Co-occurring grassland species vary in their responses to fine-scale soil heterogeneity

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Abstract

Questions: How does fine-scale soil heterogeneity impact on co-occurring species? Which species are advantaged in heterogeneous soils?

Location: Greenhouse experiment using European grassland species (University of Tartu, Estonia).

Methods: We grew plant assemblages consisting of 15 species in five soil treatments – comprising three spatially uniform fertility levels (low, medium or high), and two heterogeneous conditions created using checkerboard combinations of low- and high-fertility patches at two spatial scales (6.25 x 6.25 cm or 12.5 x 12.5 cm patches, overall medium fertility). We compared species' responses (aboveground biomass) between heterogeneous and homogeneous treatments. Additionally, we compared species' responses within low-fertility patches in heterogeneous treatments to the homogeneous treatment of the same fertility.

Results: Larger, dominant species were advantaged in heterogeneous compared to homogeneous conditions (with the same or lower overall fertility), whereas the growth and survival of smaller, subordinate species was reduced. Larger, dominant species also had greater aboveground biomass within the low-fertility patches in heterogeneous compared to homogeneous low-fertility conditions, but the opposite was true for smaller, subordinate species. In general, species' responses in heterogeneous conditions did not differ from the homogeneous high-fertility treatment although the heterogeneous conditions had lower overall fertility.

Conclusions: In our experimental grasslands, species differed in their responses to fine-scale soil heterogeneity. Patchy resource distribution directly benefits larger, dominant species that can forage among patches and produce more aboveground biomass compared to conditions where the same amount of resources is distributed homogeneously. Smaller, subordinate species that are more likely confined to a uniform soil patch are disadvantaged by heterogeneity due to

increased root and shoot competition from neighbouring species. These species-specific responses to fine-scale soil heterogeneity and altered competitive interactions have important implications for plant community structure and productivity.

Keywords: Aboveground biomass; Community composition; Light competition; Niche; Root competition; Root foraging; Soil fertility; Soil resources

Running head: Competing species' responses to soil heterogeneity

Introduction

In natural ecosystems, soil resources are distributed heterogeneously at different spatial scales (Ettema & Wardle 2002), and this impacts on plant communities, populations and individuals (Hutchings et al. 2003). Heterogeneity occurring at large scales is considered a universal driver of species coexistence (Tilman & Pacala 1993; Stein et al. 2014). More species can co-exist if soil heterogeneity allows niche partioning, and high-fertility patches favour strong competitors while low-fertility patches provide safe sites for subordinates (Chesson & Huntley 1997; Day et al. 2003a, b; Hutchings et al. 2003; Mommer et al. 2012). However, in the case of fine-scale soil heterogeneity, plant individuals are not confined to a specific patch, but can forage throughout the soil (Hutchings et al. 2003). Soil heterogeneity occurring at smaller scales than root extent can alter community structure in varying ways if coexisting species differ in how they perceive and respond to heterogeneity, and this impacts on competitive interactions (Hutchings et al. 2003; Lundholm 2009; Tamme et al. 2010). Much of the available research about plant responses to fine-scale soil heterogeneity comes from experiments where plants were grown in monocultures (reviewed in Hutchings et al. 2003; Kembel & Cahill 2005) or in pair-wise competition (Fransen et al. 2001; Day et al. 2003c; Mommer et al. 2012). Only a few studies have explored how individual species respond to soil patchiness in multi-species assemblages (see Wijesinghe et al. 2005; Maestre & Reynolds 2007; Rajaniemi 2010), and further research is needed to explicitly test how fine-scale soil heterogeneity impacts on plant community structure.

Plant individuals respond to fine-scale soil heterogeneity using a variety of root foraging strategies, e.g. allocating more roots into resource-rich patches (foraging precision), developing extensive root systems (foraging scale), or occupying resource-rich patches rapidly (foraging rate; reviewed in Kembel & Cahill 2005). A trade-off between foraging precision and scale has been reported (Campbell et al. 1991; Wijesinghe et al. 2001; Grime 2007), but this is not universal among species (Kembel & Cahill 2005; Kembel et al. 2008), and some species exhibit multiple strategies to benefit from patchy resource distribution (Farley & Fitter 1999; Rajaniemi & Reynolds 2004; Kembel et al. 2008). Therefore, soil heterogeneity itself can be considered a ‘niche axis’ along which species sort. While some species prefer heterogeneous conditions that enable them to take advantage of high-fertility patches, other species do better in conditions where the resources are distributed homogeneously (Hutchings et al. 2003; Tamme et al. 2010).

