

RESEARCH ARTICLE

Plant community evenness responds to spatial plant–soil feedback heterogeneity primarily through the diversity of soil conditioning

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Abstract

1. Plant–soil feedback (PSF) has been identified as a key driver of local plant diversity and evenness in competitive communities. However, while it has been shown that spatial PSF heterogeneity can alter plant performance and competitive interactions, there is no proof of principle that spatial PSF heterogeneity enhances community diversity.
2. Using a grassland model system, we separated two aspects of spatial heterogeneity: the number of species conditioning the soil and spatial distribution of the PSFs.
3. Our data show that PSFs promoted a higher plant evenness when the soil was conditioned by multiple species (mixed-conditioned) than when the soil was conditioned by a single species (mono-conditioned). On mono-conditioned soils, heterospecifics typically outperformed the focal species. In addition, there was a trend for increasing community evenness from uniform, via fine-grained to coarse-grained mixed-conditioned soils, but this was not significant.
4. On mixed-conditioned soils, performance of all competing species was intermediate to the best and the worst mono-conditioned soils, leading to higher community evenness.
5. Our data demonstrate that PSFs play a role in promoting plant evenness. Across mono-conditioned soils, PSF led to altered competitive hierarchies. However, on soils conditioned by multiple species, competitive ability among species was more similar and this led to higher plant evenness. The spatial distribution of the heterogeneity, on the other hand, did not significantly affect plant evenness. Our data therefore show that community evenness was more strongly related to the number of plant species that conditioned the soil than the spatial distribution of the PSF heterogeneity. Future studies need to investigate the importance of PSFs in the field across plant life stages and multiple generations.

KEYWORDS

competition, plant diversity, plant–soil interactions, spatial heterogeneity

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1 | INTRODUCTION

A long-standing question in ecology is how high plant diversity is maintained at local spatial scales (Hutchinson, 1961; Wilson, Peet, Dengler, & Pärtel, 2012), as competitors are known to exclude one another (Hardin, 1960). Differences in competitive abilities lead to a decline in community evenness and eventually to local extinction of subordinate species (Booth & Grime, 2003; Silvertown, 2004; Wilsey & Polley, 2004). Several authors have proposed that at small spatial scales, plant antagonists, particularly soil-borne pathogens, may act as key drivers of plant evenness and diversity (Bennett & Cahill, 2016; Bever, Mangan, & Alexander, 2015; Bradley, Gilbert, & Martiny, 2008; De Kroon et al., 2012).

When growing in soil, plants induce changes in the composition of the soil community (Bezemer et al., 2010; Lundberg et al., 2012) and these changes, in turn, affect plant performance. This phenomenon is known as plant–soil feedback (PSF; Bever, 1994, 2003; Van der Putten et al., 2013). Most direct PSF effects, that is the effect of growing on self-conditioned soil, are reported to be negative, and this may prevent species from becoming mono-dominant in the community (Kulmatiski, Beard, Stevens, & Cobbold, 2008; Petermann, Fergus, Turnbull, & Schmid, 2008). The particular soil organisms that cause the PSF effect may vary between soils and may be different for each plant

species in the community (Bever et al., 2015). Furthermore, interactions with other soil organisms can strongly alter the effects of mutualists and pathogens on plants (Bradley et al., 2008; Hersh, Vilgalys, & Clark, 2012; Morris et al., 2007). PSF studies quantify the net effect of changes in the whole soil community on plant performance and as such incorporate the complex web of interactions below-ground (Bever, Westover, & Antonovics, 1997; Van der Putten et al., 2013).

Theoretical models of spatial plant communities show that PSF effects can mediate plant diversity if they are highly localized in space (Abbott et al., 2015; Bonanomi, Giannino, & Mazzoleni, 2005; Fukami & Nakajima, 2013; Mack & Bever, 2014). Recent empirical work has confirmed that spatial heterogeneity in PSFs can affect plant performance (Brandt, De Kroon, Reynolds, & Burns, 2013; Burns, Brandt, Murphy, Kaczowka, & Burke, 2017; Hendriks, Visser, et al., 2015; Wubs & Bezemer, 2016), seedling establishment (Burns & Brandt, 2014) and can alter competitive hierarchies (Hendriks, Ravenek, et al., 2015). Furthermore, individual grassland plant species growing in open field communities are known to have specific soil communities that are distinct from neighbouring individuals of other species (shown using 5-cm-diameter cores; Bezemer et al., 2010). However, thus far PSF studies have been limited to inferences based on data from monocultures or pairs of plant species. Empirical evidence of the impact of heterogeneity of plant–soil feedback on plant diversity in

