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RESEARCH ARTICLE

Naturalized alien plants experience less negative soil-legacy effects and gain competitive advantages through spatial heterogeneity

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Abstract

1. With the number of naturalized alien plant species continuously increasing, it has become of major interest to understand how they can coexist with or even outcompete native species. Plant–soil interactions and soil spatial heterogeneity are thought to play major roles in the coexistence of plant species. Depending on the strengths of conspecific and heterospecific soil feedbacks, size inequalities between competing plants might either decrease (i.e. promote coexistence) or increase. However, how spatial heterogeneity in soil legacies affects individual growth, competitive balance and thus coexistence of competing plants, and how this depends on the plant origins has never been tested.
2. Here, we first conditioned soil with each of five naturalized alien and five native species separately. Thereafter, we grew all 45 pairwise species combinations under four homogeneous soil-legacy conditions (including unconditioned soil as one of the homogeneous conditions) and two heterogeneous soil-legacy conditions.
3. Soil legacies overall had a negative effect on biomass production, irrespective of the origins of the competing species. Biomass inequality between the competing plants was the smallest when they grew on soil conditioned only by the larger one of the two species. Both alien and native plants suffered strongly from conspecific soil legacies. However, alien plants could benefit from another co-growing alien species on homogeneous-conspecific soil, which thus mitigated negative soil-legacy effects, or benefit from heterogeneous soil conditions to increase the competitive advantage over native plants.
4. Our findings show that the performance of competing plants may depend on their origins as well as on soil legacies. This may ultimately affect species competition and coexistence in natural environments where soil legacies are likely to be heterogeneous.

KEYWORDS
coexistence, conspecific, exotic, homogeneous, interspecific competition, invasion ecology, invasional meltdown, plant–soil feedback

1 | INTRODUCTION

In the last centuries, the numbers of alien species that have established self-sustaining populations have dramatically increased all over the world (Dawson et al., 2017; Pyšek et al., 2017). Consequently, a major research question is how these naturalized alien species can coexist with native ones or even outcompete them. Moreover, with the continuing increase in the number of naturalized alien species (Seebens et al., 2021), it also becomes more likely that alien species interact with other alien species. Among the few studies on alien-alien interactions in plants, some found that naturalized alien species might provide resistance against the establishment of other alien species (Haeuser et al., 2019), whereas other studies suggest that alien organisms can have positive interactions (Simberloff & Von Holle, 1999), particularly through soil-legacy effects (Bourgeois et al., 2005; Zhang et al., 2020). Therefore, more research is needed on how interactions between plant species depend on whether the species are alien or native.

The interactions between plants and soil are considered to play a key role in plant competition and coexistence (Fahey et al., 2020; Wolfe & Klironomos, 2005). Plants alter the biotic and abiotic properties of the soil, and these soil legacies affect the growth of subsequent plants (Bever et al., 1997; Crawford et al., 2019; Kulmatiski et al., 2008; van der Putten et al., 2013). Plant–soil feedback usually becomes stronger and more negative when the former (i.e. the conditioning plant) and later plant (i.e. the test plant) are conspecifics (Lozano et al., 2022; McCarthy-Neumann & Kobe, 2010). This would imply that when two species compete on soil conditioned by the larger of the two species, the size advantage of the larger species should decrease, thereby diminishing the size inequality and thus promoting coexistence of the two species. However, size inequality should increase when the two species compete on soil conditioned by the smaller of the two species, and could ultimately, through asymmetric competition for light, result in mortality of the smaller species.

In nature, plant diversity results in a mosaic of soil patches conditioned by different plant species, and this soil-legacy heterogeneity should also affect plant coexistence (Brandt et al., 2013). For example, heterogeneity in soil legacies could provide refuges in which the growth of plants is less strongly limited by negative conspecific plant–soil feedback, thereby favouring species coexistence (Burns et al., 2017; Hendriks et al., 2015). Indeed, spatially heterogeneous plant–soil-feedback effects can reduce growth inequalities between competing species (Xue et al., 2018). However, ultimately, the effects of heterogeneous soil legacies on plant growth should depend on whether each species is growing in a patch conditioned by a conspecific or by the other species, or even in a mixture of both. To the best of our knowledge, it has not yet been tested how different homogeneous and heterogeneous soil-legacy scenarios affect the growth of plant individuals, the competitive balance, and thus species coexistence.

Alien plants are, due to the potential release from species-specific natural enemies (Keane & Crawley, 2002; Mitchell & Power, 2003), often less negatively or sometimes even positively affected by conspecific soil legacies (Klironomos, 2002). This should give the alien plants an advantage over the native plants, resulting in larger size inequalities, at least if the alien plants are larger than the native ones, as is frequently the case for invasive aliens (van Kleunen et al., 2010). Furthermore, as naturalized plants frequently take more advantage of heterogeneous conditions than native species do (Parepa et al., 2013; Wei & van Kleunen, 2022), it could be that the alien plants will benefit more from heterogeneous soil legacies. On the contrary, if two alien plants compete with each other, the lack of strong soil-legacy effects for both species may have little influence on size inequalities. In this case, invasional meltdown mediated by soil legacies could happen (Chen & van Kleunen, 2022; Zhang et al., 2020). Consequently, it should be tested whether homogeneous and heterogeneous soil legacies affect plant growth and coexistence differently depending on the origin of the competing species.

To test how growth and the competitive balance depend on the sizes and origins of the plant species, and on different homogeneous and heterogeneous soil legacies, we conducted a two-phase plant–soil feedback experiment. We first conditioned soil by five herbaceous species native to central Europe and another five that are naturalized aliens. Thereafter, we grew all 45 pairwise combinations of those species (25 alien-native, 10 alien-alien and 10 native-native species pairs) under four homogeneous and two heterogeneous soil-legacy conditions (Figure 1). We then measured biomass production and inequalities of the two competing plants. We tested the following main questions and hypotheses: (1) How do different soil-legacy scenarios affect biomass production and inequalities of competing plants? We hypothesize that soil-legacy effects on plant biomass production should be negative at the pot level. Soil-legacy effects will reduce size inequalities of the competing species when grown on soil conditioned by the larger of the two species only, and will increase size inequalities when grown on soil conditioned by the smaller of the two species only. (2) How is the growth of plant individuals affected by both competitor origins and soil-legacy patches? We hypothesize that focal plants will experience negative conspecific soil-legacy effects at the patch level, but alien plants will be less affected than native ones. For alien focal plants, this negative conspecific effect will be mitigated when the neighbouring species is also alien or when the soil-legacy patch mosaic is heterogeneous. (3) How do