In multi-species assemblages, plant responses to soil heterogeneity are further modified by the presence and identity of neighbours, and are often not predictable from experiments where species were grown separately (Day et al. 2003c; Maestre et al. 2006; Cahill et al. 2010; Mommer et al. 2011, 2012; Padilla et al. 2013) or even in pairwise combination (Dormann & Roxburgh 2005). Competitive interactions in heterogeneous conditions are also expected to differ from these in homogeneous conditions and can be asymmetric belowground, if species with greater root foraging ability can reach and deplete high-fertility patches quicker (Schwinning & Weiner 1998; Hutchings et al. 2003; Rajaniemi & Reynolds 2004; Maestre & Reynolds 2006). Some experiments have found fine-scale soil heterogeneity to affect pair-wise competition (Fransen et al. 2001; Day et al. 2003c; Mommer et al. 2011), others have reported weak, or no effects, of heterogeneity on the outcome of competitive interactions (Cahill & Casper 1999; Bliss et al. 2002; Rajaniemi 2007).

Differential root responses to fine-scale soil heterogeneity can also affect resource acquisition and competition aboveground if successful root foraging allows plants in high-fertility quadrats to grow taller and produce more shoot biomass (Cahill 1999). In addition, individuals that establish in low-fertility patches can still produce more aboveground biomass if they are able to forage for high-fertility patches belowground, causing greater light competition also in low-fertility patches that otherwise would act as safe sites from strong competitors (Day et al. 2003a, b; Hutchings et al. 2003). Therefore, plant responses in heterogeneous conditions may by similar to those in homogeneous conditions with higher overall fertility. Several monoculture experiments have shown that the yield of individuals or populations grown in heterogeneous soils is higher than in homogeneous conditions with equivalent resource supply (Cahill & Casper 1999; Day et al. 2003a). In multi-species assemblages, the total productivity of the community is often also higher in heterogeneous than in homogeneous conditions even if the amount of resources remains the same (Wijesinghe et al. 2005; Maestre et al. 2006; Gazol et al. 2013). Whether this is due to all species equally benefitting from heterogeneity, or some species benefitting more from heterogeneous conditions and outcompeting others is not yet clear.

Using 15 grassland species in a mesocosm experiment, we compared species' responses (measured as aboveground biomass) in homogeneous (low-, medium- or high-fertility) and heterogeneous (checkerboard combinations of low- and high-fertility patches at two spatial scales, with overall medium-fertility) soil. We compared plant species' responses between the treatments (community-level analysis) and between the same fertility patches in different treatments (patch-level analysis). Specifically, we expected: 1) species to segregate along the 'heterogeneity niche axis' – some species grow better in heterogeneous treatments while others do better in homogeneous conditions (community-level analysis); 2) species' responses to soil heterogeneity are similar to species' responses to homogeneous high-fertility conditions, leading to equal growth in heterogeneous and high-fertility homogeneous treatments (community-level analysis); 3) species that benefit from heterogeneity can exclude smaller species in competition, especially in low-fertility patches that otherwise would act as safe sites for smaller species (patch-level analysis). We expected that these responses vary depending on the size of the soil patches, since the average distance to high-fertility patches decreases with the spatial scale of heterogeneity.

Material and methods

Experimental design and sampling

We conducted a mesocosm experiment in a greenhouse at the University of Tartu in Estonia between the 15^{th} February and 11^{th} June 2011. The experiment consisted of five treatments, each with 10 replicates, including three homogeneous treatments (low-, medium- or high-fertility) and two heterogeneous treatments (small or large patches). We used galvanized steel boxes (25 x 25 x 20 cm) and different combinations of commercial sand and potting compost (*Biolan Must Muld*®; N = 100 mg/l; P = 200 m/l; K = 400 mg/l) for growing substrate. The low-fertility treatment (Low) was created using a 1:4 mixture of compost and sand, the medium-fertility treatment (Med) consisted of a 1:1 mixture of compost and sand, and the high-fertility treatment (High) was a 4:1 mixture of compost and sand. The heterogeneity treatments with large and small patches (HetL and HetS, respectively) were created using checkerboard combinations of Low and High treatment mixtures. HetL treatment consisted of four 12.5 x 12.5 cm patches filled to a depth of 20 cm, while the HetS treatment was made up of 16 6.25 x 6.25 cm patches filled to a depth of 20 cm. Hence, the two heterogeneous treatments had the same overall fertility as treatment Med, but varied in the spatial distribution of resources.

We obtained seeds of 15 Northern European grassland species (Table 1) from a commercial supplier (B & T World Seeds, Paguignan C.P. 34210, Aigues-Vives, France). The chosen species resembled a diverse community in terms of plant traits and are known to commonly co-occur in seminatural grasslands (Pärtel et al. 1999). For each replicate box, we mixed an approximately equal number of seeds (at least 32) from each species with sieved natural soil (to include microbial communities) and spread the mixture uniformly onto the growing substrate. Owing to varying germination success, the number of individuals varied between species, but not between treatments (see Online Resource 1 in Gazol et al. 2013). For the first 15 days, the boxes were covered with a plastic sheet and watered every second day to aid germination. Each box was divided into 16 6.25 x 6.25 cm quadrats for sampling purposes. We randomly selected four 6.25 x 6.25 cm quadrats in each box (200 quadrats in total) for species-specific aboveground biomass sampling. In the heterogeneous treatments, two quadrats of both the low- and high-fertility patches were included. During the course of the experiment, we recorded the number of individuals for each species in all pre-selected quadrats (Appendix S1). This was done every two weeks following germination to ensure that species' absence in a quadrat at the time of the biomass sampling can be attributed to mortality and was not due to random seed distribution or failed germination.