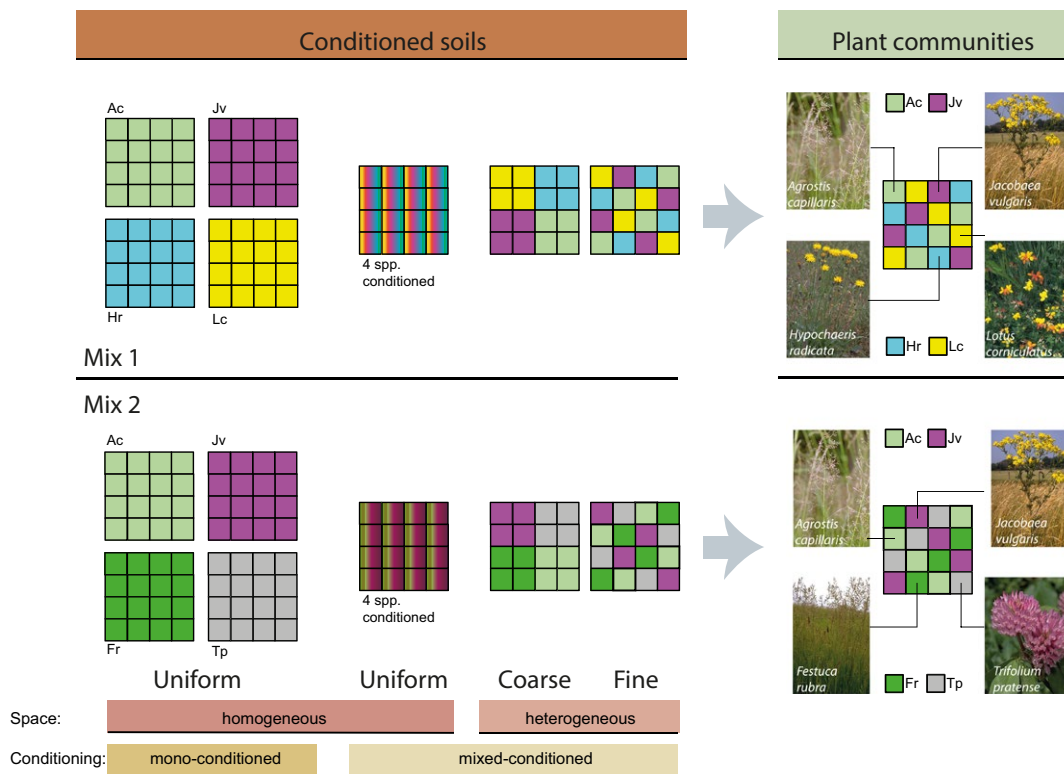


FIGURE 1 Experimental design. Two plant communities (mix 1 and mix 2) were planted each on seven conditioned soils with different levels of conditioning diversity and at different spatial grain. Soils were either homogeneous (uniform) or heterogeneous (fine- or coarse-grained heterogeneity). Heterogeneous soils were conditioned by the same four species as in the respective plant mixture. The homogeneous soils (uniform) were either conditioned by one species (mono-conditioned) or simultaneously conditioned by four species in mixture (mixed-conditioned). Ac = *Agrostis capillaris*; Fr = *Festuca rubra*; Hr = *Hypochaeris radicata*; Jv = *Jacobaea vulgaris*; Lc = *Lotus corniculatus*; Tp = *Trifolium pratense*

communities consisting of more than two species is lacking (Hendriks, Ravenek, et al., 2015). In addition, spatial PSF heterogeneity consists of two components that have hitherto not been teased apart: conditioning diversity (CD) and spatial grain (Figure 1).

With CD, we mean the number of plant species that conditioned the soil, where soil conditioned by one species is called mono-conditioned soil, while we refer to soil conditioned by multiple species as mixed-conditioned soil. With spatial grain, we refer to how the PSF is spatially distributed (e.g. fine- or coarse-grained). We examined spatial grain effects only in mixed-conditioned soils as a mono-conditioned equivalent of a heterogeneous soil does not exist by default.

Here, we test in model grassland communities whether spatial PSF heterogeneity drives community evenness at a scale where plants interact with neighbouring plants and with the soil community. All communities consisted of four plant species, and hence, we focused on plant community evenness as a measure of plant diversity (sensu De Deyn et al., 2003). Differences in species richness are difficult to detect within glasshouse experiments as it can take several years before species go locally extinct (Booth & Grime, 2003; Hillebrand, Bennett, & Cadotte, 2008; Wilsey & Polley, 2004). However, rates of local extinctions have been shown to be higher in communities with lower evenness, and differences in evenness are thus expected to translate into differences in species richness over time (Wilsey & Polley, 2004). In this experiment, we explicitly tested whether the effects of CD or spatial grain were the dominant drivers of PSF effects on community evenness.

We predicted that plant evenness would be higher in mixed-conditioned treatments. This is because in uniform soil conditioned by one species (mono-conditioned), heterospecific plants are expected to become dominant as they would not encounter their own soil-borne antagonists within their rooting zones (Casper, Schenk, & Jackson, 2003). In contrast, in soils conditioned by multiple species, each species would be kept in check by its own set of soil-borne antagonists. Therefore, we predicted that the competitive abilities among species in a community would be more equal in mixed-conditioned soils compared to mono-conditioned soils and that this led to a higher community evenness.

In addition, we manipulated the grain of the spatial heterogeneity while keeping the ratios of the differently conditioned soils the same (i.e. all mixed-conditioned soils). Some plant species are known to be competitively superior when abiotic soil resources are distributed heterogeneously, because of their superior root placement ability (Gazol et al., 2013). Likewise, specific root placement ability in response to heterogeneous PSFs also differs among species (Hendriks, Ravenek, et al., 2015). This suggests that in heterogeneous mixed-conditioned soils, some species may have a competitive advantage as they can place their root preferentially in patches with the least negative PSF, suggesting that evenness will decline in heterogeneous conditions (evenness: coarse-grained < fine-grained < uniform). However, in contrast to soil-borne resources, soil biota are mobile to some extent and this may blur the initial heterogeneity (e.g. after a plant, or a root, dies). If the latter effect is dominant, then each species is equally likely to encounter its enemies regardless of their exact spatial location (Wubs

& Bezemer, 2016). In that case, we predict that spatial grain would have no effect on plant performance and evenness, and therefore, we predicted that uniform soils conditioned by multiple species (mixed-conditioned) would have the same effect on plant evenness as spatially heterogeneous treatments.

2 | MATERIALS AND METHODS

To test our hypotheses, we conducted a glasshouse PSF experiment where we grew two plant communities on four soil conditioning treatments, where we explicitly manipulated the spatial PSF heterogeneity (Figure 1). This study builds on the work reported in Wubs and Bezemer (2016) as it uses the same soil conditioning and spatial heterogeneity treatments. However, the data reported from the test phase are new and the study addresses the new question of how spatial PSF heterogeneity affects plant community composition and evenness. Six plant species were selected that are typical for old fields on sandy soils in north-west Europe: *Agrostis capillaris* L. and *Festuca rubra* L. (both grasses), *Hypochaeris radicata* L. and *Jacobaea vulgaris* Gaertn. (syn. *Senecio jacobaea* L.; both forbs) and *Lotus corniculatus* L. and *Trifolium pratense* L. (both legumes). Plant-soil feedback experiments typically consist of two phases, first one in which plants condition the soil (conditioning phase) and subsequently a phase in which the effects of the soil conditioning on plant growth are tested (test or feedback phase).

2.1 | Phase 1: Soil conditioning phase

We collected topsoil (to 30 cm deep) from an ex-arable grassland (Mossel, Planken Wambuis, Ede, the Netherlands, GPS: 52°04'0N 05°45'0E) that had been under restoration for 17 years. The soil was sieved (5 mm mesh size) and used to fill containers (17 × 17 × 17 cm; 5 kg of soil per container). We subsequently conditioned the soil for 8 weeks, by growing all six plant species in monocultures in the soil in a glasshouse. All seeds were surface-sterilized (1 min in <2.5% NaClO solution), rinsed with water and allowed to germinate on sterilized glass beads in a climate chamber (16:8-hr day-night cycle, continuous 20°C) for 2 weeks. Sixteen individuals of a species were planted in each container, and there were 58 containers per species, except for *A. capillaris* and *J. vulgaris* with 77 containers each. More soil of the latter two species was needed to create the spatially heterogeneous treatments in the test phase (see below). In addition, we implemented a mixed-conditioning treatment where two sets of four species simultaneously grew in the soil. The first set was planted with *F. rubra*, *H. radicata*, *J. vulgaris* and *L. corniculatus*, while the second set was planted with *A. capillaris*, *F. rubra*, *J. vulgaris* and *T. pratense*. Here, we planted four individuals per species in a Latin square design. In both sets, 37 pots of soil were conditioned. Pots in each conditioning treatment were randomly allocated to one of three soil replicates, and the soils of these replicates were kept separate throughout the experiment to ensure they were fully independent. Containers were placed randomly in the glasshouse, and plants were allowed to grow (16:8-hr day:night, natural light supplemented with 600-W metal-halide lamps,

