogeneity treatments × 5 alien species) with 1,360 alien plants and 7,200 native plants.

From 15 to 19 June 2020, we transplanted the seedlings into the 12-L pots filled with homogeneous and heterogeneous soils. First, 24 native seedlings were transplanted to create the different diversity levels (Figure 1). In Diversity 1 pots, eight seedlings of the same native species were transplanted into each patch. In Diversity 4 pots, two seedlings of each of the four species were transplanted into each patch. In Diversity 8 pots, only one seedling of each of the eight species was transplanted into each patch. After planting the native seedlings, four seedlings of one of the alien species were transplanted into each pot—one in the middle of the pot, and one in the middle of each of the three patches (Figure 1). In Diversity 0 pots, we only transplanted the four alien seedlings. So, effectively, we had in each pot a small population of four individuals of the alien species, and in the heterogeneous pots, each individual experienced different soil conditions.

We replaced seedlings that had died within the first week after transplanting. The positions of all pots were randomized at the beginning of the experiment, and we re-randomized the position after 4 weeks on 27 July 2020. To reduce heat stress, the area was covered with a shading net (Nitsch & Sohn GmbH & Co KG), which reduced light intensity by 30%. Plants were watered two to three times a week, to saturation. From the fifth to the eighth week of the experiment, we added same amount of nutrient solution (1 g/L Universol®



Blue; ICL Deutschland, Nordhorn, Germany) once per week to each pot to maintain the soil fertility. The experiment lasted for 8 weeks from 29 June to 24 August 2020. The air temperature in the botanical garden during the experiment was between 9 and 35°C.

2.3 | Measurements

Shortly after transplanting, from 23 to 25 June 2020, we measured on each alien seedling the length and width of the largest leaf, and we counted the number of leaves. From these measurements, we estimated the initial leaf area of the alien seedlings as length × width of the largest leaf × the number of leaves (e.g. Speißer et al., 2021). At the end of the experiment, from 24 to 27 August 2020, above-ground biomass of each native species was harvested separately per patch. Above-ground biomass of the four alien individuals in each pot were also harvested separately. All the plant materials were then dried in a drying oven at 70°C for at least 72 hr to constant weight before weighing.

We calculated the patch-level total above-ground biomass as the sum of the patch-level above-ground biomass of the native

FIGURE 1 Illustrations of soil heterogeneity treatments, planting positions of the alien plants (red crosses), planting positions of the native species (heptagonals with different colours for each species) in the different diversity treatments (Diversity 0, Diversity 1, Diversity 4 and Diversity 8) and pictures of the divider, soil heterogeneity treatments and transplanted plants. (a) Soil-heterogeneity treatment. The heterogeneous soil treatment was created by filling only sand, only peat and a 1:1 (v:v) mixture of sand and peat into each of the three equally sized sections of the pots. The homogeneous soil treatment was created by filling the mixture soil into the three sections. (b) Planting positions of alien plants and native plants (illustrated on heterogeneous soil). In Diversity 0 pots, only four alien plants were transplanted: one in the middle of the pot and one in the middle of each of the three patches. In Diversity 1, Diversity 4 and Diversity 8 pots, four alien plants and 24 native plants were transplanted. Therefore, Diversity 0 refers to the competition-free treatment, and Diversity 1, Diversity 4 and Diversity 8 refer to competition treatment of different species richness. In Diversity 1 pots, eight plants of the same native species were transplanted into each patch. In Diversity 4 pots, two plants of each of the four native species were transplanted into each patch. In Diversity 8 pots, only one plant of each of the eight native species was transplanted into each patch. (c) The divider used to divide the circular 12-L pots (Ø 30.7 cm × Ø 24.5 cm × 24.5 cm, upper × bottom × height) into three equally sized sections. (d) The divider in the 12-L pot used in the experiment. The edges of each patch were marked on the pot rim with white permanent marker. (e) Heterogeneous soil treatment after removing the divider from the pot. (f) Homogeneous soil treatment after removing the divider from the pot. (g) Plants transplanted in heterogeneous soil after 1 week. (h) Plants transplanted in homogeneous soil after 1 week

community and the above-ground biomass of the alien plant in the same patch. Pot-level above-ground production was calculated as the sum of the above-ground biomass of all native species and the four plants of the alien species in the pot. The proportional above-ground biomass of the alien species at the patch level was calculated as patch-level above-ground biomass of the alien plant divided by the total patch-level above-ground biomass in the same patch. Similarly, the proportional above-ground biomass of the alien species at the pot level was calculated as pot-level above-ground biomass of the alien plants divided by the total pot-level above-ground biomass.