After the experiment had run for 105 days and communities had reached their peak aboveground biomass, we harvested the aboveground biomass separately for each species in all of the four preselected quadrats in each box. The biomass was then oven-dried (24 h at 80 ºC) and weighed. We used plant aboveground biomass as a measure of plant responses as it is shown to be a good indicator of species' root extent (Rajaniemi & Reynolds 2004; Kembel & Cahill 2005) as well as competitive ability (resource uptake above- and belowground; Grime 1973).

Data analysis

We included data from nine species in the analyses (*Antennaria dioica*, *Briza media*, *Centaurea jacea*, *Cirsium acaule*, *Festuca rubra*, *Hypericum perforatum*, *Plantago media*, *Prunella vulgaris*, *Trifolium montanum*, hereafter referred to by genus name), and excluded six species that had very small aboveground biomass values in all of the experimental treatments (*Anthyllis vulneraria*, *Erophila verna*, *Filipendula vulgaris, Galium verum*, *Primula veris*, *Viola rupestris*). To examine how co-occurring species are influenced by soil resource heterogeneity, we used aboveground biomass of each of the nine species at the end of the experiment as a measure of species' response. To account for species' survival differences between treatments, we assigned a biomass of 0 to species that had germinated in the quadrat but did not survive until the final sampling. All statistical analyses were performed for the nine species separately and we included data from quadrats where the species had established. We tested for the homogeneity of variance across treatments using Levene's test (Zar 1999) and $\log_{10}$-transformed (one unit was added to all values beforehand) the aboveground biomass data to meet the assumption of normality. We used linear mixed-effects models in all analyses, with species' aboveground biomass in a quadrat as the response variable and treatment as a fixed factor. We included box identity as a random factor and a constant variance function structure to account for the different number of included quadrats in the treatments (Zuur et al. 2009).

We performed both community- and patch-level analyses to test our expectations. In the community-level analysis, we used data from all treatments in species-specific models, and made multiple comparisons following our *a-priori* expectations. To test whether, and which, species segregated along the 'heterogeneity niche axis', we compared HetL and HetS treatments to both Low and Med treatments. We included both of these homogeneous conditions to test if the addition of high-fertility patches or simply the heterogeneous distribution of soil fertility is necessary for species segregation along the ‘heterogeneity niche axis’. Since heterogeneous treatments have higher overall fertility than the Low treatment, we included a comparison between Med and Low treatments to discern whether plants were affected by heterogeneity or changes in overall fertility. To test whether heterogeneous treatments provided conditions similar to high-fertility conditions, we compared HetL and HetS treatments to the High treatment. We included an additional comparison between Med and High treatments to ensure that the potential similarities between heterogeneous and high-fertility conditions were not expected based on the overall fertility levels of the treatments. Hence, we performed eight comparisons for each species. We performed patch-level analyses to compare species’ aboveground biomass in quadrats within low-fertility patches in heterogeneous conditions and in quadrats within homogeneous low-fertility treatment. Therefore, we only included data from the Low treatment and from the low-fertility quadrats in HetL and HetS treatments in these analyses.

All analyses were performed in the R environment (R Foundation for Statistical Computing, Vienna, AT). We used the *car* package (Fox & Weisberg 2011) for Levene’s test, *nlme* package (Pinheiro et al. 2014) for fitting the models, and the *glht* function from the *multcomp* package (Hothorn et al. 2008) for multiple comparisons. We used analysis of variance (ANOVA) to test the overall effect of treatment on species’ responses.

Results

Species sort along the ‘heterogeneity niche axis’

We found that six of the nine analysed species responded to soil heterogeneity at the community level, but the responses varied between species and the spatial scale of heterogeneity (Fig. 1, Table 2). When heterogeneous treatments were compared to the medium-fertility treatment, Med), *Festuca* and *Plantago* had higher aboveground biomass in the heterogeneous treatment with small patches (HetS), whereas *Antennaria* showed an opposite pattern. *Antennaria* and *Hypericum* also had lower aboveground biomass in the heterogeneous treatment with large patches (HetL) compared to the Med treatment. When heterogeneous treatments were compared to the low-fertility treatment (Low), *Festuca* had higher aboveground biomass in both heterogeneous treatments, whereas *Antennaria* showed an opposite pattern. Moreover, *Centaurea* had higher biomass in HetL and *Prunella* in HetS compared to the Low treatment. Since the aboveground biomass for these species did not differ between Med and Low treatments, these responses were not affected by the overall increase in fertility. *Briza* and *Plantago* had significantly higher aboveground biomass in both HetL and HetS compared to the Low treatment, but these responses were at least partly induced by the overall change in soil fertility, since the same differences were found when comparing Med and Low treatments. *Cirsium* and *Trifolium* showed no significant responses to a patchy distribution of soil fertility at the community level. While the strength of the effect of soil heterogeneity depended on the spatial scale of heterogeneity, in general, the direction of the effect did not – the only exceptions were *Hypericum* (when compared to Low) and *Prunella* (when compared to Med).