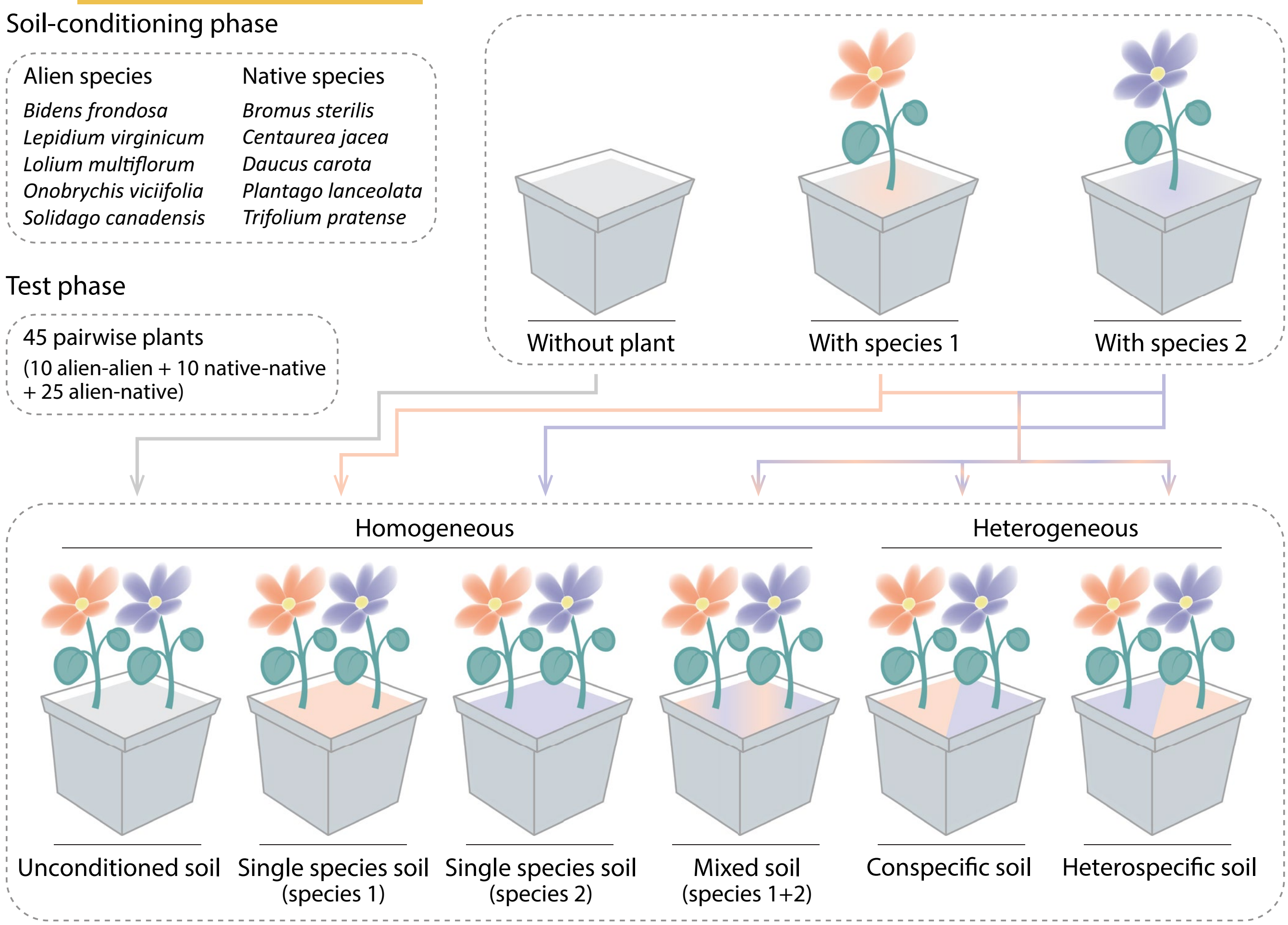

FIGURE 1 Overview of the experimental design. In the soil-conditioning phase, each of the five alien and five native species was separately planted in pots to condition the soils. The soil without any plant conditioning was used to create unconditioned control soil. In the test phase, the 10 species were combined into 45 species pairs (25 alien-native, 10 alien-alien and 10 native-native) and were grown as focal plants and competitors in six soil-legacy treatments created from the soils of the conditioning phase. Pots were divided in half along their diagonals, and these halves were filled separately with soil from the conditioning phase to create various homogeneous and heterogeneous soil-legacy environments in which the two plants of the species pair were planted. Note that there was no physical barrier between the two pot halves. This resulted, from the perspective of a focal species (i.e. the orange species 1 in the figure), in four homogeneous and two heterogeneous soil-legacy treatments per species pair.

homogeneous and heterogeneous soil legacies alter the coexistence of alien and native plant species? We hypothesize that the competitive advantage of alien species will be reduced on soil conditioned by conspecifics, but this negative effect will be weakened in the heterogeneous soil-legacy scenario. As a consequence, alien plants will have a relatively large competitive advantage over natives in their heterogeneous-conspecific soil legacies.

2 | MATERIALS AND METHODS

2.1 | Study species and pre-cultivation

We selected 10 species from six families to be used in both the soil-conditioning phase and the test phase (Table S1). Five of the species are naturalized aliens (*Bidens frondosa* L., *Lepidium virginicum* L., *Lolium multiflorum* Lam., *Onobrychis viciifolia* Scop., *Solidago canadensis* L.), and five species are native to Germany (*Bromus sterilis* L., *Centaurea jacea* agg., *Daucus carota* L., *Plantago lanceolata* L. and *Trifolium pratense* L.). All study species are widely distributed in Germany and can be found in similar habitats (Table S1). Whether a species is naturalized or native was based on information from the FloraWeb website (www.floraweb.de, accessed March 2021). Seeds of the 10 species were either ordered from Rieger-Hofmann GmbH or taken from the seed collection of the Botanical Garden of the University of Konstanz (Table S1).

To make sure that all seedlings would be in a similar developmental stage at transplanting, we sowed seeds of the different species on 12, 19 or 21 April 2021 (Table S1). This was done based on prior knowledge about the time each species requires for germination. Each of the 10 species was separately sown into trays (18 cm × 14 cm × 5 cm) filled with potting soil (Topferde; Einheitserde Co., Sinntal-Altengronau, Germany), and the trays were placed in a greenhouse with a temperature between 18 and 25°C.

2.2 | Experimental set-up

2.2.1 | The soil-conditioning phase

The experiment was conducted in greenhouse compartments of the Botanical Garden of the University of Konstanz, Germany (47°41′32″ N, 9°10′41″ E). On 26 April 2021, we collected field soil from a native grassland site near the Botanical Garden, where all five native study species occurred but none of the alien study species. This ensured that the soil had a shared ecological history with all native species but reduced the likelihood of specialist enemies of the alien species already being present. We sieved the field soil by using a 1-cm metal mesh to remove plant fragments and pebbles. The substrate used in the soil-conditioning phase consisted of a mixture of the field soil, sand and vermiculite (v:v:v = 2:3:3), and was then filled into 2-L pots (14 cm × 14 cm × 14.5 cm). On 3 May 2021, we transplanted one seedling into the centre of each pot. For each of the 10 species, we had 115 pots to make sure that we would obtain sufficient amounts of conditioned soil to be used in the next phase. As a control (i.e. unconditioned soil), we additionally had 225 pots without any plants, resulting in 1375 pots in total. Seedlings that died within 2 weeks after transplanting were replaced. All pots were randomly allocated to positions in three greenhouse compartments (24°C/18°C day/night temperature, 16/8 h day/night), and each pot was placed on a separate plastic dish (Ø = 17 cm). To reduce potential effects of environmental heterogeneity within and among greenhouse compartments, positions of all pots were re-randomized 5 weeks after the start of the soil-conditioning phase. We watered all pots every 2–3 days and fertilized them four times with 150 mL of a water-soluble fertilizer (1‰ m/v, Universol Blue with a NPK ratio of 3:2:3).

It is generally thought that the soil-conditioning phase should last at least 8 weeks (van der Heijden, 2004); we thus harvested the plants and soils 11 weeks after the start of the soil-conditioning phase. From 19 to 23 July 2021, we collected and sieved the soils from each pot, including pots without any plants, through a 5-mm mesh to remove the roots. The mesh was sterilized with 70% ethanol between different pots. The sieved soil was immediately stored at 4°C until use in the test phase.