2.4 | Statistical analyses

Linear mixed-effects models were used to test whether the growth of alien species was related to soil heterogeneity and diversity levels of the native community. All the analyses were conducted using the *lme* function of the NLME package (Pinheiro et al., 2020), and figures were made using the *ggplot* function of the GGPLOT2 package (Wickham, 2016) in R 4.0.3 (R Core Team, 2020). We graphically checked for all models whether the residuals were normally distributed using histograms and quantile–quantile plots. The homoscedasticity of the residuals was checked by plotting them 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). Moreover, as the variance differed among the alien species and among native communities, we used the *varIdent* and *varComb* functions of the NLME package to allow each species and native community to have different variances (Table S3; Pinheiro et al., 2020). The significance of fixed effects was assessed with likelihood-ratio tests when comparing models with and without the effect of interest (Zuur et al., 2009).

For individual-plant-level and patch-level analyses, we ran two separate analyses on subsets of the data. Firstly, to test whether the different soil patches in the heterogeneous pots affect plant growth differently, we analysed the subset of data collected from heterogeneous pots. We included patch type (sand, mixture and peat), competition (competition-free and competition), diversity of the native community (a continuous variable with the values 1, 4 and 8), the interaction of patch type and competition, and the interaction of patch type and diversity as fixed effects. We considered diversity of the native community as continuous variable as this allows us to specifically test whether the resistance against invaders changes with increasing diversity. In the model, we fitted the effect of diversity after the effect of competition, as diversity only applied to pots with competition (i.e. pots with a native community). Specifically, this means that the effect of diversity was tested by comparing a model that included both competition and diversity with a model that only included competition, and that the effect of competition was tested by comparing the latter with a model that did not include competition (and also not diversity). To account for variation among the five alien species, and for variation due to the different compositions of the native community, we included alien species identity and native species mixture as random effects in the model. In addition, to account for non-independence of patches within the same pot, we included pot identity as a random effect in the model.

Secondly, we tested whether it matters whether plants on the mixed soil patches were in the homogeneous pots or in the heterogeneous pots (i.e. surrounded by two other mixed soil patches or by a sand and a peat patch). We analysed the subset of data of patches with mixed soil, and because the homogeneous pots had three such patches, we randomly chose one. We included soil heterogeneity (heterogeneous and homogeneous), competition (competition-free and competition), diversity of the native community (a continuous variable with the values 1, 4 and 8), the interaction of patch type and competition, and the interaction of patch type and diversity as fixed effects. Again, we fitted the effect of diversity after the effect of competition, as diversity only applied to pots with competition (i.e. pots with a native community). We included alien species identity and native species mixture as random effects.

For population-level and pot-level analyses, total above-ground biomass of alien plants, total above-ground biomass of native community and proportional above-ground biomass of alien plants were analysed as response variables. In these models, we included soil heterogeneity (heterogeneous and homogeneous), competition (competition-free and competition), diversity of the native community (a continuous variable with the values 1, 4 and 8) as fixed main effects. We also included the interaction of soil heterogeneity and competition, and the interaction of soil heterogeneity and diversity as fixed terms. We included alien species identity and native species mixture as random effects in the model.

When in any of the models described above a response variable was not available for the competition-free treatment (i.e. above-ground biomass of native community, proportional above-ground biomass of alien plant and total above-ground biomass of native and alien plants combined), the factor competition was not included. When the response variable was above-ground biomass of the alien plant or proportional above-ground biomass of the alien plant, we accounted for initial variation in alien plant size by including initial leaf area of the alien plant as covariate in the model.

