

RESEARCH ARTICLE

Small-scale heterogeneity shapes grassland diversity in low-to-intermediate resource environments

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Abstract

Questions: Soil resource heterogeneity influences the outcome of plant–plant interactions and, consequently, species co-existence and diversity patterns. The magnitude and direction of heterogeneity effects vary widely, and the processes underlying such variations are not fully understood. In this study, we explored how and under what resource conditions small-scale heterogeneity modulates grassland plant diversity.

Location: Oderhänge Mallnow, Potsdam, Brandenburg, Germany.

Methods: We expanded the individual-based plant community model (IBC-grass) to incorporate dynamic below-ground resource maps, simulating spatial heterogeneity of resource availability. Empirical centimeter-scale data of soil C/N ratio were integrated into the model, accounting for both configurational and compositional heterogeneity. We then analyzed the interplay between small-scale heterogeneity and resource availability on the interaction and co-existence of plant species and overall diversity.

Results: Our results showed significant differences between the low- and high-resource scenarios, with both configurational and compositional heterogeneity having a positive effect on species richness and Simpson's diversity, but only under low-resource conditions. As compositional heterogeneity in the fine-scale C/N ratio increased, we observed a positive shift in Simpson's diversity and species richness, with the highest effects at the highest level of variability tested. We observed little to no effect in nutrient-rich scenarios, and a shift to negative effects at the intermediate resource level. The study demonstrates that site-specific resource levels underpin how fine-scale heterogeneity influences plant diversity and species co-existence, and partly explains the divergent effects recorded in different empirical studies.

Conclusions: This study provides mechanistic insights into the complex relationship between resource heterogeneity and diversity patterns. It highlights the context-dependent effects of small-scale heterogeneity, which can be positive under low-resource, neutral under high-resource, and negative under intermediate-resource conditions. These findings provide a foundation for future investigations into small-scale heterogeneity–diversity relationships, contributing to a deeper understanding of the processes that promote species co-existence in plant communities.

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KEYWORDS

agent-based modeling, below-ground resource heterogeneity, individual-based modeling, niche separation, plant diversity, species co-existence, trait-based approach

1 | INTRODUCTION

The “environmental heterogeneity hypothesis” (EHH) holds that spatial heterogeneity in biotic and abiotic environmental conditions increases biodiversity (MacArthur & MacArthur, 1961; MacArthur et al., 1966; MacArthur & Wilson, 1967; Ricklefs, 1977). Following this hypothesis, the heterogeneity–diversity relationship (HDR) is typically assumed to be positive, as environmental heterogeneity not only allows for the presence of additional niches, but also modulates the breadth of existing ones. Soil moisture, organic matter, nitrogen or other nutrients, light, precipitation, and temperature are known sources of environmental heterogeneity. Some experimental studies also included heterogeneity in the microsite texture (Grime et al., 1987) and soil depth (Baer et al., 2004). However, there are contradictory empirical findings, raising doubts about the universality of this simple heterogeneity–diversity relationship (Williams & Houseman, 2013). Field et al. (2009) showed that empirical studies found positive, neutral, or even negative effects of heterogeneity on the diversity of plant communities, with HDR being predicted to typically be positive for coarse-grained heterogeneity at the intercommunity level, but to be non-existent or even negative with smaller patch sizes. Additionally, many studies have reported different correlations between at least one source of heterogeneity and species diversity, showing positive, negative, and unimodal relationships (Williams & Houseman, 2013). In sum, one of the major findings is that the relationship seems to be highly scale- and potentially resource-dependent, lending support to the assumption that soil chemistry, texture, and depth, for example, have the greatest impact on community composition at small spatial scales, with climatic variables becoming increasingly important as scale increases (e.g., Palmer, 2007; Costanza et al., 2011).