1 per 4 m⁻², c. 225 µmol light quanta m⁻² s⁻¹ at plant level, 21:16°C day:night, 50%–70% relative humidity) for 8 weeks. Subsequently, shoot biomass was clipped and all root systems were removed from the soil of each pot. Soil from containers in which the same species had grown and that were a priori allocated to the same soil replicate were pooled and carefully homogenized. To obtain a sufficient amount of soil for the experiment, each of the soil replicates was mixed with sterilized (>25K Gray gamma radiation; Isotron, Ede, the Netherlands) field soil collected from the same site in an 8.4:1.6 (conditioned: sterile w:w) ratio. From each of the homogenized soil replicates, a sample (200 g) was taken for chemical analysis after addition of the sterilized soil. We measured mineral nitrogen (KCl extraction), PO₄ (P-Olsen extraction) and soil organic matter (ashed at 430°C for 24 hr) content as well as soil acidity (in 1:2.5 w:w dry soil:water suspensions; see Table S1). Furthermore, three soil samples, one per soil replicate, were taken from each of the mono-conditioned soils (n = 18) and analysed for differences in fungal community composition using terminal restriction fragment length polymorphism (T-RFLP) analysis of the ITS marker (see Methods S1 for the protocol).

2.2 | Phase 2: Feedback phase

In the test phase, three different levels of spatial grain were created (spatially homogeneous, spatially heterogeneous coarse-grained and spatially heterogeneous fine-grained; Figure 1). Each container (length × width × height: 26 × 22 × 22 cm) was divided using a custom-made metal grid into 4 × 4 cells, each with a surface area of c. 35 cm² (the length and width of the cells differed slightly to account for the rounded corners of the containers), extending to the bottom of the container. The size of the grid cells was chosen because at this grain size systematic differences in soil community composition were detected in open communities in the field (Bezemer et al., 2010).

In each container, independent of the treatment, all 16 grid cells were filled individually and any given grid cell was always filled with a single conditioned soil type. Each container was filled with 2.5 kg sterilized gravel (quartz, 4–8 mm) and then with 8 kg of conditioned soil (500 g per grid cell). All containers were filled with conditioned soil in the same way: weighing 500 g of the appropriate conditioned soil type and then carefully pouring the soil into the respective grid cell. Immediately after filling the containers, the metal grid was removed so that during the test phase, the soil patches in each container were in full contact.

For the homogeneous treatment, all cells in a container were filled with one conditioned soil (either mono- or mixed-conditioned), while for spatially heterogeneous treatments (coarse- and fine-grained), grid cells were filled with soil mono-conditioned by four different species (Figure 1). The four soils in the fine-grained treatment were applied following a Latin square design, while for the coarse-grained treatment, four contiguous square blocks of four cells each were created in each container. The two spatially heterogeneous treatments (coarse- and fine-grained) were created with two different mixes of soil conditioned by four plant species (soil mix). Soil mix 1 consisted of soils conditioned by *A. capillaris*,

H. radicata, *J. vulgaris*, and *L. corniculatus*; soil mix 2 consisted of *A. capillaris*, *F. rubra*, *J. vulgaris* and *T. pratense*. Consequently, both soil mixes had at least one representative each of the grass, forb and legume plant functional types. Containers in the mixed-conditioned uniform treatment received the soil that was simultaneously conditioned by four species in all grid cells. As the mixed-conditioned uniform soils were homogenized at the end of the conditioning phase, as was true for all conditioned soils, we expect that any spatial differences will have been evened out and therefore consider it as a spatially uniform treatment. Conditioned soils from all six focal species were used separately to create spatially homogeneous containers with mono-conditioned soil.

After preparation of the soil treatments, the conditioned soils were planted with two mixtures of four plant species, which were the same as the species that conditioned the two soil mixes mentioned above. Data from both mixes were analysed only when growing on soils in their own mix. Consequently, each plant mixture grew on seven soil-by-spatial heterogeneity treatments (four mono-conditioned uniform, one mixed-conditioned uniform, one coarse heterogeneous and one fine heterogeneous). The four species were planted in a Latin square design, which was selected randomly with the constraint that each plant species would be planted on all four soils in the spatially heterogeneous treatments (i.e. a Graeco-Latin square for the fine-grained heterogeneous treatment). The whole set-up was replicated three times, using the three independent soil replicates. In total, there were 42 containers in the test phase (7 soil treatments × 2 plant communities × 3 replicates).

Each container was planted with 32 seedlings, planting two individuals of the same species into each grid cell (each seedling 1 cm from the grid cell mid-point). The experimental design ensured that all plant species were grown on all soils in the heterogeneous treatments. Seeds were germinated in the same way as in the conditioning phase. Seedlings that died upon transplantation were replaced once during the first week. The containers were placed in the glasshouse in a complete randomized design under the same conditions as during the conditioning phase and allowed to grow for 8 weeks. The soil was kept moist by regular watering (two or three times per week depending on evapotranspiration rates). After 8 weeks of growth, above-ground plant biomass was clipped flush with the soil, dried (72°C, 48 hr) and weighed separately per grid cell for each of the containers (i.e. 16 observations per container, with known locations of each observation within the container).

Below-ground biomass was sampled by inserting a soil corer (Ø 3.3 cm) into the middle of a grid cell and gently pushing it to the bottom of the container. While extracting the corer, it was made sure that all soil in the column, down to the gravel underneath, was collected. To make sure the soil cores were taken exactly in the middle of each grid cell, a metal grid (the same dimensions as before, but only 1 cm high) was placed on top of the soil when taking soil cores. Roots were extracted from the soil cores by careful washing over a sieve (2 mm mesh) and subsequently dried and weighed. For the spatially heterogeneous treatments (coarse- and fine-grained), all 16 grid cells were sampled, while eight cores were taken from the spatially

homogeneous treatment. Roots could not be identified to species level and so root biomass values were summed per container to estimate total root biomass.

2.3 | Data analysis

We calculated the evenness index (J' , this is Shannon diversity rescaled to 0–1 by dividing by the natural logarithm of the number of species in the sample) based on the shoot biomass of each species present in each container as a measure of plant diversity (Pielou, 1966). Both plant evenness and total shoot and root plant biomass in each container were analysed with simple fixed-effects models. In each case, we analysed two models, one comparing the effect of CD (only including the mono- and mixed-conditioned uniform treatments) and one directly comparing the effect of spatial grain when soils were mixed-conditioned. In both analyses, plant mixture and the interaction between plant mixture and, respectively, CD or spatial grain were included as fixed effects. When the spatial grain effect was significant, we used planned contrasts to compare fine- and coarse-grained heterogeneity to the mixed-conditioned uniform treatment.

Shifts in competitive hierarchies were analysed using relative abundance of each species per container. Relative abundance was calculated as the ratio of shoot biomass of a given species to the total container shoot biomass. These data were analysed per community using linear mixed models (LMMs) with container as a random factor. Test plant species, conditioned soil and level of spatial heterogeneity and their interactions were included as fixed factors.