3 | RESULTS

3.1 | Individual-plant-level and patch-level performance measures in the heterogeneous pots

For the subset of heterogeneous pots, the above-ground biomass of the individual alien plants in each of the three patches per pot was significantly affected by the type of patch (Table 1, $F = 48.75$, $p < 0.001$). The above-ground biomass of individual alien plants increased significantly from sand (mean ± *SE*: 2.39 ± 0.14 g) via mixture (mean ± *SE*: 5.52 ± 0.35 g) to peat (mean ± *SE*: 7.91 ± 0.47 g) patches. Individual alien plants produced on average 28.8% more biomass when grown without native communities than when grown with native communities (Table 1, $F = 4.80$, $p = 0.029$; Figure 2a). Diversity of the native community, however, had no significant effect on the above-ground biomass of individual alien plants (Table 1; Figure 2a).

Similarly, above-ground biomass of the native community, total above-ground biomass of native and alien plants combined (Table S4; Figure S1) and proportional above-ground biomass of the alien plants were significantly different between the three patch types of the heterogeneous soil treatment (Table 1; Figure 2). Like for the alien plants, total above-ground biomass of the native community, and thus also total above-ground biomass of the native and alien plants combined, was highest in the peat patches and lowest in the sand patches (Figure 2b; Figure S1). However, the individual alien plants benefited more from the peat patches, as the proportional above-ground biomass of the alien plants was highest there (Table 1; Figure 2c).

The effect of diversity of the native community on above-ground biomass of the native community, total above-ground biomass of native and alien plants combined (Table S4; Figure S1) and the proportional above-ground biomass of the alien plants was not significant (Table 1; Figure 2). However, the effect of diversity on total above-ground biomass of native and alien plants combined was significantly affected by patch types (significant patch type × diversity interaction in Table S4, $F = 6.46$, $p = 0.040$). With increasing diversity of the native community, the total above-ground biomass of native and alien plants combined in sand patches slightly increased, whereas in the peat patches, it slightly decreased (Figure S1).

3.2 | Individual-plant-level and patch-level performance measures in the mixture-soil patches

For the subset of mixture soil patches, individual alien plants produced on average 25.5% more above-ground biomass in the

TABLE 1 Individual-plant-level and patch-level effects of patch type (P), competition (C), diversity of the native community (D) and their interactions on above-ground biomass of alien plants, above-ground biomass of the native community and proportional above-ground biomass of alien plant in different patches of the heterogeneous pots. Significant effects ($p < 0.05$) are shown in bold

Model terms	Above-ground biomass of alien plant			Above-ground biomass of native community			Proportional above-ground biomass of alien plant		
Fixed effects	*df*	χ^2	*p*	*df*	χ^2	*p*	*df*	χ^2	*p*
Initial leaf area	1	48.749	**<0.0001**	–	–	–	1	48.890	**<0.0001**
Patch type (P)	2	201.775	**<0.0001**	2	135.964	**<0.0001**	2	65.705	**<0.0001**
Competition (C)	1	4.796	**0.029**	–	–	–	–	–	–
Diversity (D)	1	0.506	0.477	1	1.880	0.170	1	1.063	0.303
P × C	2	0.450	0.799	–	–	–	–	–	–
P × D	2	3.021	0.221	2	1.311	0.519	2	0.597	0.742
Random effects			*SD*			*SD*			*SD*
Alien species[a]			0.520			0.090			0.121
Native community			0.220			0.272[b]			0.133
Pot			0.000			0.065			0.000
Residual			0.483			0.224			0.147

[a]The *SD*s shown in the table are for the alien species *Veronica persica* Poir., and the *SD*s for all alien species are shown in Table S7.

[b]The *SD* shown in the table is for the native community No.1, and the *SD*s for all native communities are shown in Table S8.

