

Spatial heterogeneity in plant–soil feedbacks alters competitive interactions between two grassland plant species

Wei Xue¹  | Frank Berendse² | T. Martijn Bezemer^{1,3} 

¹Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

²Nature Conservation and Plant Ecology Group, Wageningen University, Wageningen, The Netherlands

³Institute of Biology, Section Plant Ecology and Phytochemistry, Leiden University, Leiden, The Netherlands

Correspondence

Wei Xue, Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, The Netherlands.
Email: W.Xue@nioo.knaw.nl

Funding information

China Scholarship Council (CSC), Grant/Award Number: 201406510030

Handling Editor: Miranda Hart

Abstract

1. The effects of plants on soil vary greatly between plant species and in mixed plant communities this can lead to spatial variation in plant-soil feedback (PSF) effects. Such spatial effects are thought to influence plant species coexistence, but the empirical evidence for this hypothesis is limited.
2. Here, we investigate how spatial heterogeneity in PSFs influences plant growth and competition. The experiment was carried out with high and low nutrient soils to examine how these effects depend on soil fertility. We collected soil from field plots planted for three years with monocultures of *Anthoxanthum odoratum* and *Centaurea jacea* and tested the performance of the two species in a greenhouse experiment in heterogeneous soils consisting of patches of “own” and “foreign” soils and in soils where the “own” and “foreign” soils were mixed homogeneously. In the test phase, plants were grown in monocultures and in 1:1 mixtures in live or sterilized soils.
3. Overall, *A. odoratum* in monocultures produced less aboveground biomass in heterogeneous soils than in homogeneous soils. *Centaurea jacea* produced less belowground biomass in live heterogeneous soils than in live homogeneous soils, but there was no difference between sterile heterogeneous and homogeneous soils. The belowground biomass per patch varied more in pots with live heterogeneous soils than in pots with live homogeneous soils for both plant species, but there was no difference between pots with sterile heterogeneous and homogeneous soils. In pots with plant mixtures, the difference in aboveground biomass between the two competing species tended to be smaller in heterogeneous than in homogeneous soils. In pots with heterogeneous soils, both plant species grown in mixtures produced more aboveground biomass in “foreign” soil patches than in “own” soil patches. The responses of plants to heterogeneous PSFs were not different between low and high nutrient soils.
4. Our results show that spatially heterogeneous PSFs can influence plant performance and competition via reducing the growth inequality between the two competing species by allowing selective growth in foreign soil patches, independent of initial soil nutrient availability. Such effect may slow down exclusion processes and thus promote the coexistence of competing species at the local scale in mixed plant communities.

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KEYWORDS

intra- and interspecific competition, patchy distribution, plant–plant interactions, plant–soil feedback, plant–soil interactions, soil heterogeneity, soil nutrient, soil origin

1 | INTRODUCTION

Plants change the properties of the soil they grow in, and this can influence the performance of the same or other plant species that grow later in this soil, a phenomenon termed plant–soil feedback (Bever, Westover, & Antonovics, 1997; van der Putten et al., 2013). Most plant species perform worse in soil where another individual of the same species grew previously (“own soil”) than in soil where another plant species had been grown before (“foreign soil”), and hence, most conspecific plant–soil feedback effects are negative (Kulmatiski, Beard, Stevens, & Cobbold, 2008; but see Bennett et al., 2017; Teste et al., 2017). As each plant individual in a plant community influences its local soil in a specific manner, soil characteristics and plant–soil feedbacks may vary spatially in the field. Spatial variation in plant–soil feedbacks (i.e. spatial plant–soil feedback heterogeneity) has been theoretically suggested to influence plant performance and coexistence (Abbott et al., 2015; Bonanomi, Giannino, & Mazzoleni, 2005; Fukami & Nakajima, 2011; Mack & Bever, 2014; Zee & Fukami, 2015). However, the vast majority of empirical plant–soil feedback studies so far have ignored such spatial aspects of plant–soil feedback (but see Brandt, de Kroon, Reynolds, & Burns, 2013; Burns, Brandt, & Lau, 2014; Burns, Brandt, Murphy, Kaczowka, & Burke, 2017; del Pino, Brandt, & Burns, 2015; Hendriks, Ravenek et al., 2015; Hendriks, Visser et al., 2015; Wubs & Bezemer, 2016, 2017a).

In spatially heterogeneous soils, a plant can preferentially forage for nutrients in “foreign” soil patches thereby avoiding contact with its antagonists in “own” soil patches (Hendriks, Visser et al., 2015). How plant–soil feedback heterogeneity will influence plant growth in the presence of neighbouring plants is less clear as competing plants may also change their foraging behaviour in heterogeneous soils (e.g. Cahill et al., 2010; Xue, Huang, Dong, Zhang, & Yu, 2013). In monospecific communities, spatial plant–soil feedback heterogeneity may not be beneficial because competing individuals will employ the same strategy (Bennett et al., 2017; Bliss, Jones, Mitchell, & Mou, 2002; Teste et al., 2017). A recent study even reported that plants in monocultures performed worse in spatially heterogeneous soils than predicted from their performance in homogeneously conditioned soils (Wubs & Bezemer, 2016).