To examine how PSF effects change with spatial heterogeneity, we analysed differences in shoot biomass as well as relative abundance (shoot biomass per grid cell relative to total shoot biomass in the container) on grid cell level using LMMs. The uniform mixed-conditioned soil treatment was excluded from these analyses because in this treatment the soil effects on plant performance could not be attributed to individual species that had conditioned the soil. These models included random effects for container and grid cell. The grid cell factor was introduced to account for positional effect within containers, but given the rotational symmetry in the within container design, the grid cell factor had three levels (corner [4 per container], edge [8] or centre [4] of the container). Test plant species, conditioned soil and level of spatial heterogeneity (uniform mono-conditioned, heterogeneous fine and heterogeneous coarse) and their interactions were included as fixed factors, and analyses were conducted separately for the two plant communities. We constructed separate own–foreign soil planned contrasts for each species as a measure of PSF at each level of spatial heterogeneity (Adbi & Williams, 2010; Brinkman, Van der Putten, Bakker, & Verhoeven, 2010). Here, own soils were given positive contrast weights, while foreign soils were given negative weights that in total sum to zero: as a result, negative contrast values indicate negative direct PSF (i.e. biomass on own soil is lower than on foreign soil).

We analysed the effects of PSFs on plant competition in two ways. First, we analysed whether PSF effects were strong enough to alter competitive hierarchies. To do so, we calculated the number

of rank reversals within both plant mix 1 and 2 across all six possible pairs of mono-conditioned uniform soils. We ranked the species based on their relative abundance within each container and calculated the number of reversed ranks among all pairs of conditioned soils, always directly comparing experimental units from the same soil replicate. We summed the number of rank reversals across all pairs and replicates and used the χ^2 distribution to test whether the number of rank reversals was more or less than 50% (Kitajima & Bolker, 2003). We interpreted significantly more rank reversals than 50% as evidence that PSFs altered the competitive ranking of the plants species.

In the second analysis, we assessed how the differences in species competitive abilities (following Weigelt & Jolliffe, 2003) within each experimental community changed with the PSF treatments. We calculated the competitive ability (CA) of each species across the seven soil treatments relative to (1) the respective shoot biomass in monoculture and (2) a perfectly “even” community (i.e. relative shoot biomass of the four species = 0.25:0.25:0.25:0.25):

$$CA1 = \log(RA_{i,r,mix}/RA_{i,r,mono}) \quad (1)$$

and

$$CA2 = \log(RA_{i,r,mix}/0.25) \quad (2)$$

where $RA_{i,r,mix}$ is the relative shoot biomass of species i in replicate r when grown in mixture and $RA_{i,r,mono}$ is the relative shoot biomass of species i in replicate r when grown in monoculture. Monoculture data were taken from Wubs and Bezemer (2016) and rescaled to relative shoot biomass by dividing grid cell biomass by the total container shoot biomass. For the comparison of plant performance in plant mixtures and monocultures, data from the monocultures were selected so that matching values were obtained from the same plant species, conditioned soil, soil replicate and grid cell as the data obtained in the mixtures, so as to account for positional effects within containers. Relative shoot biomass values were summed per species within each container, and competitive abilities were calculated (i.e. four values per container). Subsequently, the absolute differences between the highest and lowest CA across the species in each container were taken as a measure of the spread in CA within each community. These data were analysed in the same way as plant evenness (see above).

In some of the grid cells, seedlings died in the course of the experiment even after the first week. Seedling mortality can be an integral part of plant responses to PSF. We analysed seedling mortality at grid cell level, where we treated mortality as a binary variable, which takes the value of 1 when one or both of the plants of a grid cell had died. Plant mortality data were analysed using generalized linear mixed models (GLMMs) with a binomial error distribution. These data were analysed per plant mix with the same random- and fixed-effects structure as the LMMs described before.

Differences in abiotic soil conditions and shoot biomass at the end of the conditioning phase were tested with one-way ANOVAs. Spearman correlations were used to assess the relationship of the soil abiotic variables at the end of the conditioning phase and the

shoot biomass at the end of the test phase. These correlations were calculated for each plant community separately using all uniform soils that corresponded with the plant community ($n = 15$). Differences between soils in fungal community composition (T-RFLP data) were visualized using non-metric multidimensional scaling (NMDS) and tested using a multiple-response permutation procedure. Prior to analysis, we removed singleton loci from the T-RFLP data. To test whether plant and fungal community composition were correlated, we calculated a community dissimilarity matrix (Bray–Curtis index) for both the plant and the T-RFLP data and tested their association using a Mantel test. Community dissimilarity was calculated for the mono-conditioned uniform treatments, and we only compared experimental units that occurred within the same plant mix (i.e. 4 mono-conditioned uniform soils \times 3 replicates per plant mix). We pooled these values into a single Mantel analysis, where permutations were restricted within plant mix (999 permutations; Spearman's rho was used as the test statistic). The same analysis was performed for plant community composition and the dissimilarities in abiotic conditions (Euclidian distance).

All analyses were conducted in R v. 3.3.0 (R Core Team, 2016), and model assumptions were checked graphically. Heteroscedasticity was modelled using generalized least squares (Pinheiro & Bates, 2000; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Planned contrasts were analysed using the MULTCOMP v1.4-6 package (Hothorn, Bretz, & Westfall, 2008). LMMs were fitted with NLME v. 3.1-128 (Pinheiro, Bates, DebRoy, Sarkar, & R Development Core Team, 2016), GLMMs were fitted with LME4 v. 1.1-12 (Bates, Mächler, Bolker, & Walker, 2015) and post hoc comparisons were conducted in LSMEANS v. 2.23 (Lenth, 2015). Type I errors of multiple comparisons were controlled using the false discovery rate (Benjamini & Hochberg, 1995).

3 | RESULTS

Plant evenness was higher in spatially uniform containers with soils that were conditioned by more species (mixed-conditioned) than in uniform containers with soil conditioned by a single species (Figure 2a,b; Table S2). Evenness in the mixed-conditioned soils was