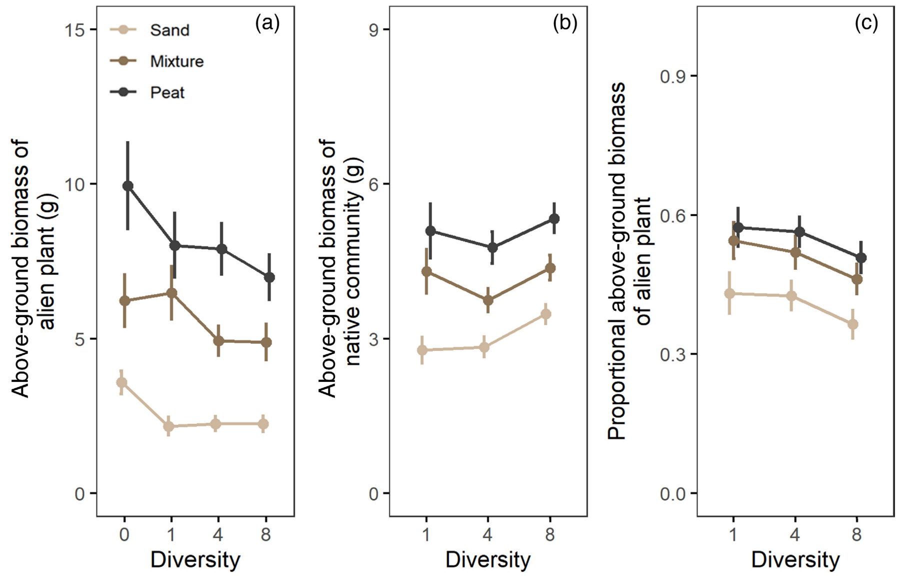


FIGURE 2 Individual-plant-level and patch-level effects of patch (sand, mixture and peat) and diversity levels of the native community (Diversity 0, Diversity 1, Diversity 4 and Diversity 8) on above-ground biomass of alien plants (a), above-ground biomass of the native community (b) and proportional above-ground biomass of alien plants (c) in different patches of the heterogeneous pots. Data shown are mean values (±*SE*s). Diversity 0 refers to the competition-free treatment

TABLE 2 Individual-plant-level and patch-level effects of soil heterogeneity (H), competition (C), diversity of the native community (D) and their interactions on above-ground biomass of alien plants, above-ground biomass of the native community and proportional above-ground biomass of alien plant in the mixture patch of the homogeneous and heterogeneous pots. Significant effects ($p < 0.05$) are shown in bold and marginally significant effects ($0.05 \le p < 0.1$) are shown in italics

Model terms	Above-ground biomass of alien plant			Above-ground biomass of native community			Proportional above-ground biomass of alien plant		
Fixed effects	***df***	χ^2	***p***	***df***	χ^2	***p***	***df***	χ^2	***p***
Initial leaf area	1	33.248	**<0.0001**	–	–	–	1	33.301	**<0.0001**
Heterogeneity (H)	1	7.383	**0.007**	1	1.262	0.261	1	6.206	**0.013**
Competition (C)	1	3.248	*0.072*	–	–	–	–	–	–
Diversity (D)	1	1.572	0.210	1	1.991	0.158	1	1.248	0.264
H × C	1	2.207	0.137	–	–	–	–	–	–
H × D	1	0.255	0.614	1	0.020	0.887	1	0.244	0.621
Random effects			***SD***			***SD***			***SD***
Alien species[a]			0.489			0.055			0.106
Native community			0.270			0. 393[b]			0.125
Residual			0.530			0.323			0.176

[a]The *SD*s shown in the table are for the alien species *Veronica persica* Poir., and the *SD*s for all alien species are shown in Table S7.

[b]The *SD* shown in the table is for the native community No.1, and the *SD*s for all native communities are shown in Table S8.

heterogeneous pots than in homogeneous ones (Table 2, $F = 7.38$, $p = 0.007$; Figure 3a). The total above-ground biomass of native and alien plants combined in the mixture patch of heterogeneous pots were on average 23.8% higher than in the homogeneous pots (Table S5, $F = 16.90$, $p < 0.001$; Figure S3), though the above-ground biomass of native community did not significantly differ between heterogeneous and homogeneous pots (Table 2; Figure 3b). Proportional above-ground biomass of alien plants in the mixture patch of heterogeneous pots were 2.4% higher than in the homogeneous pots (Table 2, $F = 6.21$, $p = 0.013$; Figure 3c).

The effects of diversity of the native community on above-ground biomass of alien plants, above-ground biomass of the native community, total above-ground biomass of native and alien plants combined (Table S5; Figure S3) and the proportional above-ground biomass of the alien plants in the mixture patch in both the heterogeneous and homogeneous pots were not significant (Table 2; Figure 3). However, the above-ground biomass of alien plants grown alone in the mixture patch was 40.1% higher than when grown with native communities, irrespective of the diversity (marginally significant competition effect in Table 2, $F = 3.25$, $p = 0.072$; Figure 3a).