2.2.2 | The test phase

On 5 and 12 July 2021, we sowed the 10 species again to produce seedlings for the test phase (Table S1). The pre-cultivation conditions were the same as for the soil-conditioning phase. From 24 to 27 July 2021, to test the effects of homo- and heterogeneous plant–soil feedback on each of the 45 pairs of species (i.e. 25 alien-native, 10 alien-alien and 10 native-native interspecific combinations), we divided each of 1350 pots (1.3-L; 12 cm × 12 cm × 13.2 cm) in half along their diagonals using a plastic divider. We then filled the two halves of the pots with the same (homogeneous soil legacies) or different (heterogeneous soil legacies) conditioned soils. The divider was removed once a pot had been filled and was sterilized with 70% ethanol before using it to fill the next pot. For heterogeneous pots, one half was filled with soil conditioned by one species of the species pair that would be planted in the pot and the other half with soil conditioned by the other species of that pair (Figure 1). To test whether heterogeneity in soil legacies affects plant growth, we compared them to the two homogeneous treatments in which both halves of the pot were filled with soil conditioned by only one of the two species in a pair. To test whether the plants responded differently when soil legacies of both species of a species pair were present in a homogeneous treatment compared to when only a soil legacy of one of the two species was present, and whether it differed from when soil legacies of both species were present in a heterogeneous treatment, we further conducted a homogeneous treatment with a 1:1 mixture of soils conditioned by the two species. This treatment was done by randomly mixing the soils from two conditioned pots, and two diagonal patches of one pot were randomly filled with mixed soils from different conditioned pots, respectively. In addition, to test the overall effect of plant–soil feedback, we also had a homogeneous treatment with unconditioned control soil in both halves of the pot. To avoid the effects of the heterogeneous treatments arising simply because the two halves in a test pot were filled with soils from two conditioning pots, irrespective of whether they were from two different species or not, the patches in the homogeneous treatments were also filled with soils from two replicate conditioning pots, but of the same species.

On 27 July 2021, we transplanted for each of the 45 species pairs one seedling of each of the two species per pot (Figure 1). So, each pot half received one seedling. For each species pair, there were four homogeneous soil-legacy treatments that had in both pot halves (1) unconditioned soil (homogeneous-unconditioned), (2) soil conditioned by the larger of the two species (homogeneous-larger-species), (3) soil conditioned by the smaller of the two species (homogeneous-smaller-species) and (4) a mixture of soil conditioned by both species (homogeneous-mixed). For homogeneous treatments 2 and 3, the information on which species was larger was based on the growth of the species in the homogeneous-unconditioned treatment (Figures S3 and S4). For each species pair, there were furthermore two heterogeneous soil-legacy treatments in which either (1) each species was planted in the pot half filled with soil conditioned by a conspecific plant (heterogeneous-conspecific) or (2) each species was planted in the pot half filled with soil conditioned by the other species (heterogeneous-heterospecific). Each species pair by treatment combination had five replicate pots, so, ideally, we would have had a total of 1350 pots (45 species pairs × 6 treatments × 5 replicates). However, because we did not have enough seedlings for the alien species *O. viciifolia*, we decreased the number of replicates for species pairs and treatment combinations that included this species but ensured that each had at least three replicates. Therefore, we finally had 1214 pots in the test phase.

All pots were randomly allocated to positions in two greenhouse compartments (24°C/18°C day/night temperature, 16/8 h day/night) and each of them was placed on a separate plastic dish (Ø = 15 cm).

Positions of all pots were re-randomized 5 weeks after the start of the test phase. We watered all pots every 2–3 days and fertilized them two times with 100 mL of a water-soluble fertilizer (1‰ m/v, Universol Blue).

2.3 | Measurements

On 28 and 29 July 2021, at the start of the test phase, we measured the length and width of the largest leaf on each seedling and counted the number of leaves. The initial leaf area of each seedling was then estimated as the number of leaves × length of the largest leaf × width of the largest leaf. On 4 and 5 October 2021, 10 weeks after the start of the test phase, we harvested the above-ground biomass of each of the two plants per pot separately. The below-ground biomass was not harvested because it was not possible to separate the roots of the two plants in each pot. The plant materials were dried at 70°C to constant weight and then weighed.

2.4 | Replication statement

Scale of inference	Scale at which factor of interest as applied	Number of replicates at the appropriate scale
Plant	Species	10 species
Plant	Species origin	5 alien, 5 native species
Plant	Species pair	25 alien-native, 10 alien-alien, 10 native-native species pairs
Plant	Pot	5 replicates for each pot

2.5 | Statistical analysis

To test whether the various homogeneous and heterogeneous soil-legacy treatments affected the growth of the alien and native test plants, we fitted different linear mixed effect models, both at the pot and patch levels, with the *lme* function of the *nlme* package (Pinheiro et al., 2019) in R 4.2.2 (R Core Team, 2022). To improve the homoscedasticity of the model residuals, we allowed the variance to vary among the test species or species pairs using the *varIdent* and/or *varComb* functions. In all models, we used log-likelihood ratio tests to assess the significance of each fixed effect by comparing models with and without the effect of interest (Zuur et al., 2009).

2.5.1 | Pot-level analyses

To test whether the four homogeneous and two heterogeneous soil-legacy treatments affected the biomass production and size inequality of the two plants in the pots of the test phase, we first fitted two models to the combined above-ground biomass of the two plants per pot and to the coefficient of variation (CV) of the biomass values of the two plants per pot. In these models, soil-legacy treatment (homogeneous-unconditioned, homogeneous-larger-species, homogeneous-smaller-species, homogeneous-mixed, heterogeneous-conspecific or heterogeneous-heterospecific), origin combination (alien-native, alien-alien or native-native) and their interaction were included as fixed effects. To account for variation due to the 45 different combinations of test species, we included the identity of the species pair as a random effect. Furthermore, to account for the differential response of multiple species pairs to soil-legacy treatments, we included the interaction of the identity of the species pair and the soil-legacy treatment as a random effect. To account for differences in initial sizes of the plants in the test phase, we also included the combined initial leaf area of the two plants per pot as a covariate.

To test whether the competitive balance between alien and native plants was affected by the various soil-legacy treatments, we fitted two models using the subset of pots from the alien-native competition treatment. In these models, the CV of the biomass values of the two plants per pot and the proportional biomass of the alien plant, calculated as $\text{biomass}_{\text{alien}}/(\text{biomass}_{\text{alien}} + \text{biomass}_{\text{native}})$, respectively, were included as the response variable. We used soil-legacy treatment as the fixed effect, and we used the identity of the alien-native species pair and the interaction of the identity of the species pair and the soil-legacy treatment as random effects. Most of the soil-legacy treatments were the same as in the model that included all origin combinations, but now the two homogeneous soils conditioned by only one species were defined according to whether the soil was conditioned by the alien species (homogeneous-alien-species) or the native species (homogeneous-native-species), instead of by the larger or smaller species. The combined initial leaf area of the two plants per pot was included as a covariate in the first model, while the proportional initial leaf area of the alien species was included as a covariate in the second one.

To meet the assumption of normality, plant biomass was square-root transformed and the CV was box-cox transformed ($\lambda = 0.63$). Post hoc multiple comparisons for the above models at the pot level were done separately with the *emmeans* function of the '*emmeans*' package (Lenth et al., 2023).