When different plant species grow together in spatially homogeneous soils, interspecific competition generally enhances the plant–soil feedback effects (e.g. Crawford & Knight, 2016; Jing, Bezemer, & van der Putten, 2015; Kardol, Cornips, van Kempen, Bakx-Schotman, & van der Putten, 2007; Petermann, Fergus, Turnbull, & Schmid, 2008; van der Putten & Peters, 1997). Similar to what is observed when soil resources are distributed heterogeneously, in soils with spatially heterogeneous plant–soil feedbacks, plants growing

in “own” soil patches will experience a competitive disadvantage and inferior competitors may benefit in these patches (Burns et al., 2017; Day, John, & Hutchings, 2003; Hendriks, Ravenek et al., 2015; Hutchings, John, & Wijesinghe, 2003). Hence, competing species may all preferentially forage in “foreign” patches and this may reduce competitive imbalances between species.

Several studies have shown that plants generally respond less strongly to plant–soil feedbacks in fertilized soils than in nutrient-poor soils (De Deyn, Raaijmakers, & van der Putten, 2004; Gustafson & Casper, 2004; Kardol et al., 2013; Kos, Tuijl, de Roo, Mulder, & Bezemer, 2015; Manning, Morrison, Bonkowski, & Bardgett, 2008; van der Putten & Peters, 1997; Wubs & Bezemer, 2017b). However, how soil nutrient availability influences the impact of a plant on the soil (i.e. the soil conditioning effect in the conditioning phase) is less well understood. As plants generally interact more strongly with soil biota in nutrient-poor conditions (Teste et al., 2017; van der Heijden, Bardgett, & van Straalen, 2008), we may also expect that the effects of plant–soil feedback heterogeneity on plant performance in the test phase will be stronger when the soil was originally nutrient-poor than when the soil was nutrient-rich during the conditioning phase.

In this study, we examine how plant–soil feedback heterogeneity influences the performance and competitive interactions between two grassland plant species, and how these effects depend on soil fertility. We grew the grass *Anthoxanthum odoratum* and the forb *Centaurea jacea* in field plots in monocultures in either high-nutrient or low-nutrient soil. After three years, we collected soil from these monocultures and tested the performance of *A. odoratum* and *C. jacea* in monocultures and in 1:1 mixtures in a greenhouse experiment in homogeneous mixtures of “own” and “foreign” soil, and in spatially heterogeneous soils with distinct patches of “own” and “foreign” soil. The experiment was carried out with live and sterilized soil to test the impact of soil biota on the response of the two plant species to spatial plant–soil feedback heterogeneity. We tested four hypotheses: (a) in monocultures (intraspecific competition), plants will produce similar amounts of biomass in pots with two conditioned soils placed in discrete patches (heterogeneous soil) as in evenly mixed soil (homogeneous soil) as, at the pot level, on average the biotic composition and abiotic composition of both soils are identical. However, there will be more variation in biomass among the soil patches within heterogeneous soils than within homogeneous soils. (b) In plant mixtures (interspecific competition), at the pot level, the difference in growth between the two competing species will be smaller in heterogeneous soils than in homogeneous soils, as each of the competing species will produce more biomass in “foreign” soil patches than in “own” soil patches within the heterogeneous soils. (c) Effects of plant–soil feedback heterogeneity in the test

phase will be stronger when the soil was initially nutrient-poor than when the soil was initially nutrient-rich during conditioning, as plant-soil feedback effects generally diminish with increasing soil fertility. (d) Plant-soil feedback heterogeneity effects will disappear in sterile soils.

2 | MATERIALS AND METHODS

2.1 | Plant species

We used a grass species, *Anthoxanthum odoratum* L. (Poaceae), and a forb, *Centaurea jacea* L. (Asteraceae). Both species can reproduce by seeds and vegetative growth (Hartemink, Jongejans, & de Kroon, 2004). *Anthoxanthum odoratum* produces closely connected ramets, while *C. jacea* forms extensive branches underground (Jongejans & de Kroon, 2005). Both species are native in western Europe and commonly coexist in meadows (van Ruijven & Berendse, 2003). Both plant species experience negative conspecific plant-soil feedbacks (Supporting Information Figure S1B,D; less root biomass in “own” than “foreign” live soils for *A. odoratum*, and less root and shoot biomass for *C. jacea*).

2.2 | Soil conditioning in monoculture field plots

In an outdoor experimental garden (from April 2013 to September 2015), we planted monocultures (144 seedlings/plot) of *A. odoratum* and *C. jacea* in plots filled with either high-nutrient soil

(N-NH₄: 3.31 mg/kg; P-PO₄: 1.88 mg/kg; N-NO₃: 41.10 mg/kg) or low-nutrient soil (N-NH₄: 2.44 mg/kg; P-PO₄: 0.36 mg/kg; N-NO₃: 0.09 mg/kg). There were 20 plots (2 levels of nutrient availability × 2 plant species × 5 replicate plots) of 1 m² each distributed over five replicated blocks in a randomized block design. Weeds were regularly removed during the experiment. In September 2015, all plants in the central 60 × 60 cm² of each plot were clipped at a height of 1 cm. Above-ground biomass in each plot was determined after being oven-dried to constant weight. Productivity of both plant species in high-nutrient and low-nutrient soils is shown in the supporting information (Supporting Information Figure S2). In February 2016, we collected all topsoil (20 cm deep) from the central area of 60 × 60 cm² in each experimental plot and kept soil from different plots in different sealed bags. Then, soil collected from each plot was sieved (1.5 cm mesh) and further separated into two parts both kept in separate sealed bags. One of the two bags from each plot was sterilized by γ -irradiation (minimum 25KGray; Isotron, Ede, The Netherlands). Hence, there were 40 different conditioned soils (2 nutrient levels × 2 plant species × 5 replicate plots × 2 sterilization treatments). In the greenhouse experiment, for each of the two nutrient levels and for sterile and non-sterile soil, we created two levels of PSF heterogeneity (spatially homogeneous PSF and spatially heterogeneous PSF) using soils conditioned by *A. odoratum* and *C. jacea* from the same field block (Figure 1). A total of 120 pots (2 nutrient levels × 2 sterilization treatments × 2 PSF heterogeneity treatments (described below) × 3 planting treatments (described below) × 5 replicates) of 4.6 L each were used in the greenhouse experiment.