3.3 | Population-level and pot-level performance measures

The combined biomass of the population of four alien plants in each pot was on average 22.8% higher on the heterogeneous soils than on the homogeneous soils (Table 3, $F = 32.46$, $p < 0.001$;

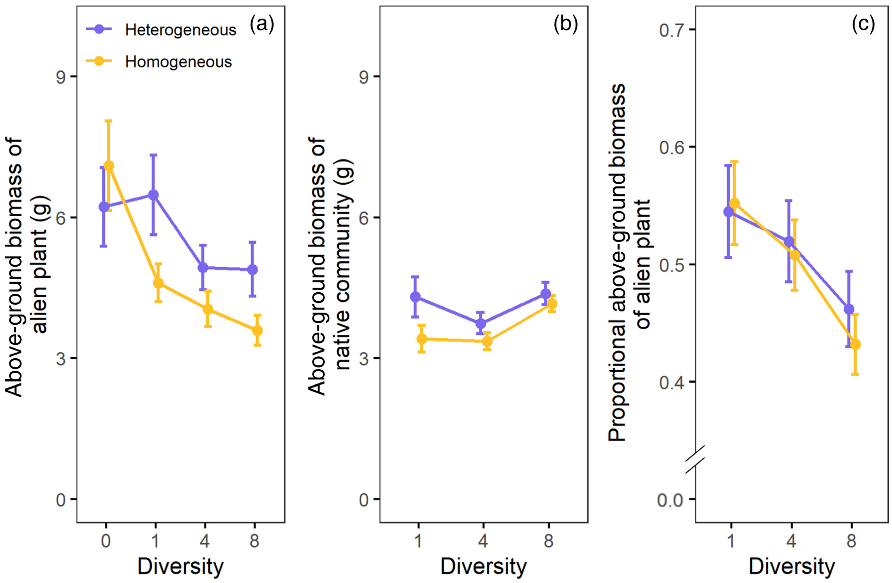


FIGURE 3 Individual-plant-level and patch-level effects of soil heterogeneity (heterogeneous and homogeneous) and diversity levels of the native community (Diversity 0, Diversity 1, Diversity 4 and Diversity 8) on total above-ground biomass of alien plants (a), above-ground biomass of the native community (b) and proportional above-ground biomass of alien plants (c) in the mixture patches of the homogeneous and heterogeneous pots. Data shown are mean values (±*SE*s). Diversity 0 refers to the competition-free treatment

TABLE 3 Population-level and pot-level effects of soil heterogeneity (H), competition (C), diversity of the native community (D) and their interactions on the total above-ground biomass of alien plants, total above-ground biomass of the native community and proportional above-ground biomass of alien plants. Significant effects ($p < 0.05$) are shown in bold, and marginally significant effects ($0.05 \le p < 0.1$) are shown in italics

Model terms	Total above-ground biomass of alien plants			Total above-ground biomass of native community			Proportional above-ground biomass of alien plants		
Fixed effects	*df*	χ^2	*p*	*df*	χ^2	*p*	*df*	χ^2	*p*
Initial leaf area	1	32.253	**<0.0001**	–	–	–	1	26.298	**<0.0001**
Heterogeneity (H)	1	32.457	**<0.0001**	1	0.007	0.934	1	21.242	**<0.0001**
Competition (C)	1	3.593	*0.058*	–	–	–	–	–	–
Diversity (D)	1	1.490	0.222	1	2.412	0.120	1	0.672	0.412
H × C	1	3.143	*0.076*	–	–	–	–	–	–
H × D	1	0.007	0.933	1	1.368	0.242	1	0.695	0.404
Random effects			*SD*			*SD*			*SD*
Alien species[a]			0.361			0.073			0.048
Native community			0.194			0.351[b]			0.053
Residual			0.289			0.196			0.074

[a]The *SD*s shown in the table are for the alien species *Veronica persica* Poir., and the *SD*s for all alien species are shown in Table S7.
[b]The *SD* shown in the table is for the native community No.1, and the *SD*s for all native communities are shown in Table S8.