2.5.2 | Patch-level analyses

To test the effects of the various soil-legacy treatments on the alien and native plant individuals in each patch, we fitted two models using different subsets of the data and using square-root transformed above-ground biomass of the individual plants as the response variable. First, using the subset of pots with four homogeneous soil-legacy treatments, we tested whether individual biomass in patches was affected by the presence of diverse soil legacies and the origins of the focal plant and its competitor. Origin of the focal plant (alien or native), origin of the competitor (alien or native), soil-legacy treatment of patch (homogeneous-unconditioned, homogeneous-mixed, homogeneous-conspecific or homogeneous-heterospecific) and their interactions were included as fixed effects. We also included three orthogonal hierarchical contrasts for the soil-legacy treatment of a patch to test (1) the effect of soil legacies ($Patch_{Unconditioned/Conditioned}$), which compares the unconditioned control soil patch with the average of the other three soil-legacy patches, (2) the effect of soil mixing ($Patch_{Mixed/Single}$), which compares the mixed soil-legacy patch with the average of the conspecific and heterospecific soil-legacy patches, and (3) the effect of whether the focal plant grew on soil conditioned by a conspecific or heterospecific plant ($Patch_{Conspecific/Heterospecific}$), which compares homogeneous conspecific with homogeneous-heterospecific patches. We included the identity of the focal species and the competitor species as random effects. To account for the differential responses of multiple focal species and competitors to soil-legacy treatments in patches, we further included the interactions of their identities and the soil-legacy treatment in the patch as random effects. As each plant was used both as a focal plant and as a competitor, we accounted for the nonindependence of the two plants within the same pot by including pot identity as a random factor. We also accounted for variation in the initial size of the plants by including initial leaf area as a covariate.

In addition, we also tested whether individual biomass was affected by the soil legacy of the focal plant's patch, soil-legacy heterogeneity of the pot, and whether it depended on the origins of the focal plant and its competitor. We therefore used the subset of pots from the homogeneous-conspecific, homogeneous-heterospecific, heterogeneous-conspecific and heterogeneous-heterospecific treatments. Origin of the test species, origin of the competitor, soil-legacy heterogeneity of the pot (homogeneous or heterogeneous), soil-legacy of the focal plant's patch (conspecific or heterospecific) and their interactions were included as fixed effects. Identity of the focal species and the competitor species, interactions of their identities and the soil-legacy treatment, and pot identity of the test phase were included as random effects. We also included the initial leaf area of focal plants as a covariate.

3 | RESULTS

3.1 | Pot-level effects of soil-legacy treatments on competing plants

Overall, irrespective of their origins, the competing plants produced the most biomass per pot on unconditioned control soil (Table S2a, Figure 2a). Among the five soil-legacy treatments with conditioned soil, the combined biomass per pot did not significantly differ (Table S2a, Figure 2a). Averaged across the soil-legacy treatments, there were no significant differences among the three origin combinations of the species, and there were also no significant differences in the responses of the three origin combinations to the soil-legacy treatments (Table S2a).

Across all soil-legacy treatments, the coefficient of variation in biomass (CV) between the two plants in a pot was the smallest when the soil had been conditioned by the largest of the two species only (i.e. homogeneous-largest-species treatment; Table S2b, Figure 2b). This reduction in size inequality of this soil-legacy treatment was the most pronounced for alien-alien species pairs and the least pronounced for native-native species pairs relative to the other soil-legacy treatments (Figure 2b).

3.2 | Patch-level effects of homogeneous and heterogeneous soil legacies on individual plants

Across the four homogeneous soil-legacy treatments, there were no significant differences between the alien and native focal plants (Table S3). However, the differences in individual biomass of alien and native focal plants were larger on the homogeneous soil conditioned by a single species (+16.9%) than on the homogeneously mixed soil from both species (+3.7%; Table S3, Figure S1a), particularly when the competing plants were alien (significant $Origin_{focal} \times Origin_{comp} \times Patch_{Mixed/Single}$ interaction in Table S3, Figure S1b). Furthermore, the negative soil-legacy effects on focal plants were stronger when the soil had been conditioned by conspecifics instead of heterospecifics (−10.4%; Table S3, Figure 3a). However, in the conspecific soil-legacy treatment, alien focal plants produced more biomass when grown with an alien competitor than when grown with a native competitor (+4.5%), whereas the reverse was true in the heterospecific soil-legacy treatment (−5.7%; significant $Origin_{focal} \times Origin_{comp} \times Patch_{Conspecific/Heterospecific}$ interaction in Table S3, Figure 3a). As a consequence, alien focal plants experienced weaker negative conspecific soil-legacy effects when they were in the presence of another alien plant.

In addition, among homogeneous and heterogeneous treatments with conspecific or heterospecific soil legacies, focal plants grew worse on conspecific than on heterospecific soil patches (−5.8%; Table S4, Figure S2a). Soil-legacy heterogeneity overall had no significant effect on the biomass of focal plants across these four treatments (Table S4). However, the negative conspecific soil-legacy effect was mainly driven by the homogeneous treatments (significant Hetero × Patch interaction in Table S4; Figure S2b). Furthermore, in the heterogeneous soil-legacy treatments, the negative effect of conspecific soil remained for alien focal plants competing with aliens (−6.7%), but it disappeared for the native focal plants competing with natives or aliens, and even reversed for alien focal plants competing with natives (+12.4%; significant $Origin_{focal} \times Origin_{comp} \times Hetero \times Patch$ interaction in Table S4, Figure 3b, Figure S2).

3.3 | Effects of soil-legacy treatments on competitive symmetry between alien and native plants

For the subset of pots with alien-native species pairs, the alien biomass proportion and the CV of biomass of the alien and native plants