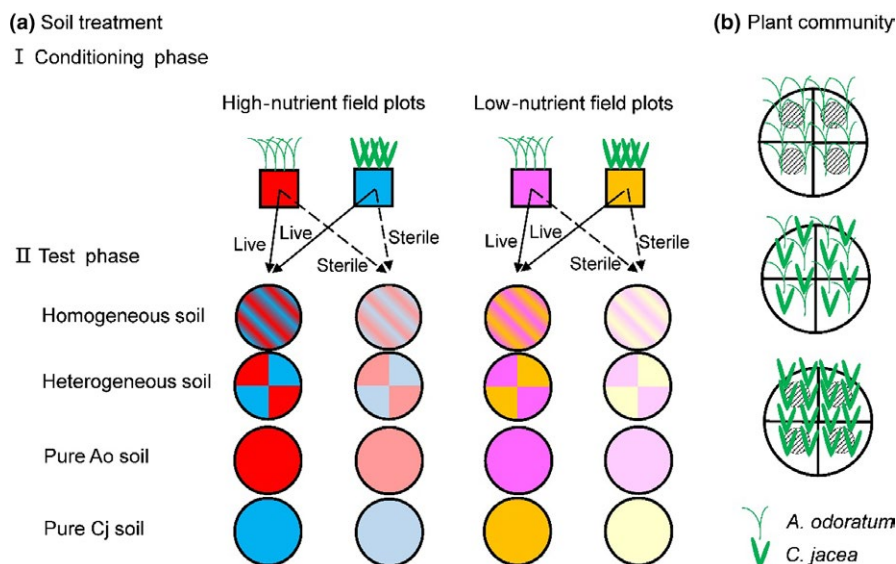


FIGURE 1 Experimental design. (a) In the conditioning phase (I), high-nutrient and low-nutrient soils were conditioned separately by monocultures of *Anthoxanthum odoratum* (Ao soil) and *Centaurea jacea* (Cj soil) for three years in field plots. The initial planting density was 144 seedlings/plot. Soil was collected from the plots and conditioned soils were either sterilized or not (i.e. live and sterile), resulting in eight different soils (different colours). In the test phase (II), pots with heterogeneous soils were created by filling with Ao soil and Cj soil in an alternated way, while pots with homogeneous soil (striped pot) were created by filling with 1:1 (w:w) mixtures of Ao soil and Cj soil. Additional pots were filled with pure Ao soil or pure Cj soil. The pure soil treatments (pure Ao soil and pure Cj soil) were not included in the main analysis; these results are presented in the supporting information. (b) Planting design. Each pot was planted with either 16 plants of *A. odoratum* or *C. jacea* in monocultures or eight plants of each of the two species in mixtures. The shaded circles within the monoculture pots represent the positions where soil samples were taken

2.3 | Greenhouse experiment

In the greenhouse experiment, two levels of PSF heterogeneity (spatially homogeneous PSF and spatially heterogeneous PSF) were created using soil conditioned by *A. odoratum* and *C. jacea* from the same field block (Figure 1). In the heterogeneous soil treatments, each pot was equally divided into four patches using a metal grid and each patch was alternately filled with 1.4 kg soil conditioned by monocultures of *A. odoratum* or *C. jacea*. In the homogeneous soil treatments, each pot was filled with 5.6 kg of a 1:1 (w:w) homogenized mixture of soil conditioned by monocultures of *A. odoratum* and *C. jacea* (Figure 1). In this way, there were pots that differed in spatial variation in plant–soil feedbacks, while the abiotic and biotic soil conditions in the homogeneous and heterogeneous soils were kept constant. We allocated pots filled with soils originated from the same field block in the same block in the greenhouse experiment so that there were five blocks. Pots of different treatments were randomized within each block. Holes were made in the bottom of each pot to allow vertical movement of water. To prevent soil from passing through holes, a piece of filter paper (15 cm in diameter) was placed at the bottom of each pot before filling the pot with soil. Each pot was placed on a tray to prevent possible contamination through leachate. The metal grid was removed after each pot was filled so that plants could grow freely across different patches. We randomly selected three field blocks and collected subsamples from the soil of each plot in those blocks for soil chemical analysis. We measured soil organic matter content, nutrient content (NH_4 , NO_3 and PO_4), water content and pH (Supporting Information Table S1). The amount of NH_4 , NO_3 and PO_4 (mg/kg dry soil) was determined by adding 30.0 ml of 0.01 mol/L CaCl_2 solution to soil samples (3.0 g), shaking mechanically for at least 2 hr at room temperature (20°C), filtering the solution and analysing the nutrients in the soil extracts in a flow analyser (SKALAR SAN plus system). Soil pH- H_2O was determined by adding 25.0 ml demi-water to soil samples (volume 5.0 ml), shaking for 5 min and measuring 2 hr later. Soil organic matter was determined by measuring the difference between weights of the oven-dried (105°C) soil samples (5.0–10.0 g) before and after being heated in a furnace at 550°C. The weight of each sample was determined after cooling it down in the air to handwarm temperature and further cooling it for at least 45 min in a desiccator. Soil moisture content was determined by measuring the difference between the weights of each soil samples before and after oven-drying (105°C).