Figure 4a). The population of alien plants produced on average 28.5% less above-ground biomass when grown in competition with the native communities than when grown without native communities (marginally significant competition effect in Table 3, $F = 3.59$, $p = 0.058$; Figure 4a). Moreover, the positive effect of soil heterogeneity on total above-ground biomass of the aliens tended to be stronger when grown in competition with native communities (+26.7%) than when grown without native communities (+4.2%; marginally significant soil heterogeneity × competition interaction in Table 3, $F = 3.14$, $p = 0.076$; Figure 4a). Although there was a trend that the total above-ground biomass of alien plants declined with increasing diversity of the native community, this effect was not statistically significant (Table 3; Figure 4a). When we analysed above-ground biomass of only the single alien plant individual in the centre of each pot, the results were very similar (Table S6; Figure S5a). However, there was no significant trend that the soil-heterogeneity response was stronger with than without competition (Table S6; Figure S5a).

Above-ground biomass of the native communities in the pots did not significantly differ between heterogeneous and homogeneous soils (Table 3; Figure 4b). However, the combined above-ground biomass of the alien and native plants was on average 18.8% higher on heterogeneous than on homogeneous soils (Table S6, $F = 41.16$, $p < 0.001$; Figure S5b). This effect on combined above-ground biomass was mainly due to the alien plants, which was also reflected in the significantly higher proportional above-ground biomass of the

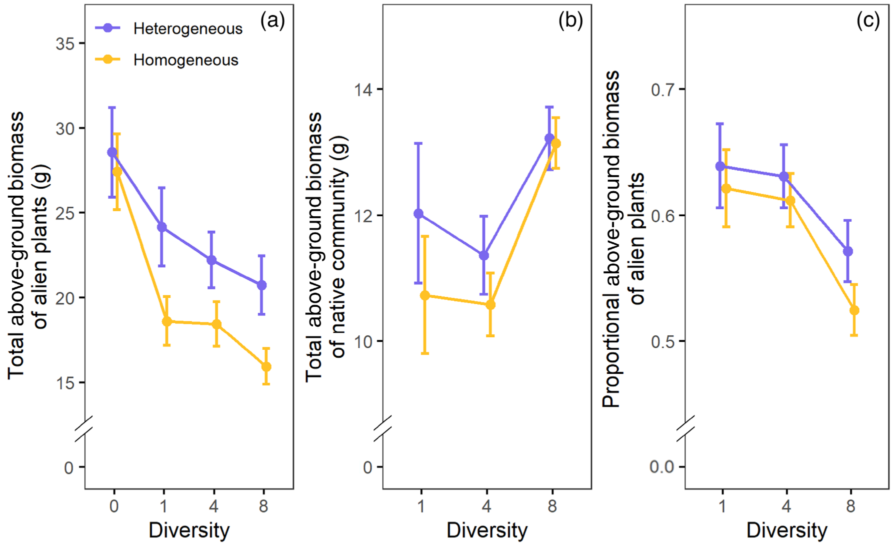


FIGURE 4 Population-level and pot-level effects of soil heterogeneity (heterogeneous and homogeneous) and diversity levels of the native community (Diversity 0, Diversity 1, Diversity 4 and Diversity 8) on total above-ground biomass of the alien plants (a), total above-ground biomass of the native community (b) and proportional above-ground biomass of the alien plants (c). Data shown are mean values (±*SE*s). Diversity 0 refers to the competition-free treatment

alien plants on heterogeneous soils (mean ± *SE*: 0.61 ± 0.02) than on homogeneous soils (mean ± *SE*: 0.59 ± 0.01; Table 3, $F = 21.24$, $p < 0.001$; Figure 4c). Furthermore, although the biomass of the native communities was highest and the proportional biomass of the aliens was lowest at Diversity 8, the overall diversity effects were not significant (Table 3; Figure 4b,c).

4 | DISCUSSION

Our mesocosm study tested whether spatial environmental heterogeneity may facilitate the growth of alien plants in communities of different diversities of native plants. We found that the populations of naturalized alien plants in each pot benefited from the heterogeneous soil conditions, and this tended to be particularly the case when a native community was present. The underlying mechanism for this population-level heterogeneity effect might be that individual alien plants benefited more strongly from the resource-rich peat soil than the native communities did. In addition, individual alien plant in the mixture patch of the heterogeneous pots produced over-proportionally more biomass than when they were in the homogeneous pots. The native communities did not respond to soil heterogeneity, but their presence had a negative effect on the alien plants. However, against the predictions of Elton's (1958) diversity-invasibility hypothesis, the strength of this competitive effect on the alien plants did not significantly depend on the diversity of the native community. Overall, our findings suggest that environmental heterogeneity might promote the invasion success of alien plants, irrespective of the diversity of the native communities.