Heterogeneous conditions resemble high-fertility homogeneous conditions

We found that heterogeneous conditions resembled high-fertility homogeneous conditions in the community-level analysis (Fig. 1, Table 2). Aboveground biomass responses did not differ between HetS or HetL and the homogeneous high-fertility (High) treatments for any of the species despite the heterogeneous treatment having lower overall fertility. Moreover, the aboveground biomass of *Antennaria*, *Festuca* and *Plantago* differed significantly between Med and High treatment.

Low-fertility patches do not act as safe sites

In the patch-level analyses, we found that *Briza*, *Festuca* and *Plantago* had higher aboveground biomass in the low fertility patches in both HetS and HetL compared to the Low treatment (Fig. 2, Table 3). Additionally, *Prunella* produced more aboveground biomass in the low fertility patches in HetL compared to the Low treatment. *Antennaria* showed a contrasting pattern, with less aboveground biomass in low fertility patches in both heterogeneous treatments compared to the Low treatment, while *Trifolium* had lower biomass only in the HetL treatment. In general, the direction of species' responses in low-fertility patches did not depend on the spatial scale of heterogeneity, but when significant, the responses in smaller patches were always stronger than in the larger patches.

Discussion

Using experimental communities of temperate grassland species, we found that co-occurring plant species respond to soil heterogeneity in varying ways. Some species benefit from the patchy resource distribution, while others are negatively affected in heterogeneous conditions, indicating that species segregate along the 'heterogeneity niche axis' when grown with neighbours. Our results show that species benefitting from heterogeneity gain higher aboveground biomass especially in low-fertility patches that otherwise would act as safe sites for smaller and slow-growing species (Hutchings et al. 2003), and can outcompete others in light competition (Gazol et al. 2013). Despite having lower overall fertility, heterogeneous conditions resemble high-fertility homogeneous conditions in terms of individual species' aboveground biomass as well as taxonomic and functional diversity (Gazol et al. 2013; Price et al. 2014). Soil heterogeneity can alter community structure if species advantaged by heterogeneity exclude others in root or shoot competition (Hutchings et al. 2003; Tamme et al. 2010; Gazol et al. 2013).

Species differ in their responses to soil heterogeneity and sort along the 'heterogeneity niche axis'

We found that four out of nine species were advantaged in heterogeneous conditions, two species grew better in homogeneous conditions, and three species were not affected by the spatial distribution of soil resources (Fig. 1, Table 2). Three forbs (*Centaurea*, *Plantago* and *Prunella*) as well as the grass *Festuca* benefitted from soil heterogeneity and were most likely able to forage among the high-fertility patches. Forbs have been found to be more precise foragers that can allocate roots to high-fertility patches (Kembel & Cahill 2005), whereas grasses can gain a competitive advantage over forbs in heterogeneous conditions by rapidly reaching and occupying high-fertility patches (Šmilauerová & Šmilauer 2010; Kiær et al. 2013). Other experimental studies have also found that rhizomatous or clonal species are most advantaged in heterogeneous conditions (Collins & Wein 1998; Baer et al. 2004; Wijesinghe et al. 2005; Maestre & Reynolds 2007; Reynolds et al. 2007; Eilts et al. 2011). In plant communities, more complicated competitive hierarchies and indirect interactions determine the outcome of competition (Rajaniemi 2007; Mommer et al. 2012; Aschehoug & Callaway 2015). For example, although both species were advantaged in heterogeneous conditions in our multi-species assemblages, *Festuca rubra* was negatively affected by *Plantago lanceolata* in heterogeneous conditions when grown together in a pair-wise experiment (Padilla et al. 2013). These discrepancies among experimental studies further emphasize the importance of the identity of neighbouring plants on species' foraging and competitive abilities (Belter & Cahill 2015).

Three of the species advantaged by heterogeneity (*Festuca*, *Centaurea* and *Plantago*) were also the ones that dominated the communities in terms of aboveground biomass in all treatments (Table 1) and were some of the tallest plants in the experiment (see Table 1 in Price et al. 2014). In contrast, species that were disadvantaged in heterogeneous conditions, the forbs *Antennaria* and *Hypericum*, had the lowest relative aboveground biomass (Table 1) in all of the treatments and were the smallest plants in the experiment (Price et al. 2014). The distinct sorting of dominant and subordinate species along the 'heterogeneity niche axis' further contributes to growing evidence that dominant and subordinate species in plant communities respond to environmental factors in varying ways (Kumordzi et al. 2015).