At fine scales, environmental heterogeneity within communities is assumed to support resource partitioning between competing species (Chesson, 2000; Bolker, 2003; Costanza et al., 2011). With increasing scales, heterogeneity gradients become wider, and different communities can co-exist, resulting in large regional species pool sizes and positive heterogeneity–diversity relationships (Tamme et al., 2010). But how can the divergence in empirical findings across different scales be explained from a theoretical perspective? At the landscape scale, Kadmon and Allouche (2007) unified the island biogeography and niche theory in an elegant analytical model to challenge the positive relationship between species richness and habitat heterogeneity predicted by classical niche theory. By capturing the main elements of both theories, the model demonstrated that areal and dispersal limitations may create unimodal and even negative relationships between species richness and habitat heterogeneity. While increasing heterogeneity increases the potential number of species that may exist in a given area (as predicted by the niche theory),

the simultaneous reduction in the amount of suitable area available for each species increases the likelihood of stochastic extinction (Kadmon & Allouche, 2007). Interestingly, these contrasting mechanisms are also found in the ongoing discussion on whether landscape fragmentation per se (i.e., the spatial pattern of habitat configuration independent of habitat amount) has positive, negative, or neutral effects on species diversity (Fahrig, 2003, 2017; Fletcher et al., 2018; Rohwäder & Jeltsch, 2022). While these mechanisms are typically related to the landscape scale, a more overarching perspective emerges when two distinct components of environmental heterogeneity are explicitly distinguished: the compositional and configurational heterogeneity (Palmer, 1992; Fahrig et al., 2011; Ben-Hur & Kadmon, 2020). The former describes the magnitude of variation in environmental heterogeneity (e.g., the number of different habitat niches), and the latter refers to its spatial structure, i.e., how clumped or dispersed patches with similar conditions are distributed in space. Clearly, compositional and configurational heterogeneity may be correlated (Ben-Hur & Kadmon, 2020). In principle, both components are distinct at different scales. At the landscape level, for example, increasing compositional heterogeneity increases the available niche space and, thus, the potential to host a large number of species. At the same time, with increased niche space, the effective area occupied by a particular species is potentially reduced.

In contrast, at the local-patch scale, small-scale soil or resource heterogeneities can provide dissimilar microniches, possibly favoring particular individuals of competing species. However, it is unclear whether an increase in such microniches has negative effects, similar to the reduction in the effective area that a species can occupy at the landscape scale. A corresponding negative effect at the small scale could be that too few similar microniches lead to a very low number of individuals of the same species in the local patch, possibly causing local Allee effects (e.g., reduced pollination success, Nottebrock et al., 2013). An increase in the other component of heterogeneity, namely the configurational heterogeneity (e.g., clumping or gradual changes in resource availability), results in an increase in spatial fragmentation of the differing habitat types and their spatial distribution. This may not only negatively impact habitat connectivity and metapopulation dynamics at the landscape scale but also local population sizes. At a local scale, spatial fragmentation may either lead to micropatches that are too large to provide a safe site for an individual plant of a competitively inferior species, or patch sizes may get too small to provide sufficient resources for its survival. In the latter case, the heterogeneity may be too fine to matter. These theoretical considerations indicate that the effects of changes in compositional and configurational heterogeneity are particularly difficult to predict at a small scale. Furthermore, to date, small-scale variations in soil parameters have not been tested on a scale of centimeters, which is relevant for interactions between small plant



individuals (e.g., in grasslands; e.g., Schenk, 2006). Indeed, recent research indicates that plant-plant interactions at such scales can be crucial for understanding local plant community dynamics (e.g., Crawford et al., 2019, 2021).

In this study, we (i) present empirical data showing fine-scale heterogeneity in soil resources (here: soil carbon-to-nitrogen ratio) at the centimeter scale, and (ii) use the individual-based community model IBC-Grass (May et al., 2009; Pfestorf et al., 2016; Crawford et al., 2021) to explore how and under what conditions such fine-scale heterogeneity in soil resources impacts species co-existence and diversity of grassland communities. More specifically, we expanded and re-parameterized the model for 10 common grassland species in Mallnow Nature Reserve, Germany. Using varying scenarios in below-ground resource availability, we disentangle the effects of resource availability and compositional versus configurational resource heterogeneity on species diversity. We hypothesized that (1) the fine-scale configurational heterogeneity (patchiness) of the soil resource affects plant diversity, (2) compositional heterogeneity (i.e., variability of resources) is a major driver therein, and (3) the total resource availability of the local grid further modifies the impact of these two factors.