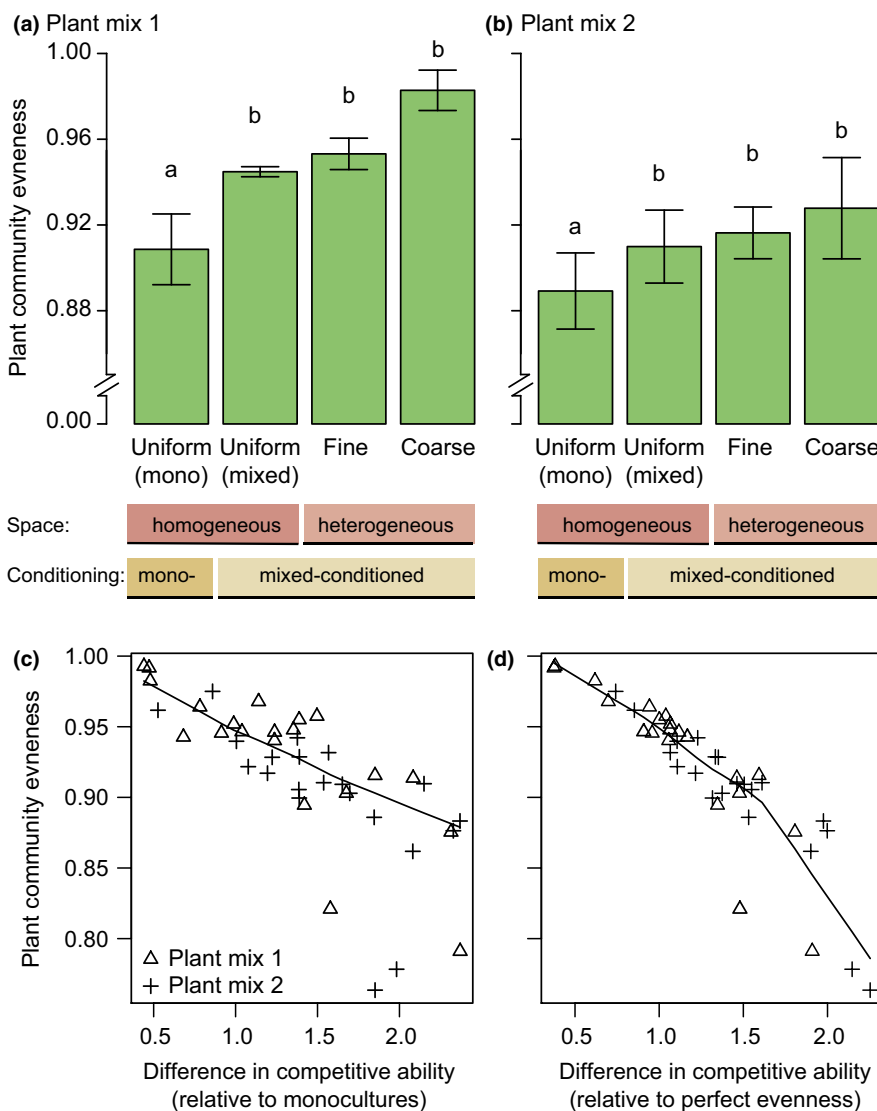


FIGURE 2 Plant evenness as a function of spatial PSF heterogeneity (a, b) and within-community differences in competitive ability (c, d). The top panels show plant evenness ($M \pm SE$) in the four spatial PSF heterogeneity treatments for both plant mixtures (a, b). Soils were either spatially homogeneous (uniform) or heterogeneous (fine- or coarse-grained) and conditioned by either one (mono) or four (mixed, fine and coarse) species. Results of statistical analyses are indicated (cf. Table S2). The bottom panels show the relationship among plant evenness in both plant mixtures as a function of the within-community differences in competitive ability measured either relative to plant performance in monocultures (c, CA1) or relative to a perfectly even community (d, CA2). In both cases, there was a significant negative correlation (Spearman's rho = -0.84 , $p < .0001$, and Spearman's rho = -0.93 , $p < .0001$, for (c) and (d), respectively). The solid lines (LOWESS fit) are included as a visual aid only

lowest in the uniform, intermediate in the fine- and highest in the coarse-grained heterogeneous soils, but this pattern was not significant (Table S2). These data suggest that the diversity of conditioning (mono- vs. mixed) has a larger impact on plant evenness than spatial grain (uniform, fine- or coarse-grained) itself.

On mono-conditioned uniform soils, heterospecific species often outperformed the plant species which self-conditioned the soil in terms of relative biomass production (Figure 3). This led to altered competitive hierarchies, indicated by significantly more rank reversals among species in the communities than expected by chance (47 of 72 potential rank reversals took place in both mix 1 and 2; $\chi^2_1 = 6.72$, $p = .01$ in both cases; Table S3). Within the same plant community, different plant species gained dominance in soils that were conditioned by different monocultures (Figure 3). However, *H. radicata* (mix 1) and *F. rubra* (mix 2) were exceptions to the general pattern, as they were still competitively superior on their own self-conditioned soil (Figure 3). Importantly, however, the performance of all species in heterogeneous soils was always intermediate to the best and the worst performance in the uniform mono-conditioned soils (Figure 3).

Furthermore, the differences in CA between the species within a community were smaller in mixed-conditioned (uniform, fine- and coarse-grained) than in mono-conditioned uniform soils (Figures S1 and S2; Table S4), and a larger difference in CA led to a lower community evenness (Figure 2c,d).

In uniform mono-conditioned soils, five out of six species experienced significant negative PSF in the mixed plant communities based on shoot biomass (Table S5; four of six based on relative abundance; cf. Table 1). Grasses performed worst on grass-conditioned soil and better on dicot-conditioned soil (Figure 4a,b; Table 1). Dicots typically showed the reverse pattern, although they also performed well on unrelated dicot-conditioned soils (e.g. *J. vulgaris* grown in *L. corniculatus* soil performed better than on *H. radicata* soil; Figure 4a). In the spatially heterogeneous soils, these patterns were altered and grasses sometimes had the highest biomass on grass-conditioned or even self-conditioned soils (e.g. *F. rubra* on *A. capillaris* soil in Coarse and *F. rubra* soil in Fine; Figure 4d,f). Similarly, forbs did not necessarily perform best on grass-conditioned soils (Figure 4) in the heterogeneous treatments. In general, direct PSFs, quantified as