In a heated greenhouse (20.0°C average temperature, 70.2% average relative humidity), seeds of *A. odoratum* and *C. jacea* (purchased from a wild seed supplier, Cruydhoeck, Nijeberkoop, The Netherlands) were sown on plastic trays filled with steamed potting soil that facilitates root development (0.03N-0.03P-0.03K, Seed Starting Potting Mix; Miracle-Gro Lawn Products, Inc., Marysville). The potting soil was watered daily so that the potting soil remained moist. One week after germination, the trays with seedlings were moved to an unheated greenhouse (12.8°C average temperature, 70.3% average relative humidity) until they were transplanted into the pots.

Similar sized seedlings of *A. odoratum* and *C. jacea* were used in the experiment. There were three planting treatments; that is, the two species were planted in monocultures and in 1:1 mixtures (Figure 1). In monocultures, we planted 16 seedlings (a similar planting density as applied in Wubs & Bezemer, 2016) of *A. odoratum* or *C. jacea* in each pot. In mixtures, we planted eight seedlings of *A. odoratum* and *C. jacea* in alternating positions (Figure 1). In this way, each seedling was surrounded by conspecific and heterospecific competitors. Dead seedlings were replaced during the first week of the experiment. We removed the dead seedlings, including the root system, and then planted a new seedling at the previous planting position. All other species emerging from the seed bank of the soil were removed manually during the experiment.

The experiment was maintained for 90 days (from 11 April to 11 July 2016) in the same unheated greenhouse. During the experiment, the mean temperature and the relative humidity in the greenhouse were 17.4°C and 67.5%, respectively. All pots were watered three times per week (300–800 ml per pot, each time depending on the weather conditions).

In this experiment, we analysed the effects of spatial plant–soil feedback heterogeneity by comparing spatially heterogeneous soils with homogeneously mixed soils that have the same origin. Hence, each pot consisted of the same initial nutritional and microbial composition. For completeness, in the experimental design we also included the two pure soil treatments (pure Ao soils and pure Cj soils; Figure 1). In these two pure soil treatments, each pot was filled with 5.6 kg of soil conditioned by monocultures of *A. odoratum* (pure Ao soil treatment) or *C. jacea* (pure Cj soil treatment) growing in either high- or low-nutrient soil and originating from the same field block. The data of root and shoot biomass in these pure soils are presented in the supplementary information (Supporting Information Table S2; Supporting Information Figure S1).

2.4 | Harvest measurements

After 90 days, we clipped all plants at soil level. Plants growing in each patch within each pot were harvested separately. In the 1:1 mixtures, the two different species were also harvested separately. After clipping, we took one soil core (4.0 cm diameter, straight down to the bottom of pot) in each of the four soil patches in each pot to measure the root mass (Figure 1). Soil cores were only taken from pots planted with monocultures as it was not possible to separate roots of the two different plant species in the mixtures. The soil samples were then washed by hand using a 0.5-mm sieve. Above-ground biomass and below-ground biomass of each plant species from each patch were oven-dried (70°C) and weighed.

2.5 | Data analysis

We analysed the above-ground biomass and below-ground biomass in the greenhouse experiment at both pot level and patch level. Data of plant monocultures and mixed plant communities were analysed separately.

For plant monocultures, at the pot level, we first calculated above-ground biomass per plant (total above-ground biomass of a species in one pot divided by the number of seedlings in the pot) and below-ground biomass per soil core of *A. odoratum* and *C. jacea* in each monoculture pot. Then, we analysed above-ground biomass and below-ground biomass separately for each of the two species planted in monocultures. We used a mixed-effect three-way ANOVA with nutrient availability (high vs. low), sterilization (live vs. sterile), soil heterogeneity (homogeneous vs. heterogeneous) and their interactions as fixed factors, and block as a random factor. A significant soil heterogeneity effect or a significant interaction with nutrient and/or sterilization would suggest that the growth of the species in monocultures is different between heterogeneous and homogeneous soils at the pot level.

The variation in above-ground and below-ground biomass among the four patches within heterogeneous and homogeneous soils was determined based on the coefficient of variation (CV) for each pot. CVs of above-ground biomass and of below-ground biomass were analysed separately for each species, using a mixed-effect three-way ANOVA with nutrient availability, sterilization, soil heterogeneity and their interactions as fixed factors, and block as a random factor. A significant heterogeneity effect or a significant interaction with nutrient and/or sterilization would suggest that the growth variation is different within heterogeneous and homogeneous soils.

At the patch level, we first calculated above-ground biomass per plant (total above-ground biomass of a species in one patch divided by the number of seedlings in the patch) and below-ground biomass per soil core of *A. odoratum* and *C. jacea* in each patch within each pot. Then, we analysed the patch-level above-ground biomass and below-ground biomass separately using a mixed-effect three-way ANOVA to test whether the two species grown in monocultures produced more biomass in “foreign” soil patches than in “own” soil patches within the heterogeneous soil. In this model, nutrient availability, sterilization, soil type (“own” vs. “foreign” soil) and their interactions were included as fixed factors, and soil type nested in pot, pot nested in block (block/pot/soil type) was included as a random effect to account for the non-independent of the growth in different patches within one pot.