2 | MATERIAL AND METHODS

2.1 | Study system

This study combined Horn et al.'s (2015) published plant community and soil properties data from a dry grassland habitat of the natural reserve in Mallnow, Lebus (Brandenburg, Germany, 52°27.778' N, 14°29.349' E) and a complementary fine-scale soil survey as benchmarks. This reserve has been managed under low-intensity sheep grazing conditions for the past 500 years (Ristow et al., 2011). The grassland plant community was inventoried using a spatially explicit design based on hierarchical nesting of three replicated macroplots along a steep gradient of soil properties. Further details regarding the sampling protocol are available in Horn et al. (2015). *Festuca* spp. dominate the community assemblage, but plant diversity can be very high locally, with more than 40 species, even in a 10 m × 10 m plot. The soil is characterized as calciferous boulder clay and very sandy (Hensen, 1995). Along the hillslopes, one can observe relatively steep gradients from sandy clayey soils on the top to almost pure sandy soils in the lower parts. To further dissect the level of small-scale variation in soil parameters on a scale of centimeters, we collected soil samples from smaller macroplots of 15 m × 5 m along this slope and divided them into three sections of 3 m × 5 m, which were 3 m apart (top, middle, and bottom parts of the hill). In each of these plots, we selected three subplots of 20 cm × 20 cm and collected 16 soil samples in each (4 × 4 soil cores of 1.5 cm in diameter and 10 cm in depth), resulting in 144 soil samples (as detailed in Appendix S1). We cut the soil cores into five 2-cm slices and determined the nitrogen content for each of these subsamples. Soil carbon and nitrogen were analyzed by direct combustion of 30 mg of pulverized soil per

core using a EuroEA Element Analyzer (HEKAtech GmbH). Oriented toward the empirical variability of carbon-to-nitrogen (C/N) ratio in the Mallnow reserve, the model explores scenarios of alternative levels of resource availability and small-scale heterogeneity (for data, see Appendix S1). The C/N ratio is considered a proxy for soil resource availability because, as Watt and Palmer (2012) noted, it is a reliable predictor of soil nitrogen fertility by implicitly accounting for the positive correlation between soil carbon content and nitrogen immobilization.

2.2 | Small-scale spatial heterogeneity maps to describe below-ground resources

With the overall aim of systematically exploring the effect of small-scale heterogeneity in soil resources on the co-existence and dynamics of grassland communities, we used the empirical fine-scale data of soil carbon-to-nitrogen (C/N) ratio described above to generate derivative resource maps with realistic features of spatial heterogeneity. Using a two-dimensional grid with a spatial resolution of 1 cm × 1 cm in cell size, we systematically varied (i) the range of resource levels occurring at this fine scale (expressed as the standard deviation from a given mean C/N ratio value) and (ii) the spatial correlation of resources in grid cells (determined by the nugget effect) at identical mean resource levels. While the earlier measure describes the range of different potential microniches (i.e., compositional heterogeneity), the latter defines the pattern of spatial aggregation (i.e., local patchiness or configurational heterogeneity).

To this end, we generated derivative fractal maps of resource availability and heterogeneity patterns following a Gaussian probability distribution, which takes a specified empirical value of the soil C/N ratio as input. The derivative maps were generated in three steps as follows. (1) A surface grid map of the recorded carbon-to-nitrogen ratio data was created, with the corresponding x- and y-coordinates as point data within a specified spatial window (e.g., 101 cm × 101 cm for this study). (2) With a weighted linear combination of known data in the nearest neighborhood, the ordinary kriging method was applied to generate estimates for unsampled locations over the entire spatial window (see, Voltz & Webster, 1990). (3) Second-order polynomial kriging with spline interpolation was applied using the R package, *gstat* (Pebesma, 2004; Gräler et al., 2016), as shown in Figure 1. From the empirical variogram of the krigged C/N ratio data, we extracted selected map parameters. This includes the nugget size, which defines the spatial autocorrelation of neighboring points; the sill, corresponding to the variance value where the empirical variogram appears to level off; the range, which marks the distance after which autocorrelation becomes independent; and the kappa coefficient, a measure of kriging accuracy. Using these parameters, we generated derivative resource maps depicting the gradient of C/N resource availability using the Gaussian field algorithm (Sciaini et al., 2018).