4.1 | Individual alien plants take advantage of nutrient-rich peat soil

Both the individual alien plants and native communities produced more biomass in the peat patches than in the sand patches of the heterogeneous pots. This is not surprising given that peat soil contains more nutrients and has a higher water-holding capacity than sand, and has many other properties that are beneficial to plant growth (Kitir et al., 2018). As we regularly watered the pots to keep the substrate moist, the main difference between the peat and sand soil in our experiment was most likely the nutrient content. Our finding that the aliens benefited more strongly than the natives did could indicate that the aliens we selected are more representative for high-nutrient habitats than the natives. However, according to Ellenberg's nutrient indicator values (Ellenberg, 1988), six of the native species as well as the five aliens that we included in our experiment are adapted to habitats with moderate or high-nutrient levels, and three of the native species are indifferent to nutrient levels (Table S1). Therefore, it is unlikely that our results reflect differences in overall nutrient preferences of the alien and native species we included. In line with our findings, previous studies also found that invasive alien plants frequently do not only benefit more in terms of biomass production in resource-rich patches of heterogeneous environments but also respond more strongly to changing environmental conditions, such as elevated temperature, CO_2 enrichment and nitrogen deposition, than natives do (Chen et al., 2019; Liu et al., 2017). Invasive alien species have also been found to exert higher plasticity of functional traits than native species that allow them to take more advantage of high resource conditions (Burns, 2004; Davidson et al., 2011; Guerrero et al., 2020). This ability may allow the alien species to achieve their potential maximum growth rates in heterogeneous soils, as there some of the resources are concentrated in patches. Nevertheless, the ability to capitalize on the resource-rich patches of heterogeneous environments also varied among the alien species we included in the experiment. In particular, plants of *Bidens frondosa* responded more strongly to the different patches than the other four alien species (Figure S2). It has, however, also been found that whether a species is common or rare may be more strongly related to its ability to take advantage of increased resource availabilities and heterogeneous environmental conditions than whether it is alien or native (Dawson, Fischer, & van Kleunen, 2012; Dawson, Rohr, et al., 2012; Tamme et al., 2016). Therefore, future studies that aim to unravel the effects of diversity and environmental heterogeneity on invasibility should also vary the commonness of the alien invaders and of the species used in the native communities.

Furthermore, we found that individual alien plants in the mixture patch of the heterogeneous treatment produced 25.5% more biomass than when grown in the mixture soil of the homogeneous treatment. Probably, this reflects that the plants in the heterogeneous treatment also accessed with their roots the more nutrient-rich peat patches. This is especially likely if the naturalized alien plants show strong adaptive root-foraging plasticity. As it was impossible to harvest the root systems of our plants, we unfortunately could not verify this. The beneficial effect of soil heterogeneity on biomass performance was particularly more pronounced for *Bidens frondosa* than for plants of the other alien species (Figure S4). This suggests that alien species also differ in their ability of root foraging. Previous studies have shown that widely naturalized plants show stronger root-foraging plasticity than less widely naturalized plants (Keser et al., 2014; Keser et al., 2015). Whether widely naturalized plants also show stronger root foraging than most native plants remains to be tested.

4.2 | Competition per se rather than diversity plays a more important role in biotic resistance against alien invaders

Not surprisingly, the presence of a native community reduced the biomass of the alien plants. We had expected—based on Elton's diversity-invasibility hypothesis—that with increasing diversity of the native community its competitive effect on the alien plants would increase. Although there were trends that above-ground biomass of the native community was highest, and absolute and relative biomass of the alien plants were lowest at the highest diversity level of the community, none of these effects was statistically significant. Our expectation that the diverse native communities should be more resistant against invaders was based on the idea that due to niche complementarity diverse communities should better fill in the available niche space, and thus use more of the available resources (Loreau & Hector, 2001). Possibly, as niche complementarity has been reported to increase over time (Fargione et al., 2007; Jucker et al., 2020), resistance of the native communities against the alien invaders might have increased with diversity if our experiment would have lasted longer.