For mixed plant communities, at the pot level, we first combined the growth of the two species in 1:1 mixtures in each pot by calculating the growth difference (D) to evaluate the effects of spatial plant-soil feedback heterogeneity on the competition between the two species. The D -value was calculated as the log-ratio of above-ground biomass of *A. odoratum* and *C. jacea* in mixtures. The D -value will be equal to zero if the two species perform equally well in mixtures; it will be positive if the biomass of *A. odoratum* is higher than that of *C. jacea*, and negative if *C. jacea* biomass is higher. We used three-way ANOVA to test the effects of nutrient availability, sterilization, soil heterogeneity and their interactions on D , and block was included as a random factor. A one-sample t test was used to test whether D for each combination of nutrient availability, sterilization and soil heterogeneity differed from zero. A significant soil

heterogeneity effect or a significant interaction with nutrient and/or sterilization would suggest that the difference in the growth between the two competing species in the 1:1 mixture is different in heterogeneous and homogeneous soils. We also analysed the plot-level above-ground biomass (total above-ground biomass of a species in one pot divided by the number of seedling in the pot) separately for each of the two species grown in the 1:1 mixture using a mixed-effect three-way ANOVA with nutrient availability, sterilization, soil heterogeneity and their interactions as fixed factors, and block as a random factor.

At the patch level, we tested whether the two species in the 1:1 mixtures produced more biomass in “foreign” soil patches than in “own” soil patches within the heterogeneous soils. We analysed the patch-level above-ground biomass (total above-ground biomass of a species in one patch divided by the number of seedlings in the patch) separately for each of the two species grown in the 1:1 mixture, using a mixed-effect three-way ANOVA. Nutrient availability, sterilization, soil type and their interactions were included as fixed factors, and soil type nested in pot, pot nested in block (block/pot/soil type) as a random factor.

All data analyses were performed with R (version 3.3.2; <http://www.r-project.org>) in RStudio (version 1.0.44; <http://rstudio.org>). Linear mixed-effect models were fitted with *nlme* (version 3.1-128; Pinheiro, Bates, DebRoy, Sarkar, & Team, 2016). All data were checked visually for normality and homogeneity of variance using Q-Q plots and residual plots, respectively.

3 | RESULTS

3.1 | Effects of plant-soil feedback heterogeneity on the growth in monocultures

In monocultures, *A. odoratum* overall produced less above-ground biomass in heterogeneous soils than in homogeneous soils (Supporting Information Table S3A; Figure 2a), but there was no significant difference in the above-ground biomass of *C. jacea* between the two soils (Supporting Information Table S3A; Figure 2c). These results suggest that heterogeneity in PSFs did influence the above-ground biomass of *A. odoratum* but not of *C. jacea*. Both species produced much more above-ground biomass in sterile soil than in live soil (Supporting Information Table S3A; Figure 2a,c), indicating that soil biota inhibited plant growth of both species.

PSF heterogeneity also influenced below-ground biomass, but the effect varied between the two species and soil sterilization. *A. odoratum* produced similar amounts of below-ground biomass in heterogeneous and homogeneous soils (Supporting Information Table S3B; Figure 2b). *C. jacea* produced less below-ground biomass in live heterogeneous than in live homogeneous soils, but in sterilized soil, there was no difference between these heterogeneity treatments (Supporting Information Table S3B; significant sterilization \times heterogeneity effect; Figure 2d). These results suggest that heterogeneity in PSFs influenced the below-ground biomass of *C. jacea* but not of *A. odoratum*. Below-ground biomass per soil core