Species' responses in heterogeneous conditions equal species' responses in homogeneous conditions with higher overall fertility

Plant individuals that establish in, or are able to reach, high-fertility patches in heterogeneous conditions ultimately have access to a larger amount of resources than expected from the average conditions, and species interactions in heterogeneous conditions may be more similar to those in homogeneous high-fertility than in medium-fertility conditions (Grime 1973; Rajaniemi 2002). If species can rapidly access high-fertility patches belowground and grow taller, smaller species may be excluded from communities also due to light competition (Wilson 2000; Hutchings et al. 2003; Lamb et al. 2009; Hautier et al. 2009). In previous studies, we found evidence for soil heterogeneity having an indirect negative effect on species diversity by increasing the total aboveground biomass and decreasing light availability (Gazol et al. 2013), and producing communities that were assembled of functionally similar species resembling competitive high-fertility conditions in terms of trait values (Price et al. 2014). Thus, increased fertility is not a prerequisite for increased cover of dominant species or ecosystem productivity; rather varying the spatial arrangement of the same amount of resources is enough to induce changes in plant communities. The similarity of species' responses to the homogeneous high-fertility and heterogeneous treatments provides further evidence that species with good competitive ability may benefit from soil heterogeneity.

Low-fertility patches in heterogeneous conditions do not provide safe sites from competition

Low-fertility patches within heterogeneous conditions have previously been shown to provide refuges from both root and shoot competition and to benefit subordinate species in the long-term (Day et al. 2003a, c; Hutchings et al. 2003). Moreover, subordinate species have been shown to alter their foraging strategies to avoid root competition by neighbours in heterogeneous conditions (Mommer et al. 2012). However, our results show no clear evidence that low-fertility patches act as safe sites from intense competition. Subordinate species *Antennaria* and *Trifolium* that performed well in homogeneous low-fertility conditions, had lower aboveground biomass in low-fertility patches within the heterogeneous treatment (Fig. 2, Table 3). The dominant, larger species (*Briza*, *Festuca*, *Plantago*, *Prunella*) were able to increase their aboveground biomass in low-fertility patches in heterogeneous conditions most likely excluding *Antennaria* and *Trifolium* in competition for light (Wilson 2000; Hutchings et al. 2003; Lamb et al. 2009; Hautier et al. 2009, Gazol et al. 2013).

Low-fertility patches in heterogeneous conditions may help subordinate species to persist if they are large enough to allow niche differentiation and prevent good foragers from reaching high-fertility conditions and gaining a competitive advantage (Martorell et al. 2015; Letten et al. 2015). Based on the previous findings from this experiment, we did not expect species' responses to differ significantly in the two heterogeneous treatments with different patch sizes (Gazol et al. 2013; Price et al. 2014). However, there was some variability in how species responded to heterogeneous treatment with smaller or larger patches. For example, *Trifolium* had less aboveground biomass in heterogeneous conditions with larger patches than in homogeneous low-fertility treatment, but this was not true for heterogeneous conditions with smaller patches. Compared to other forbs, legumes are found to be less precise foragers (Einsmann et al. 1999), and extend their roots over relatively small areas (Hill et al. 2006). It is possible that *Trifolium* benefitted from soil heterogeneity only if the high-fertility conditions were nearby, but was not able to forage among larger patches in our experiment.

Conclusions

Co-occurring species respond to fine-scale soil heterogeneity in various ways, depending on species' foraging and competitive abilities, and behaviour in the presence of neighbours. Heterogeneity benefits large, dominant species that are able to quickly forage for patchily distributed resources in both high- and low-fertility patches. Smaller, subordinate species are negatively affected in heterogeneous conditions due to increased root and shoot competition from neighbouring species. Our results show that species-specific responses to soil heterogeneity have important implications for community structure and productivity, and help to understand the mechanisms behind a negative heterogeneity-diversity relationship that is often found at small spatial scales (Lundholm 2009; Tamme et al. 2010; Stein et al. 2014). By modifying the spatial distribution of resources, soil heterogeneity was found to decrease taxonomic (Gazol et al. 2013) and functional diversity (Price et al. 2014) in this experiment. Here, we provide evidence that the loss of species diversity was due to large and dominant species benefitting more from heterogeneous conditions and excluding smaller species from communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species' abundances (number of individuals) in 6.25 x 6.25 cm quadrats four weeks after seed addition.

Appendix S2. Full table with P values showing species' responses to soil heterogeneity at the community level.

Appendix S3. Full table with P values showing species' responses to soil heterogeneity within low-fertility patches.