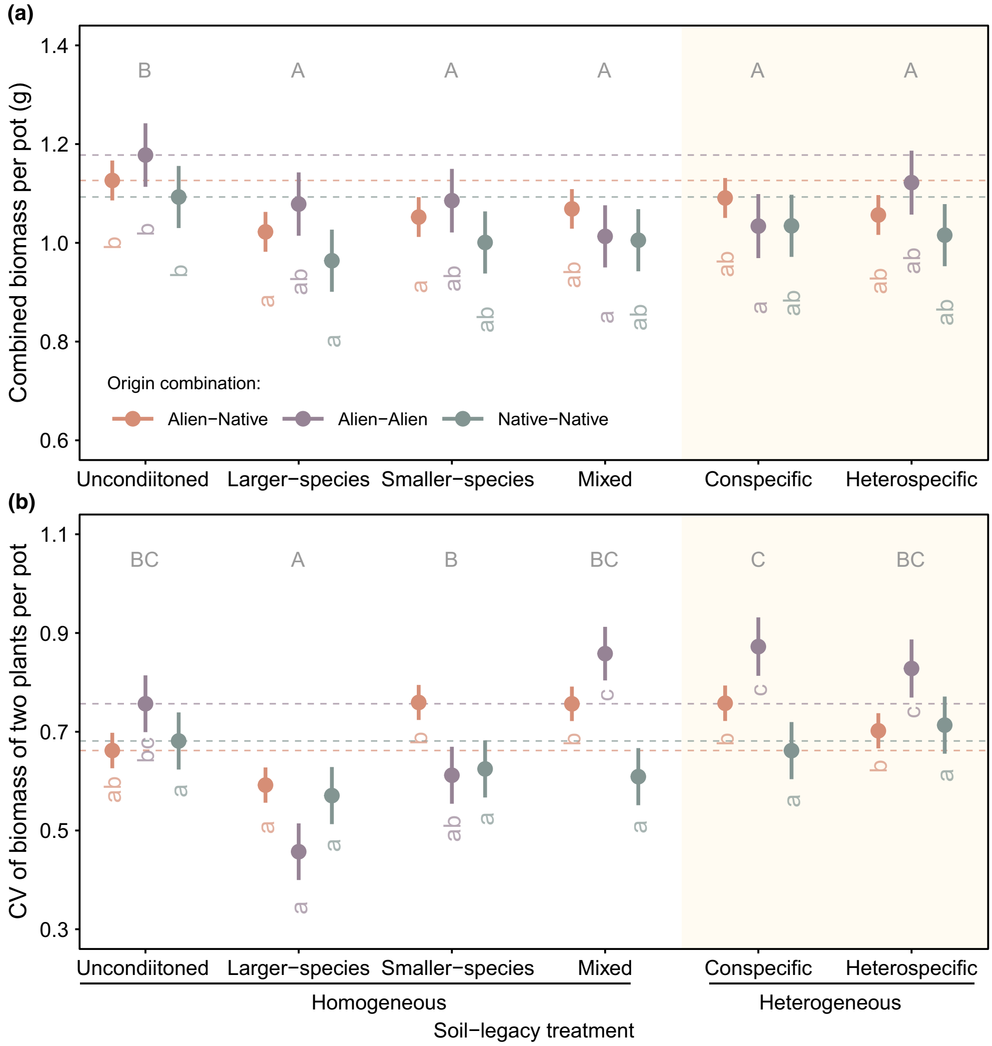

FIGURE 2 Effects of soil-legacy treatments on (a) the combined above-ground biomass per pot and (b) the coefficient of variation (CV) of biomass of the two plants per pot for alien-native, alien-alien and native-native species pairs. Shown are modelled means (±SEs). Horizontal dashed lines indicate mean values of the unconditioned control. The underlying statistical model is shown in Table S2. The uppercase letters indicate the significance ($p<0.05$) of multiple comparisons among the soil-legacy treatments (irrespective of the origin combination), and the lowercase letters indicate significances ($p<0.05$) of multiple comparisons among the soil-legacy treatments for each of the three origin combinations separately.

varied significantly among the soil-legacy treatments (Table S5). The alien biomass proportion was significantly lower in the homogeneous-alien-species treatment (i.e. on homogeneous-conspecific soil of alien species) than in any of the other soil-legacy treatments and was highest in the homogeneous-native-species treatment (i.e. on homogeneous-heterospecific soil; Figure 4a). As a consequence, the biomass inequality between competing alien and native plants was lowest on homogeneous-alien-species soil (Table S5b, Figure 4b), although it was only significantly lower than on heterogeneous-conspecific homogeneous-mixed soils (Figure 4b).

4 | DISCUSSION

Our study tested how four homogeneous and two heterogeneous soil legacies and species origins affect the growth and coexistence of competing plants. We found that all conditioned soils, relative to the unconditioned soil, negatively affected biomass production of the competing plants, irrespective of their origins. There was little variation in biomass production per pot among the five soil-legacy treatments with conditioned soils. However, the biomass was not equally partitioned between the two plants per pot. When the two competing plants grew on soil that had only been conditioned by the species that was larger in the unconditioned soil-legacy treatment, the inequality in biomass was the smallest. This indicates that the conspecific soil legacy of the larger-sized plant reduced its growth advantage relative to the smaller competitor, which should contribute to the coexistence of the two species. Both alien and native plants suffered significantly from conspecific soil legacies. However, this negative effect on alien species was mitigated when grown on homogeneous soil with another alien plant. Furthermore, alien-native species combinations had the smallest biomass

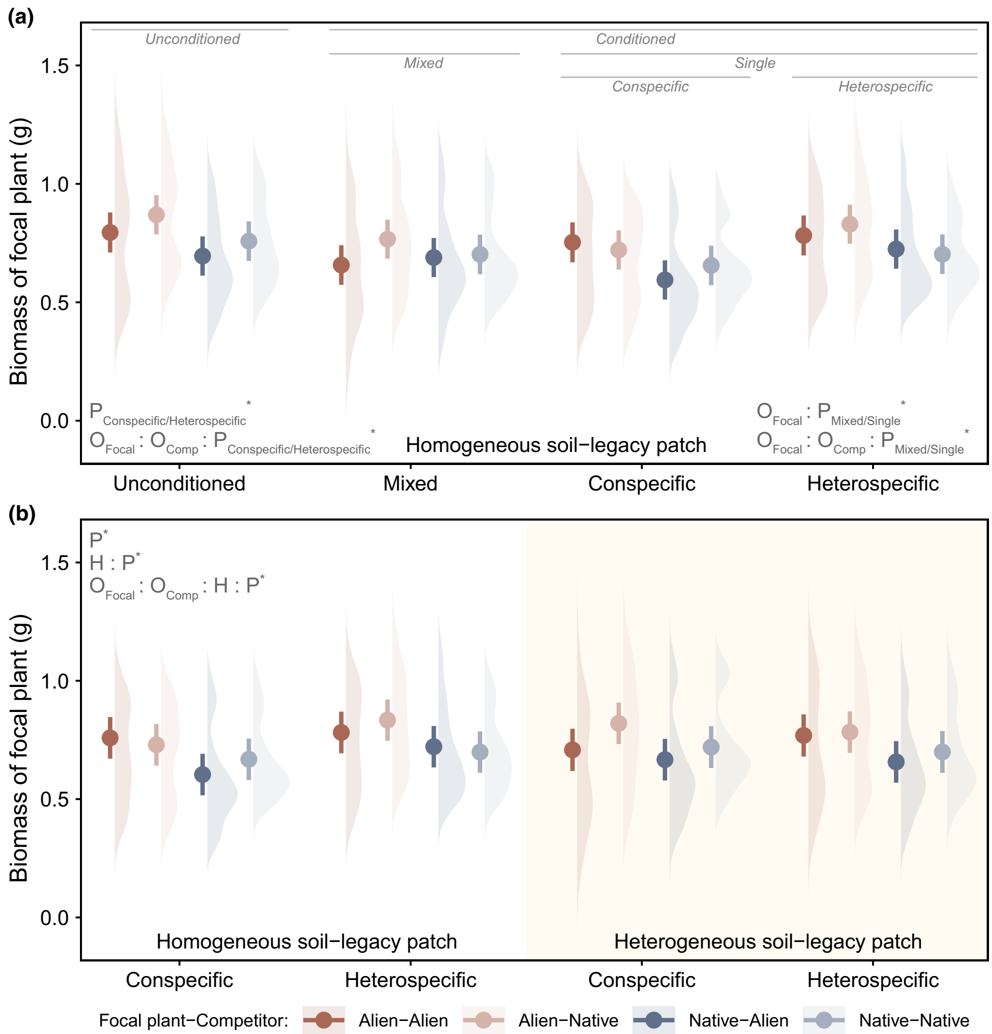

FIGURE 3 (a) Effects of the four homogeneous soil-legacy treatments on individual above-ground biomass of the alien and native focal plants at the patch level in the presence of alien or native competitors. The underlying statistical model is shown in Table S3, and significant contrasts are visualized in Figure S1. (b) Effects of conspecific and heterospecific soil legacies in patches of the focal plant and pot-level heterogeneity in soil legacies on individual biomass of alien and native focal plants in the presence of alien or native competitors. The underlying statistical model is shown in Table S4, and significant contrasts are visualized in Figure S2. Shown are modelled means (±SEs). Density ridgelines indicate the distribution of modelled values. Significant effects ($p < 0.05$) are marked with an asterisk. O, origin; P, soil-legacy treatment of patch; H, soil-legacy heterogeneity.

inequality and the lowest proportional alien biomass when grown on homogeneous-alien-species soil (i.e. homogeneous-conspecific soil for alien species), suggesting a strong negative conspecific soil-legacy effect for aliens. However, the biomass proportion of the alien species was higher when grown on heterogeneous-conspecific soil than on homogeneous-conspecific soil. This suggests that soil-legacy heterogeneity can mitigate the negative effects of conspecific soil legacies on alien plants.