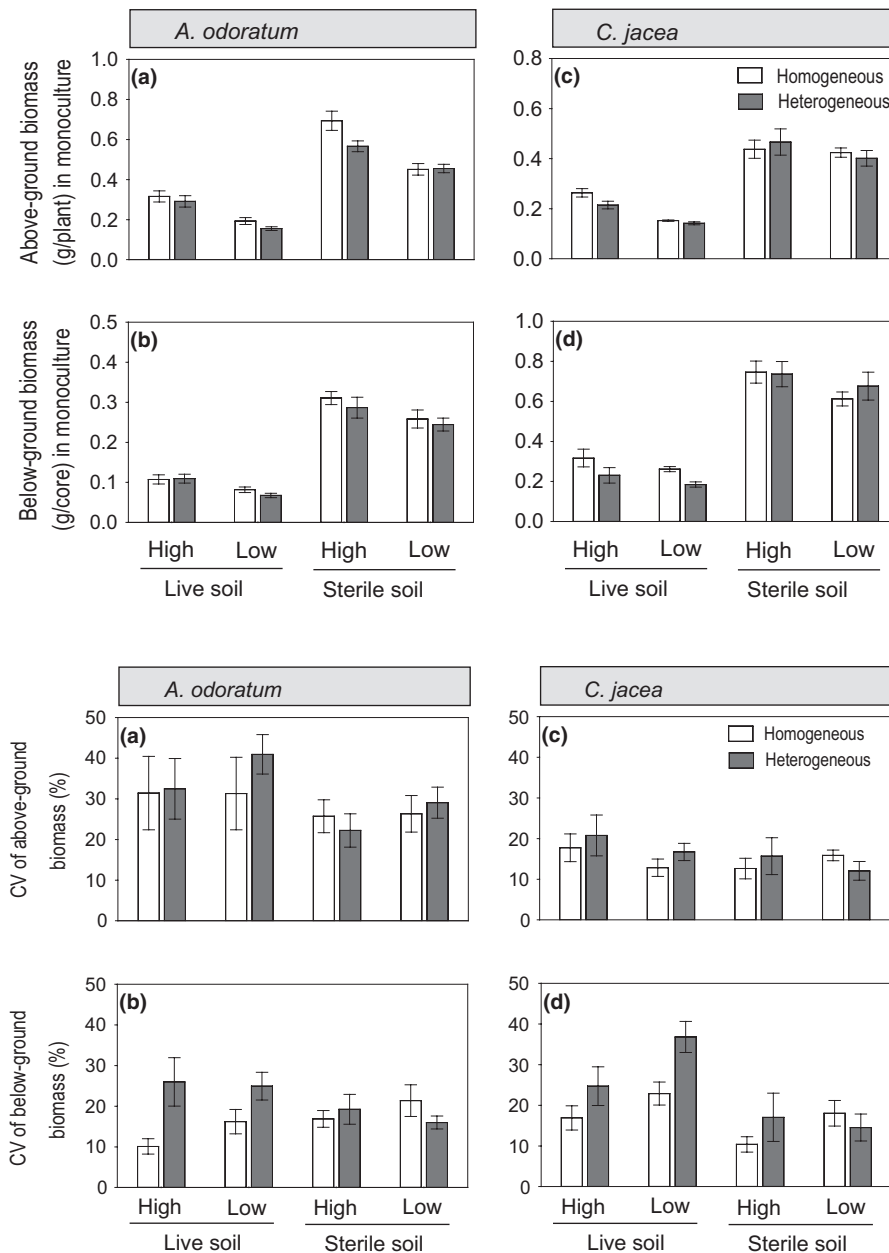


FIGURE 2 Above-ground biomass per plant (a and c) and below-ground biomass per soil core (b and d) of *Anthoxanthum odoratum* (a and b) and *Centaurea jacea* (c and d) in plant monocultures in homogeneous and heterogeneous soils at the pot level. “High” and “Low” refer to high-nutrient soil and low-nutrient soil used in the conditioning phase. “Live soil” and “Sterile soil” indicate field-collected soil and sterilized field-collected soil, respectively. Mean values (± 1 SE) are presented. See Supporting Information Table S3A,B for statistical results

FIGURE 3 Coefficient of variation (CV) of above-ground biomass (a and c) and CV of below-ground biomass (b and d) of *Anthoxanthum odoratum* (a and b) and *Centaurea jacea* (c and d) in plant monocultures among the four patches within homogeneous and heterogeneous soils. “High” and “Low” refer to high-nutrient soil and low-nutrient soil used in the conditioning phase. “Live soil” and “Sterile soil” indicate field-collected soil and sterilized field-collected soil, respectively. Mean values (± 1 SE) are presented. See Supporting Information Table S4 for statistical results

of both species was significantly greater in sterile soil than in live soil (Supporting Information Table S3B; Figure 2b,d).

Soil heterogeneity and the interaction with nutrient and/or sterilization did not affect the CV of above-ground biomass of either *A. odoratum* or *C. jacea* (Supporting Information Table S4A; Figure 3a,c). CVs of below-ground biomass of both plant species were significantly greater in live heterogeneous soil than in live homogeneous soil. In sterilized soil, there was no difference between the two heterogeneity treatments (Supporting Information Table S4B; significant and marginally significant sterilization \times heterogeneity effect for *A. odoratum* and *C. jacea*, respectively; Figure 3b,d). Hence, PSF heterogeneity increased spatial variation in root growth in live soil but not when soil biota were excluded.

In monocultures, in pots with spatially heterogeneous soil, *A. odoratum* produced more above-ground biomass in live “foreign” soil

patches than in live “own” soil patches when soil nutrient is low, but no difference was found between these two patches in high-nutrient soil or in sterile soils (Supporting Information Table S5A; significant nutrient \times sterilization \times soil interaction effect; Supporting Information Figure S3A). *C. jacea* produced more above-ground biomass in live “foreign” soil patches than in live “own” soil patches, but there was no difference between the two soil patches in sterile soils (Supporting Information Table S5A; significant sterilization \times soil interaction effect; Supporting Information Figure S3C). The same pattern was found for the below-ground biomass of *A. odoratum*, while *C. jacea* overall produced less below-ground biomass in “foreign” soil patches than in “own” soil patches (Supporting Information Table S5B; Supporting Information Figure S3B,D). These results suggest that plant monocultures showed different responses to spatially heterogeneous PSFs.

3.2 | Effects of plant–soil feedback heterogeneity on plant growth in mixtures

In mixtures, the growth difference between the two species tended to be smaller in heterogeneous soils than in homogeneous soils (Supporting Information Table S6; marginally significant heterogeneity effect; Figure 4), indicating that the growth inequality between the two competing species was reduced in heterogeneous soils. The growth difference index (D) was generally negative in live soil but positive in sterile soil; that is, *C. jacea* was superior to *A. odoratum* in live soil, while the reverse was true in sterile soil (Supporting Information Table S6; Figure 4). The above-ground

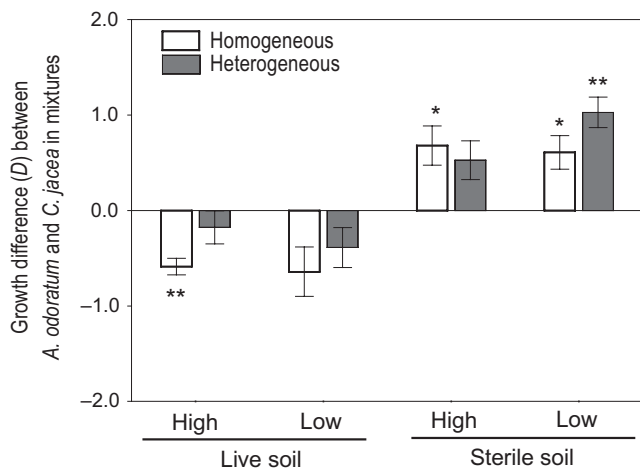


FIGURE 4 Growth difference (D , log-ratio of above-ground biomass of *Anthoxanthum odoratum* and *Centaurea jacea* in plant mixtures) in homogeneous and heterogeneous soils. Positive values indicate the biomass of *A. odoratum* is higher than that of *C. jacea*, and negative values indicate the reverse is true. “High” and “Low” refer to high-nutrient soil and low-nutrient soil used in the conditioning phase. “Live soil” and “Sterile soil” indicate field-collected soil and sterilized field-collected soil, respectively. Mean values (± 1 SE) are presented. See Supporting Information Table S6 for statistical results. Stars at the end of bars indicate which means differed from zero (one-sample t test). Symbols give p : ** $p < 0.01$ and * $p < 0.05$

biomass of both species grown in mixtures is presented in the supporting information (Supporting Information Table S3C; Supporting Information Figure S4).