Table 1. List of plant species used in the experiment, and average (SD) relative biomass (% of the total aboveground biomass accounted for by the species in a 6.25 x 6.25 cm quadrat) in the treatments. Low – low-fertility homogeneous treatment; Med – medium-fertility homogeneous treatment; HetL – heterogeneous treatment with 12.5 x 12.5 cm patches and overall medium fertility; HetS – heterogeneous treatment with 6.25 x 6.25 cm patches and overall medium fertility; High – high-fertility homogeneous treatment. The first nine species in the list were used in the analysis

Species	**Family**	**Relative biomass (%)**				
		Low	**Med**	**HetL**	**HetS**	**High**
Antennaria dioica	Asteraceae	0.38 (0.42)	0.58 (1.21)	0.09 (0.28)	0.05 (0.12)	0.02 (0.07)
Briza media	Poaceae	13.72 (22.51)	17.77 (29.99)	22.86 (27.01)	22.94 (28.53)	18.28 (23.99)
Centaurea jacea	Asteraceae	12.23 (14.22)	8.62 (14.54)	10.90 (12.21)	7.54 (12.81)	10.32 (12.03)
Cirsium acaule	Asteraceae	4.18 (11.68)	2.67 (6.72)	4.35 (10.70)	2.93 (7.40)	1.06 (2.62)
Festuca rubra	Poaceae	39.52 (19.67)	33.71 (22.61)	28.06 (20.42)	30.72 (21.83)	31.88 (19.50)
Hypericum perforatum	Hypericaceae	0.24 (0.37)	0.44 (1.14)	0.05 (0.09)	0.05 (0.17)	0.06 (0.11)
Plantago media	Plantaginaceae	27.17 (16.29)	33.76 (20.02)	31.43 (19.82)	33.34 (22.95)	36.90 (21.71)
Prunella vulgaris	Lamiaceae	0.37 (0.73)	1.02 (2.08)	0.41 (0.92)	0.74 (1.52)	0.36 (0.99)
Trifolium montanum	Fabaceae	1.50 (2.94)	0.82 (2.24)	0.28 (0.75)	0.37 (1.43)	0.07 (0.13)
Others						
Anthyllis vulneraria	Fabaceae	-	-	0.26 (1.33)	0.06 (0.37)	0.35 (1.72)
Erophila verna	Brassicaceae	0.02 (0.10)	0.00 (0.02)	-	-	-
Filipendula vulgaris	Rosaceae	0.02 (0.09)	0.26 (1.64)	-	0.04 (0.28)	-

Galium verum	Rubiaceae	-	-	0.26 (1.24)	0.07 (0.44)	-
Primula veris	Primulaceae	0.10 (0.35)	0.02 (0.11)	0.02 (0.08)	0.01 (0.04)	0.02 (0.06)
Viola rupestris	Violaceae	-	-	-	-	-

Table 2. Species' responses (measured as aboveground biomass) to soil heterogeneity and fertility at the community level, and the planned multiple comparisons among the treatment levels. Low – low-fertility homogeneous treatment; Med – medium-fertility homogeneous treatment; High – high-fertility homogeneous treatment; HetL – heterogeneous treatment with 12.5 x 12.5 cm patches and overall medium fertility; HetS – heterogeneous treatment with 6.25 x 6.25 cm patches and overall medium fertility. F values show the overall effect of the treatment, whereas z values represent the contrasts between treatment levels. The statistical significance is annotated by symbols for improved readability; see Appendix S2 for a full table with P values

Species	Treatment		Comparison to Low			Comparison to Med		Comparison to High		
			HetL	HetS	Med	HetL	HetS	HetL	HetS	Med
			z	z	z	z	z	z	z	z
Antennaria	$F_{4,177}$	**11.78** ***	**-3.44** **	**-3.42** **	0.44	**-3.34** **	**-3.31** **	1.91	2.15	**4.60** ***
Briza	$F_{4,79}$	**5.91** ***	**3.52** **	**3.28** **	**2.83** *	0.51	0.28	-0.01	-0.23	-0.49
Centaurea	$F_{4,123}$	**5.51** ***	**3.59** **	2.46 ·	1.77	0.87	0.78	0.50	0.47	-0.47
Cirsium	$F_{4,47}$	0.63	0.93	1.26	0.01	0.89	1.21	0.68	1.02	-0.31
Festuca	$F_{4,186}$	**16.59** ***	**3.62** **	**5.11** ***	1.52	2.37	**3.79** **	-2.50 ·	-1.24	**-5.33** ***
Hypericum	$F_{4,105}$	2.35 ·	-1.44	0.19	1.45	**-2.84** *	-1.05	-0.76	0.89	2.44 ·
Plantago	$F_{4,183}$	**36.61** ***	**6.20** ***	**7.29** ***	**4.61** ***	2.08	**2.78** *	-1.88	-1.35	**-4.38** ***
Prunella	$F_{4,80}$	**4.29** **	1.53	**2.73** *	2.46 ·	-0.90	0.59	-0.73	0.43	-0.05
Trifolium	$F_{4,115}$	**4.08** **	-2.12	-1.43	-0.76	-1.56	-0.78	1.58	1.32	-2.36 ·

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; · $P < 0.1$

Table 3. Species' responses (measured as aboveground biomass) to soil heterogeneity within low-fertility patches, and the planned multiple comparisons. Patch size decreases from 25 x 25 cm in the homogeneous low-fertility (Low) treatment to 12.5 x 12.5 cm in the heterogeneous treatment with large patches (HetL) and to 6.25 x 6.25 cm in the heterogeneous treatment with small patches (HetS). F values show the overall effect of patch size, whereas t values represent the contrasts between patches in the different treatments. The statistical significance is annotated by symbols for improved readability; see Appendix S3 for a full table with P values