4.1 | Plant-growth inequalities in diverse soil-legacy scenarios

Consistent with numerous plant–soil-feedback experiments (e.g. Aldorfová et al., 2020; Bennett et al., 2017; Bonanomi et al., 2005; Mangan et al., 2010) and meta-analyses (e.g. Crawford et al., 2019; Kulmatiski et al., 2008), we found that conditioned soils overall negatively affected plant growth (Figure 2a). This probably reflects that the pathogens and/or allelopathic secondary metabolites accumulated by the conditioning plants negatively affected the plants in the test phase (Bever et al., 2015; Packer & Clay, 2000). It could also reflect that the conditioning plants had depleted the soil of nutrients. However, to allow the conditioning plants to grow properly, so that they could train the soil and to avoid soil nutrient depletion, which would result in strong nutrient limitation for the subsequent plants, we fertilized the pots during both the conditioning and test phases. In addition, although soil nutrient depletion is often associated with plant size, we did not find a significant correlation between the size of conditioning plants and the size of subsequent plants (Figure S5), indicating

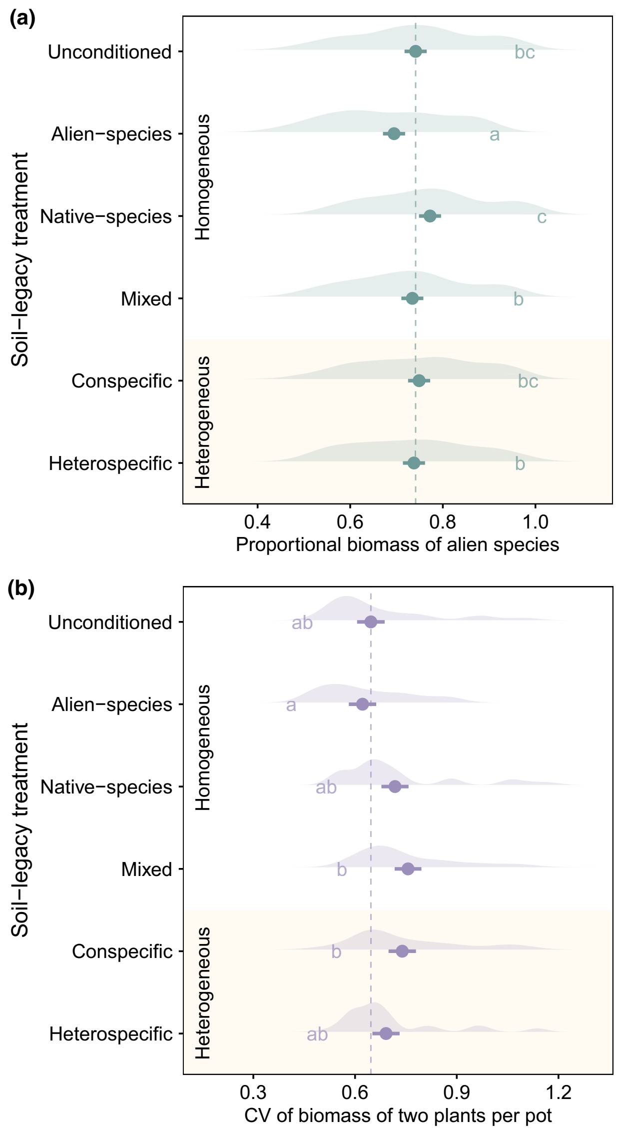

FIGURE 4 Effects of soil-legacy treatments on (a) proportional biomass of the alien plant in the presence of a native competitor and (b) the coefficient of variation (CV) of biomass of the two plants per pot for alien-native species combinations. Shown are modelled values (±SEs). Density ridgelines indicate the distribution of modelled values. Vertical dashed lines indicate mean values of the unconditioned control. The underlying statistical model is shown in Table S5. The letters indicate the significant difference ($p < 0.05$) of multiple comparisons among soil-legacy treatments.

that soil nutrient depletion probably played only a minor role in the test phase.

In line with our expectations, we found that competing plants had the smallest size inequality (CV) on soils conditioned by the larger species (Figure 2b). In other words, when a plant of the species that had a larger size under unconditioned control conditions experienced a conspecific soil legacy, its biomass was strongly reduced, making it more similar to the biomass of the competitor. When the soil had been conditioned by the smaller of the two species, the size inequality was larger than when the soil had been conditioned by the larger one. However, with the exception of the alien-native species pairs, size inequality was on average not increased relative to the unconditioned control treatment. This could reflect that slow-growing species are frequently better defended than fast-growing, acquisitive species and that they therefore accumulate fewer soil pathogens and experience less negative conspecific plant–soil feedback (Lemmermeyer et al., 2015). Furthermore, the soil-legacy effects on size inequality were the most pronounced when both plants were alien species (Figure 2b). Possibly, this reflects that many of the naturalized alien species are fast-growing species that are less defended and might therefore suffer more from soil-legacy effects mediated by generalist soil pathogens.

4.2 | Interactions between competing plant individuals mediated by soil legacies

Although growth asymmetries within alien-alien species pairs at the pot level were most sensitive to soil-legacy effects (Figure 2b), their reduction in biomass production was dependent on specific soil-legacy treatments. Specific to the patch level, on average, individual biomass of alien plants within alien-alien species pairs was higher than the biomass of native plants on soils with homogeneous soil legacies except on homogeneous-mixed soils (Figure 3a, Figure S1b). It is likely that the mixing of soil legacies from two alien species has resulted in a greater diversity of allelochemicals (Callaway & Ridenour, 2004). These novel secondary metabolites can reduce the individual growth of alien species and consequently reduce their combined biomass production on homogeneous-mixed soils. Moreover, compared to competing with native species, alien plants achieved relatively more biomass on homogeneous-conspecific soil when competing with alien species (Figure 3a). This suggests that there may be positive interactions between co-growing alien species that are mediated by the soil legacy, thereby mitigating negative conspecific soil-legacy effects. In contrast, native plants, irrespective of whether they were competing with alien or native species, experienced strong negative conspecific soil-legacy effects. Overall, these results suggest that there may be facilitation among alien plants as posited by the invasional meltdown hypothesis (Simberloff & Von Holle, 1999).

When alien and native plant species were grown in competition with one another, we found that biomass reductions of the alien and native species on their conspecific soils, relative to unconditioned control soil, were similar (−11.4% vs. −14.0%; Figure 3a). This was also true when we considered all the conditioned soils (−9.7% vs. −6.7%; Figure 3a). These findings suggest that alien plant individuals did not experience weaker soil-legacy effects than native ones. This finding is surprising as it is frequently assumed that alien species have been released from many of their species-specific natural enemies (Keane & Crawley, 2002; Mitchell & Power, 2003), and therefore should experience less negative plant–soil feedbacks (Klironomos, 2002; MacDougall et al., 2011).