In the subsequent step, we generated a set of analogous resource maps (Figure 2), in which the level of spatial autocorrelation

of resource units between grid cells is constrained by a patchiness factor (technically described as “nugget size,” see e.g., Voltz & Webster, 1990). In this study, this patchiness factor enabled the quantification and systematic comparison of the configurational heterogeneity of soil resources (i.e., C/N ratio) of specified spatial extents. The empirical nugget size of 0.06 in the Mallnow landscape was taken as a reference patchiness value. For our analysis,

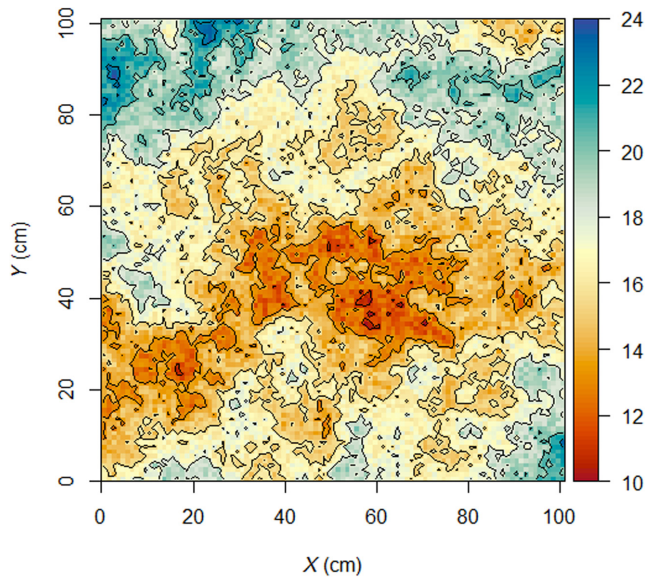


FIGURE 1 A krigged map of fine-scale C/N ratio distribution of a typical 1m x 1m plot in the Mallnow reserve.

we considered seven landscapes with patchiness ranging from 0.46 (nearly uncorrelated spatial configuration) to 0.06 (highly correlated spatial configuration; see Figure 2). As a basis for model simulations, we prepared all maps in raster format using the R package *raster* (Hijmans, 2020) and linearly transformed them to produce resource maps with specified mean values of below-ground resource availability and a coefficient of variation of 0.25, translating to a ± 4 extent of variability at a standard deviation of one unit per cm^2 .

2.3 | Modeling approach

To investigate the dynamics of the small-scale heterogeneity-diversity relationship in a grassland community, we used a refined version of the dynamic IBC-Grass model (an individual-based model of grassland community) by May et al. (2009), which simulates the fate of individual plants over time depending on above- and below-ground resource availability. With this model, different scenarios of plant-plant and plant-environmental interactions have been tested, for example, the effects of varying nutrient content and mowing (May et al., 2009), shoot and root herbivory (Crawford et al., 2021), and habitat isolation on plant communities (Weiss et al., 2014). Other examples include the effects of below-ground herbivory on the community (Körner et al., 2014; Pfestorf et al., 2016; Crawford et al., 2021), influence of grazing cessation (Weiss & Jeltsch, 2015), and role of intraspecific trait variability in species co-existence (Crawford et al., 2019). Pfestorf et al. (2016) adapted the model to allow flexible species parameterization as well as inclusion of annual