In mixtures, in pots with spatially heterogeneous soil, *A. odoratum* produced more above-ground biomass in “foreign” soil patches than in “own” soil patches (Supporting Information Table S5C; Figure 5a). A similar trend was observed for *C. jacea*, but this was not significant (Supporting Information Table S5C; Figure 5b). This result suggests that both plant species selectively grew in “foreign” soil patches in spatially heterogeneous soils.

4 | DISCUSSION

In this study, we compared the growth of plants in pots with heterogeneous soils and homogeneous soils that consisted of the same component soils. Remarkably, even though the two soils had the same starting conditions regarding nutrients and microbial composition, we observed that in heterogeneous pots with conditioned soils that were spatially separated, the performance of plant monocultures was worse than in homogeneous pots with evenly mixed conditioned soils. When competing, the difference between the growth of the two species decreased in heterogeneous pots compared to homogeneous pots. Hence, our study implies that spatially heterogeneous PSFs, that is the spatial configuration of conditioned soils, increase the negative effects for plant monocultures growing in “own” soil and decrease the growth inequality between the two competing species.

Recently, Wubs and Bezemer (2016) reported a negative effect of spatial plant–soil feedback heterogeneity on plant growth in monocultures similar to what we found. In that study, the performance of six plant species grown in monocultures in soils with spatially heterogeneous PSFs and in monospecific conditioned soil was compared. The negative effect of heterogeneity in the study by Wubs and Bezemer (2016) was explained by the more diverse microbial communities present in heterogeneous soils (where four conditioned soils were present in a pot) than in monospecific soils where only one plant species had conditioned the soil. Hence, spatial

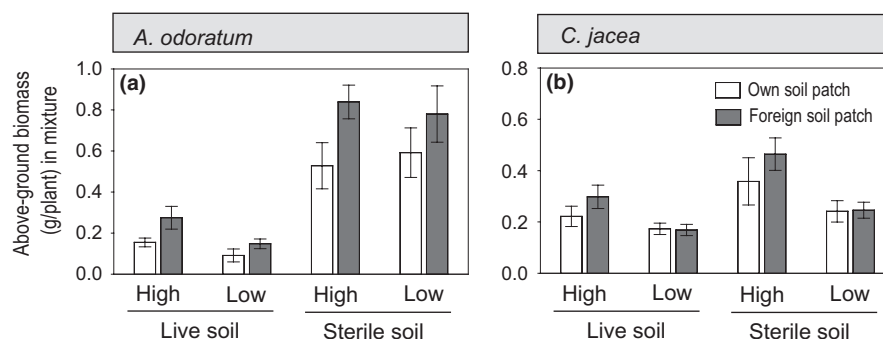


FIGURE 5 Above-ground biomass per plant per patch of *Anthoxanthum odoratum* (a) and *Centaurea jacea* (b) in plant mixtures in “own” and “foreign” soil patches for pots with heterogeneous soils. “High” and “Low” refer to high-nutrient soil and low-nutrient soil used in the conditioning phase. “Live soil” and “Sterile soil” indicate field-collected soil and sterilized field-collected soil, respectively. Mean values (± 1 SE) are presented. See Supporting Information Table S5C for statistical results

plant–soil feedback heterogeneity increased the chances of a plant to encounter specific soil pathogens, as well as the chances of co-infections by different soil pathogens (Wubs & Bezemer, 2016). In contrast, in our study, the initial composition in each pot was similar irrespective of the heterogeneity treatment, as the same set of conditioned soils were used in pots with homogeneous and heterogeneous soil. Hence, the negative effect of spatially heterogeneous PSFs in our study is less likely due to the difference in the original composition of microbial communities. However, it is important to note that we did not measure the microbial composition in the soils, and hence, we cannot exclude that mixing soil communities may have influenced the composition that established in these soils (Brinkman, van der Putten, Bakker, & Verhoeven, 2010; Reinhart & Rinella, 2016). Alternatively, evenly mixing the two soil communities implies that soil communities arranged in a patchy way in the heterogeneous pots may have been “diluted,” which allows plant monocultures to grow more in homogeneous soils than in heterogeneous soils (Hawkes, Kivlin, Du, & Eviner, 2013; Hendriks et al., 2013).

In monocultures, plant growth varied more among the four patches within the heterogeneous soils than within the homogeneous soils, indicating that spatially heterogeneous PSFs promote growth divergence. This may be explained by the greater variety of microsites within the heterogeneous soils; that is, there were two conditioned soils placed in discrete patches within the heterogeneous soils, but the two conditioned soils were evenly mixed within the homogeneous soils. Hence, plants can avoid contact with their enemies by placing more shoots/roots in the “foreign” soil patches (Supporting Information Figure S3; Hendriks, Visser et al., 2015) in the heterogeneous soils, which increases the growth variations among these patches. Importantly, we only found such difference in live soil but not in sterile soil, indicating that soil biota were likely involved in the responses of plant monocultures to spatially heterogeneous PSFs. Further studies should aim to disentangle the role of the microbial community in creating spatial heterogeneity effects on plant growth.