Possibly, the soil inoculum that we had collected in the field, where the native study species occurred, contained mainly generalist pathogens, which not only negatively affected the native species but also the alien plant species. Furthermore, it has previously been shown that negative plant–soil feedback effects on invasive plants decline with time since establishment (Diez et al., 2010). Therefore, it could be that because the naturalized alien species used in our study have been in Europe for a relatively long time (Table S1; Capinha et al., 2023) and have closely related native species, they may by now have accumulated specialist natural enemies to similar degrees as the native species.

4.3 | Effects of soil-legacy heterogeneity on coexistence of alien and native plants

When we only considered the alien-native species pairs, we found that size inequality was smallest when the alien and native plants grew on homogeneous soil conditioned by the alien species only (Figure 4b). Specifically, homogeneous-alien-species soil, where aliens thus grew on conspecific soil, reduced the biomass proportion of the alien species considerably (Figure 4a). As the alien species tended to be larger overall than the native species (Figure S3), the reduced growth of the alien species reduced the size inequality between alien and native species. However, the biomass proportion of alien species increased on heterogeneous-conspecific soil and, as a consequence, the growth inequalities between alien and native species increased again (Figure 4). This suggests that a heterogeneous soil legacy may reduce the alien species' negative conspecific plant–soil feedback and thereby increase their competitive advantage over natives. Conversely, the performance of the native plants did not differ between the homogeneous-native-species treatment, where the natives grew on conspecific soil, and the heterogeneous-conspecific treatment (Figure 3b). Indeed, studies have shown that soil-legacy heterogeneity can create refuges for plants where they experience less negative plant–soil feedback effects (Burns et al., 2017; Hendriks et al., 2015). Possibly, alien plants, due to their frequently superior plasticity relative to natives (Chen et al., 2019; Davidson et al., 2011; Keser et al., 2014; Richards et al., 2006), were likely to take more advantage of this when competing with native plants. As a consequence, in our study, alien plants achieved a higher biomass and biomass proportion on heterogeneous-conspecific soil (Figures 3b and 4a).

In addition, total biomass per pot, individual size inequality and also proportional biomass of alien plants in the heterogeneous soil-legacy treatments were similar to those in the homogeneous-mixed treatment. Possibly, this indicates that the soil microbial communities in the two halves of the heterogeneous treatments rapidly mixed so that the resulting microbial communities in the two heterogeneous soil-legacy treatments became similar to the one in the homogeneous-mixed treatment. For proportional alien biomass, the values in the homogeneous-mixed and heterogeneous treatments were intermediate to the ones in the homogeneous-alien-species and homogeneous-native-species treatments. This is not surprising because the soil legacy of the individual species was diluted, and consequently, the abundance of species-specific pathogens was also reduced correspondingly. Therefore, the competition outcomes between alien and native species may not change much when they experience soil legacies of both species.

5 | CONCLUSIONS

Our study showed that soil legacies negatively affected plant growth, irrespective of their origins. The growth inequalities between competing plants were smaller when the soil they grew on had been conditioned by the larger-sized one. Both alien and native plants suffered significantly from conspecific soil legacies. However, alien plants benefited from another co-growing alien species on homogeneous-conspecific soil, which mitigated negative soil-legacy effects. Moreover, alien plants benefited from heterogeneous soil conditions, resulting in an increase in their competitive advantage over native plants. Our findings show that the performance of competing plants may depend on their relative sizes, origins and soil legacies. This may ultimately affect the coexistence of the species in natural environments where soil legacies are likely to be heterogeneous.

AUTHOR CONTRIBUTIONS

Duo Chen conceived the idea. Mark van Kleunen and Duo Chen designed the experiment. Duo Chen conducted the experiment. Duo Chen analysed the data and wrote the first draft of the manuscript with further inputs from Mark van Kleunen.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at https://doi.org/10.6084/m9.figshare.28463939 (Chen & van Kleunen, 2025).

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REFERENCES

Aldorfová, A., Knobová, P., & Münzbergová, Z. (2020). Plant–soil feedback contributes to predicting plant invasiveness of 68 alien plant species differing in invasive status. *Oikos*, *129*(8), 1257–1270. https://doi.org/10.1111/oik.07186

Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., & Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, *355*, 181–184.

Bever, J. D., Mangan, S. A., & Alexander, H. M. (2015). Maintenance of plant species diversity by pathogens. *Annual Review of Ecology, Evolution, and Systematics*, *46*(46), 305–325.

Bever, J. D., Westover, K. M., & Antonovics, J. (1997). Incorporating the soil community into plant population dynamics: The utility of the feedback approach. *Journal of Ecology*, *85*(5), 561–573. https://doi.org/10.2307/2960528

Bonanomi, G., Giannino, F., & Mazzoleni, S. (2005). Negative plant-soil feedback and species coexistence. *Oikos*, *111*(2), 311–321. https://doi.org/10.1111/j.0030-1299.2005.13975.x

Bourgeois, K., Suehs, C. M., Vidal, E., & Medail, F. (2005). Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. *Ecoscience*, *12*, 248–256.

Brandt, A. J., de Kroon, H., Reynolds, H. L., & Burns, J. H. (2013). Soil heterogeneity generated by plant-soil feedbacks has implications for species recruitment and coexistence. *Journal of Ecology*, *101*, 277–286.

Burns, J. H., Brandt, A. J., Murphy, J. E., Kaczowka, A. M., & Burke, D. J. (2017). Spatial heterogeneity of plant-soil feedbacks increases per capita reproductive biomass of species at an establishment disadvantage. *Oecologia*, *183*, 1077–1086.

Callaway, R. M., & Ridenour, W. M. (2004). Novel weapons: Invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, *2*, 436–443.

Capinha, C., Essl, F., Porto, M., & Seebens, H. (2023). The worldwide networks of spread of recorded alien species. *Proceedings of the National Academy of Sciences*, *120*, e2201911120.

Chen, D., Ali, A., Yong, X. H., Lin, C. G., Niu, X. H., Cai, A. M., Dong, B. C., Zhou, Z. X., Wang, Y. J., & Yu, F. H. (2019). A multi-species comparison of selective placement patterns of ramets in invasive alien and native clonal plants to light, soil nutrient and water heterogeneity. *Science of the Total Environment*, *657*, 1568–1577.

Chen, D., & van Kleunen, M. (2022). Invasional meltdown mediated by plant-soil feedbacks may depend on community diversity. *New Phytologist*, *235*, 1589–1598.

Chen, D., & van Kleunen, M. (2025). Data from: Naturalized alien plants experience less negative soil-legacy effects and gain competitive advantages through spatial heterogeneity. *Figshare*. https://doi.org/10.6084/m9.figshare.28463939

Crawford, K. M., Bauer, J. T., Comita, L. S., Eppinga, M. B., Johnson, D. J., Mangan, S. A., Queenborough, S. A., Strand, A. E., Suding, K. N., Umbanhowar, J., & Bever, J. D. (2019). When and where plant-soil feedback may promote plant coexistence: A meta-analysis. *Ecology Letters*, *22*, 1274–1284.

Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, *14*(4), 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Dawson, W., Moser, D., van Kleunen, M., Kreft, H., Pergl, J., Pyšek, P., Weigelt, P., Winter, M., Lenzner, B., Blackburn, T. M., Dyer, E. E., Cassey, P., Scrivens, S. L., Economo, E. P., Guénard, B., Capinha, C., Seebens, H., García-Díaz, P., Nentwig, W., … Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, *1*(7), 0186. https://doi.org/10.1038/s41559-017-0186

Diez, J. M., Dickie, I., Edwards, G., Hulme, P. E., Sullivan, J. J., & Duncan, R. P. (2010). Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, *13*, 803–809.