Time indeed plays an important role in competition and species coexistence. A meta-analysis of experimental studies showed that negative competitive effects of alien plants on native communities declined with time since invasion (Iacarella et al., 2015). Previous studies also found that the diversity-invasibility relationships might emerge and change over time. A long-term experimental study in a grassland found a consistent positive diversity-invasibility relationship (Zeiter & Stampfli, 2012). Moreover, recent studies also indicate that the negative diversity-invasibility relationships are more often observed shortly after the invaders have been introduced, while the relationship became more positive at later stages, due to post-introduction processes (i.e. environmental disturbance, dispersal, etc.; Clark & Johnston, 2011, Clark et al., 2013). However, more long-term experimental studies are needed to disentangle how the diversity-invasibility relationship and coexistence between alien species and native communities change over time.

4.3 | Soil heterogeneity promotes invasion success of alien plants

The small populations of naturalized alien plants in each mesocosm pot produced more biomass under heterogeneous than under homogeneous soil conditions. Furthermore, the alien plant populations capitalized more strongly on the heterogeneous soil conditions than the native communities did. This is due to three effects of the heterogeneous soil treatment on the individual alien plants. First, whereas the native communities less than doubled their biomass on peat patches relative to that on sand patches, the individual alien plants more than tripled their biomass. Second, the alien plants produced 25.5% more biomass on the mixture soil in the heterogeneous treatment than on the same mixture soil in the homogeneous treatment. Third, the central alien plant in each mesocosm pot produced 49.0% more biomass in the heterogeneous than in the homogeneous treatment, even though the total amount of nutrients it had access to was the same. So, the individual alien plants in our study benefited in multiple ways from the heterogeneous soil conditions, resulting in an overall increase in biomass of the alien plant populations in each mesocosm.

The positive effect of soil heterogeneity on the biomass of the alien populations was most pronounced when native competitors were present. Actually, in the absence of competition, the biomass of the alien population in each mesocosm was almost the same under heterogeneous and homogeneous soil conditions. This could suggest that the presence of competition, and consequently overall lower resource availability, strengthens the foraging responses of the alien plants for the resource-rich peat patches. However, as the individual alien plant in the centre of the pots did not benefit more from heterogeneity in the presence than absence of competition, this explanation is unlikely to hold. Therefore, it more likely reflects that the alien plants took more advantage of the resource-rich peat patch than the native plants did. Other recent studies also found that with competition, soil heterogeneity could increase the biomass performance of alien species over native species (Chen et al., 2019; Liang et al., 2020). However, although another recent multispecies study found that soil nutrient heterogeneity had a positive effect on above-ground growth of alien plants, the relative abundance of those alien plants in competition with native communities was not changed (Gao et al., 2021). It has also been reported that temporal heterogeneity in nutrient availability might shift the competitive balance towards alien species (Parepa et al., 2013). However, again another study on temporal heterogeneity found that this might not apply to all alien plant species (Liu et al., 2018). So, more studies are required to assess under which conditions spatial and temporal environmental heterogeneity promote invasion of alien plants into native communities.

As we found no significant effect of the diversity of the native community, we also did not find support for our expectation that the alleviating effect of environmental heterogeneity would be most pronounced for the alien plants in diverse native communities. Nevertheless, in line with our expectation, environmental heterogeneity alleviated the effect of competition on the biomass of the alien populations (Figure 4a). In other words, despite the negative effect of competition, the alien plants benefited more from environmental heterogeneity in the presence of competition than in the absence of competition.

5 | CONCLUSIONS

Our study found that individual alien plants in the heterogeneous pots took more advantage of high resource patches than the native communities did. Moreover, our findings indicate that soil heterogeneity might benefit populations of alien plants in competition with native communities, irrespective of the diversity of the native community. Soil heterogeneity might have alleviated the competitive effects on the aliens, as the latter took more advantage of the high resource patches than the natives did. On the low resource patches, the natives were more dominant, and it is thus likely that soil heterogeneity promotes coexistence of the alien and native plants. This could explain why observational studies usually find positive relationships between the numbers of alien and native species.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

G.-W.W. and M.v.K. conceived the idea and designed the experiment; G.-W.W. performed the experiment; G.-W.W. and M.v.K. conducted the data analyses; G.-W.W. wrote the first draft of the manuscript; G.-W.W. and M.v.K. revised the manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data related to this paper can be accessed through the figshare repository https://doi.org/10.6084/m9.figshare.19111229.v1 (Wei & van Kleunen, 2022).

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