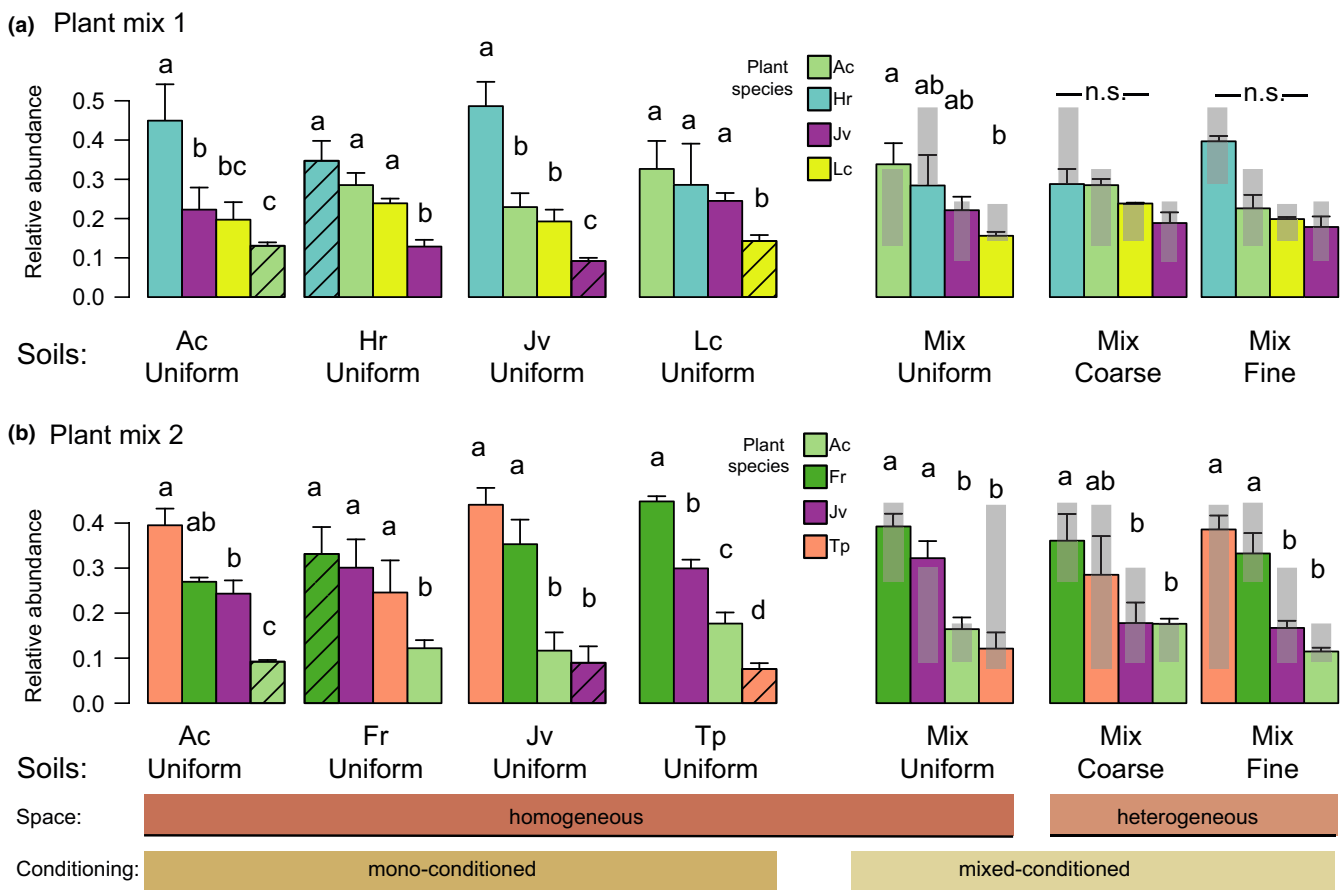


FIGURE 3 Competitive hierarchies across the different conditioned soils for two plant mixtures. Relative abundance ($M \pm SE$; shoot biomass) of the four plant species per treatment is shown, and the species are ranked from high to low abundance per treatment (a, b). The relative abundances sum to 1 per soil treatment (i.e. all test species in a given soil treatment). Different letters indicate significant differences among bars tested per soil treatment (see Table S9 for overall analyses). Hatched bars indicate the plant species in the mixture that grew on self-conditioned soil. The grey shading in the mixed-conditioned soil treatments (the right three sets of bars) indicates the highest-to-lowest performance range for each focal species on the four uniform mono-conditioned soils (the left four sets of bars). In all cases, the relative abundance of the focal species was not significantly different from this range. For abbreviations, see Figure 1

own–foreign contrasts, became less strong and non-significant in spatially heterogeneous soils (Figure 4; Table 1b and Table S5). Only *F. rubra* (mix 2) and *J. vulgaris* (mix 1) in Coarse showed significant negative direct PSF in heterogeneous soils (Table 1b). We conducted these analyses on both the relative and absolute shoot biomass, and this led to qualitatively the same conclusions (cf. Figure 4 and Figure S3; Table 1 and Table S5).

Plant mortality was low in general, but varied among the plant species (Figure S4; Table S6). In mix 1, seedling mortality of different species responded to spatial heterogeneity, with *H. radicata* having higher mortality in heterogeneous conditions, while the other species generally had lower mortality in heterogeneous soils. Mortality of *J. vulgaris* in mix 2 was elevated substantially on self-conditioned soils, which reflects its known strong negative direct PSF.

Both total community shoot and root biomass in the mixed plant communities were not affected by the spatial heterogeneity treatments (Table S7a,b). Soil conditioning altered soil nitrogen and acidity (Table S1), but community biomass in the test phase was not related to the abiotic soil variables or to shoot biomass in the conditioning phase (Table S8). Soil conditioning did lead to clear differences in fungal community composition among the six plant species;

conditioning by grasses, in particular, led to fungal communities that were different from the communities created by forbs or legumes (Figure S5; permutation $F = 1.57$, $p = .002$). Moreover, plant and fungal community composition were significantly correlated across mono-conditioned uniform treatments (Mantel $r = 0.189$, $p = .024$; Figure S6a–c), while this was not the case for plants and the abiotic variables (Mantel $r = 0.060$, $p = .318$; Figure S6d–f).

4 | DISCUSSION

In our study, we compared the PSF effects of conditioning of the soil by a single plant species and by multiple species on plant evenness and competition using experimental plant communities. Our results show that it is not the spatial distribution of PSFs per se (i.e. the grain), but rather the number of plant species that conditioned the soil that promoted plant evenness. When the soil had been conditioned by all members of the experimental community, plant evenness was higher than when only a single species conditioned the soil. In addition, there was no significant difference in evenness among the spatially heterogeneous treatments. PSFs, driven by, for example, soil-borne

TABLE 1 (a) Linear mixed-model analysis of species relative abundance (shoot biomass) in two mixtures of plant species at grid cell level. (b) Results of planned own–foreign soil contrasts (i.e. direct Plant–soil feedback (PSF)) for each species in each of the three levels of spatial grain. Negative values indicate negative feedback and vice versa

(a) Terms		df	Mix 1		Mix 2	
			F	p-value	F	p-value
Plant species (PS)		3,189	44.19	<.0001	84.50	<.0001
Conditioned soil (CS)		3,189	5.32	.002	3.03	.03
Spatial heterogeneity (SH)		215	3.37	.06	1.35	.29
PS × CS		9,189	8.07	<.0001	8.39	<.0001
PS × SH		6,189	2.33	.03	1.31	.25
CS × SH		6,189	0.97	.44	2.03	.06
PS × CS × SH		18,189	2.01	.01	1.87	.02
(b) Spatial grain	Mix 1			Mix 2		
	Species	Z	p-value	Species	Z	p-value
Uniform (mono- conditioned)	Ac	-4.19	.0002	Ac	-0.95	.38
	Hr	-1.56	.24	Fr	-3.44	.002
	Jv	-5.12	< .0001	Jv	-3.49	.002
	Lc	-3.83	.0005	Tp	-5.6	< .0001
Coarse	Ac	0.17	.87	Ac	-1.52	.19
	Hr	-1.57	.24	Fr	-3.44	.002
	Jv	-2.91	.01	Jv	-1.09	.33
	Lc	-1.02	.37	Tp	-1.12	.33
Fine	Ac	-0.77	.48	Ac	0.12	.91
	Hr	-1.22	.36	Fr	2.16	.05
	Jv	-1.15	.24	Jv	-2.23	.05
	Lc	1.22	.34	Tp	-2.6	.02

Values in bold indicate significant effects.