We expected that in plant mixtures (interspecific competition), the growth difference between the competing species would be smaller in heterogeneous soils than in homogeneous soils. In our study, we only found weak evidence for this. In heterogeneous soils, both plant species encountered patches with “own” and “foreign” soils, potentially providing both plant species with enemy free space, that is the avoidance of contact with antagonists in “own” soil patches. Indeed in mixtures, we generally found a negative conspecific PSF (less growth in “own” than in “foreign” soil patches) even though this was only significant for one of the two species. This result indicates that spatially heterogeneous PSFs can reduce the biomass inequality between competing species, but also shows that the effects are plant species-specific.

As expected, sterilizing the soil increased plant growth. Our results show that soil biota in our system have a negative effect on plant growth; that is, there are more pathogenic or harmful microbes than beneficial ones present in conditioned soil. However, it is important to note sterilization of soils also increased the soil nutrient

availability (Supporting Information Table S1), and this obviously promotes the growth of plant species. Unfortunately, we cannot distinguish to what extent the exclusion of soil biota and release of soil nutrients may have promoted the growth of the plant in sterilized soil, yet it must be a net effect of elimination of soil biota and an increase in soil nutrients (Brinkman et al., 2010). Remarkably, sterilization of soils changed the competition hierarchy of the two competing species; that is, *C. jacea* is superior to *A. odoratum* in live soil, while the reverse is true in sterile soil. One possible explanation is that *C. jacea* has a greater association with mycorrhizal fungi than *A. odoratum* under poor soil conditions as indicated by previous studies (the mycorrhizal fungi dependency of *C. jacea* and *A. odoratum* is about 64% and 35%, respectively; Grime, Mackey, Hillier, & Read, 1987; Tawaraya, 2003; van der Heijden et al., 2008). Another possible explanation may be related to the competition for different resources. *Anthoxanthum odoratum* profits from the higher nutrient supply in the sterile soil treatments. In nutrient-rich environments, competition for light is important; thus, species that can produce more leaves have a competitive advantage (Aerts, 1999). *Anthoxanthum odoratum* is a species that can produce dense tillers rapidly (Humphrey & Pyke, 1998; Lovett-Doust, 1981), and they were taller than *C. jacea* plants in the greenhouse experiment (W. Xue, *pers. obs.*). This may explain why *A. odoratum* was the stronger competitor in sterile soil. In nutrient-poor environments (live soils in the present study), competition for nutrients prevails and, hence, species with larger rooting systems may have a competitive advantage (Aerts, 1999; Grime, 2006). *C. jacea* has a deeper root system than *A. odoratum*; thus, most underground space was occupied by *C. jacea*, which may explain its competitive advantage in nutrient-poor conditions.

We hypothesized that PSF heterogeneity effects in the test phase would be stronger when the soil was originally nutrient-poor during conditioning, as PSF effects generally diminish with increasing soil fertility (De Deyn et al., 2004; van der Putten & Peters, 1997). In contrast to our hypothesis, the effects of PSF heterogeneity did not differ between the two soil fertility levels as indicated by the absence of significant nutrient \times heterogeneity effects. At the end of the conditioning period in the field, the amount of organic matter was higher in high-nutrient than in low-nutrient soils, but there were no differences in other soil chemical properties between the two soil nutrient treatments (Supporting Information Table S1). This may explain why we did not observe stronger conditioning effects on PSF heterogeneity effects in low-nutrient soils. More studies are needed to examine the role of spatial plant–soil feedback heterogeneity on plant performance and competition along a gradient of soil nutrient availability.

In conclusion, in soils with spatially heterogeneous plant–soil feedback, plants produced less biomass than in homogeneously mixed soils. However, plant growth varied more among the patches within the heterogeneous soils than within the homogeneous soils. Moreover, spatially heterogeneous plant–soil feedbacks reduced the growth inequality between the two competing species by allowing them to grow more in “foreign” soil patches

than in “own” soil patches. We did not find the evidence that initial soil fertility influences plant–soil feedback heterogeneity effects. Despite that, our results indicate that spatial plant–soil feedback heterogeneity could be a mechanism explaining species coexistence at the local scale.

ACKNOWLEDGEMENT

We thank Jan van Walsem, Frans Möller, Peiyu Zhang, Cong Chen and Ningjing Liu for the help with the experiment, and the associated editor and two anonymous reviewers for very useful comments on an earlier version of the manuscript. This work was funded by the China Scholarship Council (No. 201406510030). This is publication 6520 of the Netherlands Institute of Ecology (NIOO-KNAW).

AUTHOR CONTRIBUTIONS

W.X., F.B. and T.M.B. designed the experiment; W.X. and F.B. collected the data; and W.X. and T.M.B. analysed the data and wrote the first version of the manuscript. All authors discussed the results, contributed substantially to the draft and gave final approval for publication. There are no conflict of interests to declare.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.vm125vv> (Xue, Berendse, & Bezemer, 2018).

ORCID

Wei Xue  <http://orcid.org/0000-0002-2230-8570>

T. Martijn Bezemer  <http://orcid.org/0000-0002-2878-3479>

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How to cite this article: Xue W, Berendse F, Bezemer TM.

Spatial heterogeneity in plant–soil feedbacks alters competitive interactions between two grassland plant species. *Funct Ecol*.

2018;32:2085–2094. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2435.13124)

[2435.13124](https://doi.org/10.1111/1365-2435.13124)