Species	**Low-fertility patches**		**HetL vs Low**	**HetS vs Low**
			t	**t**
Antennaria	$F_{2,62}$	**12.70 *****	**-3.11** **	**-5.00** ***
Briza	$F_{2,28}$	**16.62 *****	**2.43** *	**5.64** ***
Centaurea	$F_{2,43}$	1.68	1.46	1.26
Cirsium	$F_{2,14}$	1.22	-1.17	0.31
Festuca	$F_{2,68}$	**7.32 ****	**2.55** *	**3.14** **
Hypericum	$F_{2,29}$	0.83	-1.09	0.28
Plantago	$F_{2,67}$	**11.52 *****	**2.55** *	**4.41** ***
Prunella	$F_{2,22}$	2.42	0.25	**2.20 ***
Trifolium	$F_{2,41}$	**3.91 ***	**-2.64** *	-0.55

*** P < 0.001; ** P < 0.01; * P < 0.05; ˙ P < 0.1

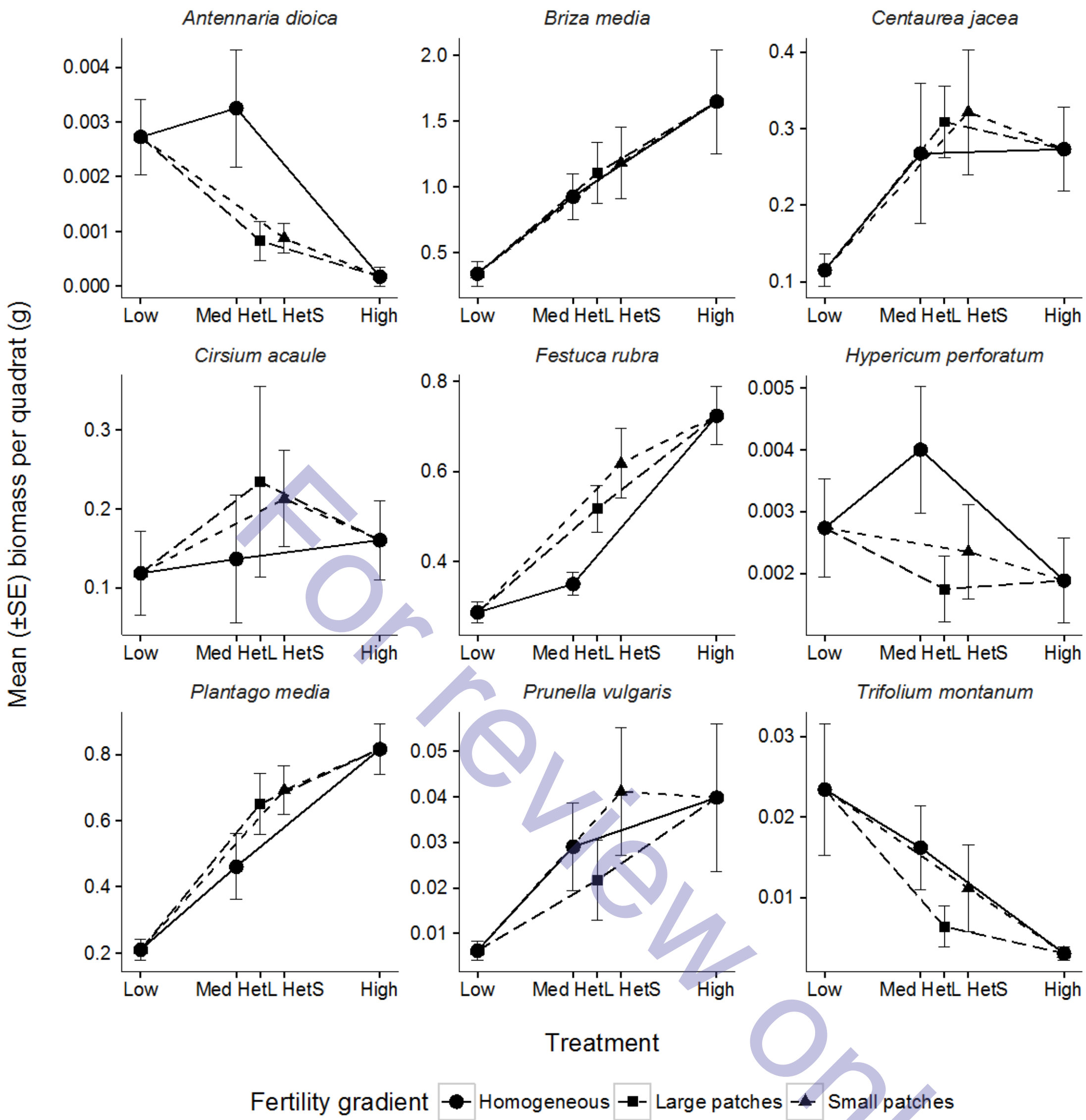

Figure 1. Species' aboveground biomass responses to the treatments at the community level. Low – low-fertility homogeneous treatment; Med – medium-fertility homogeneous treatment; High – high-fertility homogeneous treatment; HetL – heterogeneous treatment with 12.5 x 12.5 cm patches and overall medium fertility; HetS – heterogeneous treatment with 6.25 x 6.25 cm patches and overall medium fertility. Vertical bars denote ± SE. The results for comparisons of the treatments are shown in Table 2.