Fahey, C., Koyama, A., Antunes, P. M., Dunfield, K., & Flory, S. L. (2020). Plant communities mediate the interactive effects of invasion and drought on soil microbial communities. *ISME Journal*, *14*(6), 1396–1409. https://doi.org/10.1038/s41396-020-0614-6

Haeuser, E., Dawson, W., & van Kleunen, M. (2019). Introduced garden plants are strong competitors of native and alien residents under simulated climate change. *Journal of Ecology*, *107*, 1328–1342.

Hendriks, M., Ravenek, J. M., Smit-Tiekstra, A. E., van der Paauw, J. W., de Caluwe, H., van der Putten, W. H., de Kroon, H., & Mommer, L. (2015). Spatial heterogeneity of plant-soil feedback affects root interactions and interspecific competition. *The New Phytologist*, *207*(3), 830–840. https://doi.org/10.1111/nph.13394

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, *17*(4), 164–170. https://doi.org/10.1016/s0169-5347(02)02499-0

Keser, L. H., Dawson, W., Song, Y. B., Yu, F. H., Fischer, M., Dong, M., & van Kleunen, M. (2014). Invasive clonal plant species have a greater root-foraging plasticity than non-invasive ones. *Oecologia*, *174*, 1055–1064.

Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, *417*, 67–70.

Kulmatiski, A., Beard, K. H., Stevens, J. R., & Cobbold, S. M. (2008). Plant-soil feedbacks: A meta-analytical review. *Ecology Letters*, *11*, 980–992.

Lemmermeyer, S., Lörcher, L., van Kleunen, M., & Dawson, W. (2015). Testing the plant growth-defense hypothesis belowground: Do faster-growing herbaceous plant species suffer more negative effects from soil biota than slower-growing ones? *The American Naturalist*, *186*, 264–271.

Lenth, R. V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2023). Estimated marginal means, aka least-squares means.

Lozano, Y. M., Aguilar-Trigueros, C. A., Ospina, J. M., & Rillig, M. C. (2022). Drought legacy effects on root morphological traits and plant biomass via soil biota feedback. *New Phytologist*, *236*, 222–234.

MacDougall, A. S., Rillig, M. C., & Klironomos, J. N. (2011). Weak conspecific feedbacks and exotic dominance in a species-rich savannah. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 2939–2945.

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M. L., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, *466*(7307), 752–755. https://doi.org/10.1038/nature09273

McCarthy-Neumann, S., & Kobe, R. K. (2010). Conspecific plant–soil feedbacks reduce survivorship and growth of tropical tree seedlings. *Journal of Ecology*, *98*(2), 396–407. https://doi.org/10.1111/j.1365-2745.2009.01619.x

Mitchell, C. E., & Power, A. G. (2003). Release of invasive plants from fungal and viral pathogens. *Nature*, *421*, 625–627.

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, *404*, 278–281.

Parepa, M., Fischer, M., & Bossdorf, O. (2013). Environmental variability promotes plant invasion. *Nature Communications*, *4*, 1604. https://doi.org/10.1038/ncomms2632

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2019). nlme: linear and nonlinear mixed effects models.

Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., Weigelt, P., Winter, M., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., … van Kleunen, M. (2017). Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. *Preslia*, *89*, 203–274.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J., & Pigliucci, M. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, *9*, 981–993.

Seebens, H., Bacher, S., Blackburn, T. M., Capinha, C., Dawson, W., Dullinger, S., Genovesi, P., Hulme, P. E., van Kleunen, M., Kühn, I., Jeschke, J. M., Lenzner, B., Liebhold, A. M., Pattison, Z., Pergl, J., Pyšek, P., Winter, M., & Essl, F. (2021). Projecting the continental accumulation of alien species through to 2050. *Global Change Biology*, *27*, 970–982.

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*, 21–32.

van der Heijden, M. G. A. (2004). Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. *Ecology Letters*, *7*, 293–303.

van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J., Wardle, D. A., & Hutchings, M. (2013). Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology*, *101*(2), 265–276. https://doi.org/10.1111/1365-2745.12054

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*, 235–245.

Wei, G. W., & van Kleunen, M. (2022). Soil heterogeneity tends to promote the growth of naturalized aliens when competing with native plant communities. *Journal of Ecology*, *110*, 1161–1173.

Wolfe, B. E., & Klironomos, J. N. (2005). Breaking new ground: Soil communities and exotic plant invasion. *Bioscience*, *55*(6), 477–487. https://doi.org/10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO;2

Xue, W., Berendse, F., & Bezemer, T. M. (2018). Spatial heterogeneity in plant-soil feedbacks alters competitive interactions between two grassland plant species. *Functional Ecology*, *32*(8), 2085–2094. https://doi.org/10.1111/1365-2435.13124

Zhang, Z., Liu, Y., Brunel, C., & van Kleunen, M. (2020). Soil-microorganism-mediated invasional meltdown in plants. *Nature Ecology & Evolution*, *4*, 1612–1621.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

SUPPORTING INFORMATION

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

Figure S1. (a) Effects of the homogeneous-mixed and homogeneous-single (i.e. average of homogeneous-conspecific and homogeneous-heterospecific) soil-legacy treatments on individual aboveground biomass of the alien and native focal plants at the patch level. (b) Effects of the homogeneous-mixed and homogeneous-single soil-legacy treatments on individual aboveground biomass of the alien and native focal plants at the patch level in the presence of alien or native competitors.

Figure S2. (a) Effects of conspecific and heterospecific soil patches on individual aboveground biomass of the focal plants. (b) Effects of conspecific and heterospecific soil patches on individual aboveground biomass of the focal plants in homogeneous and heterogeneous soil-legacy pots.

Figure S3. Means (±SEs) of biomass of each focal plant species in unconditioned control soil treatment.

Figure S4. Differences of mean biomass of each species pair in unconditioned control soil treatment.

Figure S5. Effect of aboveground biomass produced by plants in the soil-conditioning phase on the aboveground biomass of the test-phase pots.

Table S1. Plant species used in the experiment.

Table S2. Effects of soil-legacy treatment (homogeneous-unconditioned, homogeneous-larger-species, homogeneous-smaller-species, homogeneous-mixed, heterogeneous-conspecific or heterogeneous-heterospecific), origin-combination treatment (alien-native, alien-alien or native-native) and their interaction on (a) combined aboveground biomass of the two plants per pot and (b) the coefficient of variation (CV) of the biomass of the two plants per pot.

Table S3. Effects of the origin of the focal plant (alien or native), origin of the competitor (alien or native), soil-legacy treatment of patch (unconditioned, mixed, conspecific or heterospecific) and their interactions on aboveground biomass of the focal plant in the subset of pots in the four homogeneous treatments.

Table S4. Effects of the origin of the focal plant (alien or native), origin of the competitor (alien or native), soil-legacy heterogeneity (homogeneous or heterogeneous), soil-legacy of patch (conspecific or heterospecific) and their interactions on aboveground biomass of the focal plant in the subset of pots with homogeneous and heterogeneous soil-legacies of conspecifics and heterospecifics.

Table S5. Effects of soil-legacy treatment (homogeneous unconditioned, homogeneous-alien-species, homogeneous-native-species, homogeneous-mixed, heterogeneous-conspecific or heterogeneous-heterospecific) on (a) proportional biomass of alien species and (b) the coefficient of variation (CV) in biomass of the two plants per pot in the subset of pots with alien-native species combinations.

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