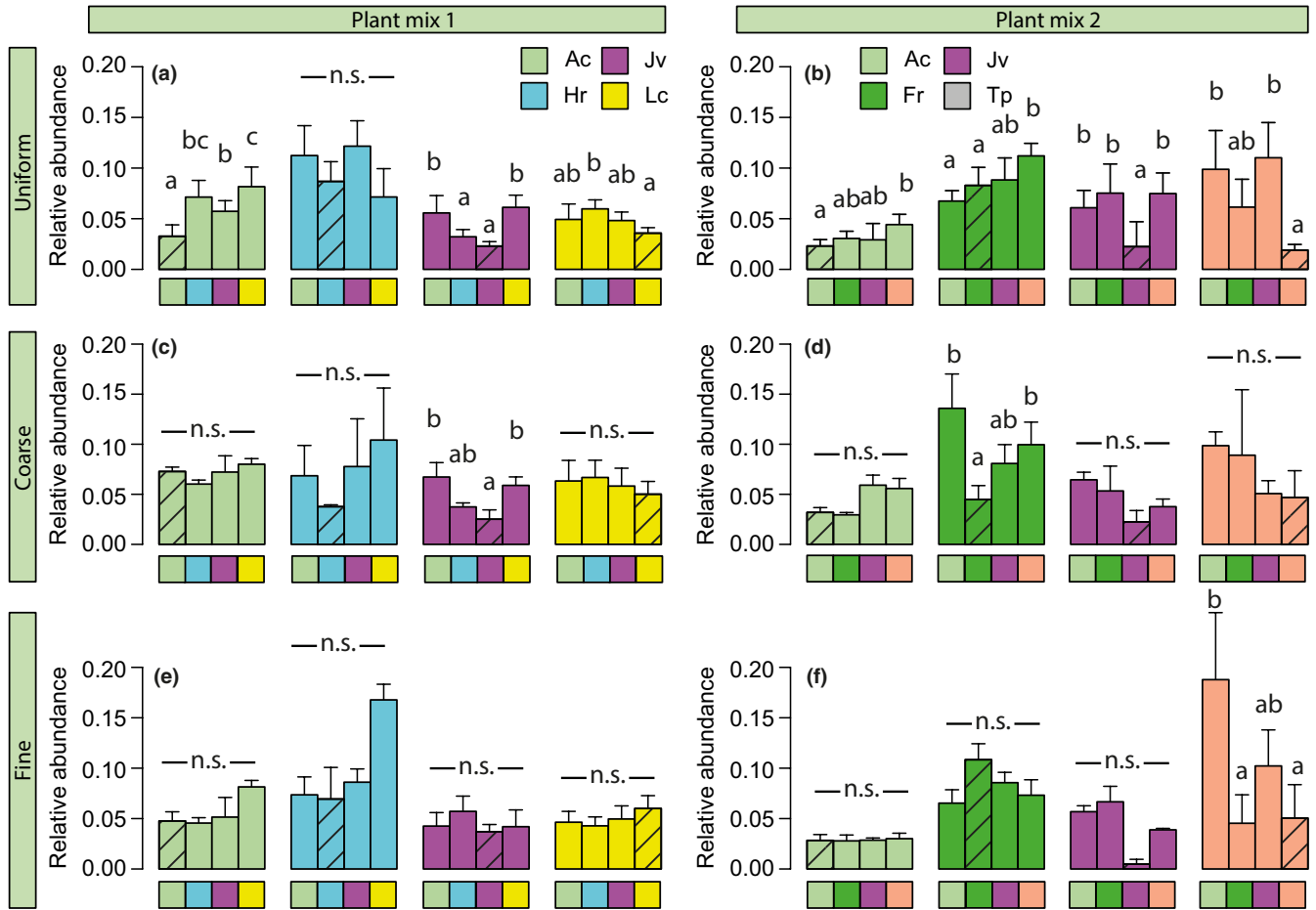


FIGURE 4 Relative abundance ($M \pm SE$; shoot biomass) per species and conditioned soil in two plant mixtures in mono-conditioned uniform (a, b) and two heterogeneous, coarse (c, d)- and fine-grained (e, f), PSF treatments. Shown are all four plant species (coloured bars) per community on all four conditioned soils (coloured squares below bars) in that mix (Figure 1). The relative abundances sum to 1 per panel (i.e. all test species \times soil patch combination per level of spatial heterogeneity). Hatched bars indicate that plants grew on self-conditioned soil. Different letters indicate significant differences among bars and those differences were tested separately per species and level of spatial heterogeneity. For abbreviations, see Figure 1, and for statistical analysis, see Table 1. For comparison, the same analyses were also conducted on shoot biomass; see Figure S3 and Table S5

pathogenic fungi and nematodes, have been suggested to maintain plant diversity at small spatial scales (e.g. Bever et al., 2015; De Kroon et al., 2012; Petermann et al., 2008). Our data now add to this by showing that the diversity of the plant species conditioning the soil drives the evenness of the plant community subsequently growing in that soil, through PSF. As low community evenness translates into higher local extinction rates (Hillebrand et al., 2008; Wilsey & Polley, 2004), we propose that these differences can result in differences in species richness over longer time frames.

We found that direct PSFs in uniform mono-conditioned soils were often negative and strong enough to alter competitive hierarchies (Hendriks et al., 2013; Jing, Bezemer, & Van der Putten, 2015; Pendergast, Burke, & Carson, 2013; Shannon, Flory, & Reynolds, 2012). This led to heterospecifics typically becoming the most abundant in the community. In soils conditioned by multiple species, PSF effects were less pronounced. In addition, the range of competitive abilities among species was smaller on mixed-conditioned soils, and this led to more equalized shoot biomass production among species

and thus higher community evenness. Although we cannot demonstrate this directly here, our data underscore the idea that PSFs, through their frequency-dependent effects on plant performance, may mediate competitive intransitivity among species (De Kroon & Jongejans, 2016; De Kroon et al., 2012; Soliveres et al., 2015), which is thought to influence dynamics of many natural communities (Soliveres et al., 2015). Alternatively, PSFs may only lead to equalized competitive abilities, which would falsify PSF as stabilizing mechanism of plant diversity. As a next step, pairwise competition experiments among all species in the community are needed to definitively demonstrate PSF-mediated intransitivity of competitive abilities (Jing et al., 2015; Laird & Schamp, 2006; Petraitis, 1979).