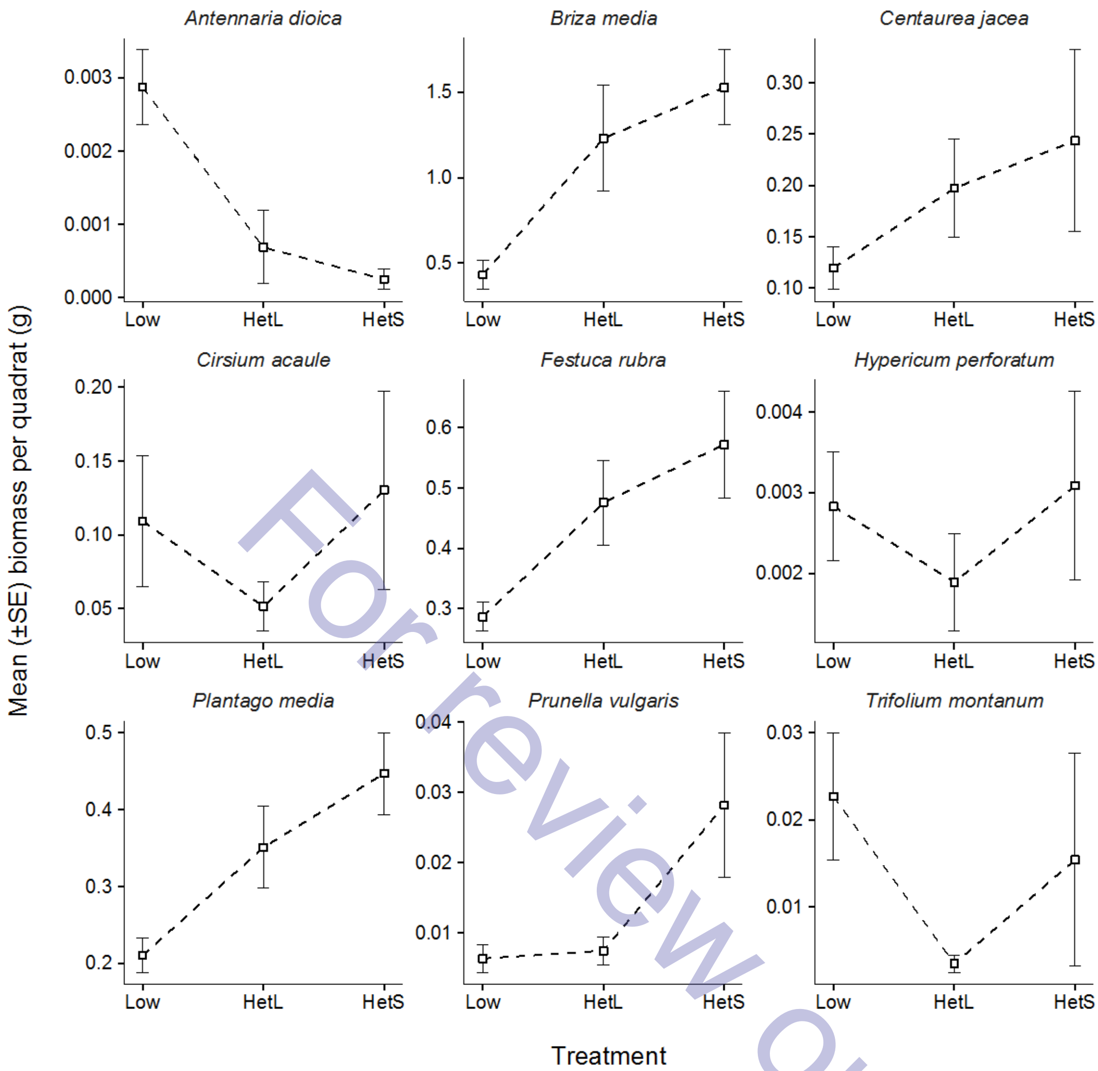

Figure 2. Species' aboveground biomass responses to soil heterogeneity within low-fertility patches. Patch size decreases from 25 x 25 cm in the homogeneous low-fertility (Low) treatment to 12.5 x 12.5 cm in the heterogeneous treatment with large patches (HetL) and to 6.25 x 6.25 cm in the heterogeneous treatment with small patches (HetS). Vertical bars denote ± SE. The results for comparisons of different patch sizes are shown in Table 3.