We found strong direct PSF effects for most plant species, in shoot biomass and also mortality, as was found in other studies (Kardol, Cornips, van Kempen, Bakx-Schotman, & Van der Putten, 2007; Kulmatiski et al., 2008; Petermann et al., 2008). However, PSFs were not strong enough to prevent all species from becoming dominant in their own self-conditioned soils. Both *F. rubra* and *H. radicata* were the

most abundant species in the communities on their own soils, even though both species had a better performance on heterospecific-conditioned soils (significant for *F. rubra*, a trend for *H. radicata* when comparing shoot biomass). We did not use seeds from the field where the soil was collected, except for *J. vulgaris*, so perhaps the soil community was naïve to these genotypes at the start of the experiment and PSF may be stronger with co-adapted plant genotypes and soil communities (Felker-Quinn, Bailey, & Schweitzer, 2011; Veen, De Vries, Bakker, Van der Putten, & Olf, 2014). In addition, PSF may also affect plant germination and establishment (Brandt et al., 2013; Burns & Brandt, 2014; Grubb, 1977), which we did not test as the experiment started from seedlings. If PSF effects are stronger during early life stages (Kardol, De Deyn, Laliberté, Mariotte, & Hawkes, 2013), PSF effects could therefore be stronger in the field than reported here, but this is insufficiently studied so far.

A long-standing alternative explanation for local plant diversity and evenness has been that spatially heterogeneous abiotic conditions, such as soil nutrient availability, create niches that can be occupied by different species (Harpole et al., 2016; Tilman, 1982). However, meta-analyses testing the effects of spatial heterogeneity in abiotic conditions on plant diversity have shown that abiotic heterogeneity only has a positive effect on local diversity at scales of heterogeneity (i.e. grain) that exceed the reach of interacting plants (sensu Casper et al., 2003). The spatial scales of interaction increase from, for example, small annuals, bunch grasses, tillering grasses to shrubs and trees (Casper et al., 2003; Schenk & Jackson, 2002). However, in general, when the heterogeneity is fine-grained (<20 × 20 cm on average across studies in meta-analyses), the effects of abiotic heterogeneity on diversity are negative (Lundholm, 2009; Tamme, Hiiesalu, Laanisto, Szava-Kovats, & Pärtel, 2010). Experiments with grassland species have shown that small-scale (e.g. patches 6.25 × 6.25 cm) abiotic heterogeneity selects for plant species that are efficient root foragers (Gazol et al., 2013; Tamme, Gazol, Price, Hiiesalu, & Pärtel, 2016). Hence, abiotic heterogeneity is unlikely to cause high plant diversity at the scale at which we conducted our PSF manipulations.

Plant–soil feedbacks can be mediated both abiotically and by the soil community (Ehrenfeld, Ravit, & Elgersma, 2005). While it was not possible in this experiment to tease out the exact causes of feedback for each plant species, we did find clear changes in fungal community composition due to soil conditioning. In addition, differences in soil abiotic conditions did not correlate with measures of plant performance or with plant community composition. However, plant community composition did correlate with the composition of the fungal community. In combination with the observation that the grain of heterogeneity did not affect plant performance, we hypothesize that changes in soil community composition, for example in soil fungi, due to soil conditioning affected plant performance, as was shown in other studies (Bever et al., 2015; Bradley et al., 2008; Hendriks et al., 2013), and community evenness. In general, our results support the notion that at small spatial scales, soil biota, not abiotic spatial heterogeneity, drives local plant diversity by preventing competitive exclusion (Bever et al., 2015; De Kroon et al., 2012; Petermann et al., 2008).

Difference in spatial grain (coarse- or fine-grained) of PSF heterogeneity did not affect small-scale plant evenness (i.e. 22 × 26 cm). Furthermore, plant evenness in pots with soil simultaneously conditioned by four species (mixed-conditioned uniform) was similar to that in the spatially heterogeneous pots but higher than in the mono-conditioned uniform treatment. It is important to highlight, however, that there might have been a difference in host–microbe interactions during soil conditioning. During conditioning in mono-conditioned soils, the host plant relative abundance was high (i.e. host relative abundance 4/4), compared to mixed-conditioning (i.e. host relative abundance 1/4), and this may have led to more pronounced effects on soil community composition. In future studies, mono-conditioned soils need to be mixed and tested alongside mixed-conditioned soils to tease apart the influence of plant relative abundance on host–microbe interactions during the conditioning phase. Nevertheless, in line with our results, Hendriks et al. (2013) showed that mixing own and foreign soil releases plants from their negative self-feedback. Models of PSF-mediated plant coexistence suggest that PSF effects need to be highly localized to maintain diversity (Abbott et al., 2015; Bonanomi et al., 2005; Fukami & Nakajima, 2013; Mack & Bever, 2014). Our study was carried out at a scale where the roots of all plant individuals could forage the entire experimental unit and be in contact with all soils (i.e. there was no physical barrier between patches) independent of the spatial configuration. Indeed, we observed that root systems spread through the entire container. Altogether, our results suggest that as long as multiple species conditioned the soil within the plant roots' zone of influence (Casper et al., 2003), the exact spatial pattern of conditioning is less important.

Field observations show that the spatiotemporal patterns of species replacement in late-successional grasslands are consistent with the model of PSF-mediated coexistence (De Kroon & Jongejans, 2016; Herben, Krahulec, Hadincová, & Kováfiiová, 1993; Van der Maarel & Sykes, 1993), suggesting that the same mechanisms may be in operation. However, an open question is how plants condition soils spatially in the field. We know that different plants in natural communities have distinct soil communities (Bezemer et al., 2010), but how they build up over the lifetime of a plant (Kardol et al., 2013; Zhang, Van der Putten, & Veen, 2016) and whether these induce the same PSF effects as in the glasshouse is unclear. It will be key to investigate how important PSFs are in driving plant community composition in relation to other mechanisms, for example the colonization–competition trade-off (Tilman, 1994), as well as in interaction with large herbivores (Chesson & Kuang, 2008; Veen et al., 2014) and across abiotic gradients (Bever et al., 2015).

In conclusion, we show that PSFs promoted plant community evenness when multiple species conditioned the soil, but that at small spatial scales, the spatial distribution of PSFs did not significantly affect plant community evenness. The presence of soil conditioned by all plant species in the community lead to more equal competitive abilities among plant species relative to soil conditioned by a single species. The spatial grain of PSF heterogeneity had no strong effect, suggesting that it is the presence, in sufficient amount, of each species' soil-borne antagonists that promotes plant

evenness. Future studies are needed to quantify the importance of PSF in the field relative to other environmental factors and across plant life stages and generations.

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AUTHORS' CONTRIBUTIONS

E.R.J.W. and T.M.B. conceived the ideas and designed the experiment. E.R.J.W. collected and analysed the data. E.R.J.W. and T.M.B. wrote the manuscript.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.11d82> (Wubs & Bezemer, 2017).

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SUPPORTING INFORMATION

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