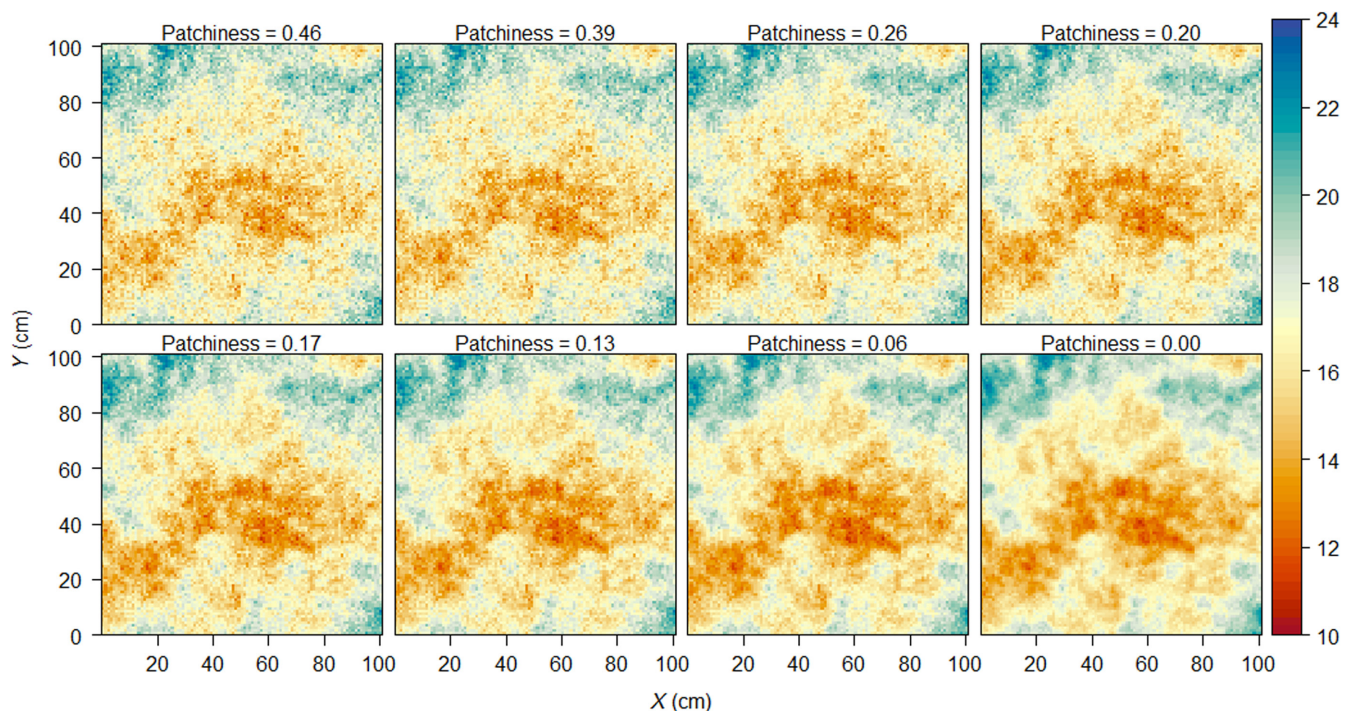


FIGURE 2 A set of derivative resource maps generated with different levels of patchiness of resource availability derived from empirical soil carbon-to-nitrogen ratio measurements. The color scheme and legend key represent the magnitude of the deviation from the mean resource level at an empirical standard deviation of 2.346 units per cm^2 .



species. For this study, we re-implemented the IBC-Grass in NetLogo 6.0.2 (Wilensky, 1999) with emphasis on a user-friendly interface and documentation. We used the IBC-Grass version of Pfestorf et al. (2016) as a base for species-level and plant functional type (PFT) parameterization, as well as model testing. We further expanded the model to integrate the below-ground resource map as a dynamic input to simulate the spatial heterogeneity of resource availability, representing the C/N ratio of the grid cells per time step. To ensure software quality, we conducted intensive model testing and evaluation (including global sensitivity analyses) based on the two-person rule (Kusumoto et al., 1998). This pair programming approach engages at least two persons in crucial software development, testing, and quality control tasks, leveraging their expertise and perspectives to minimize the likelihood of mistakes and to detect and rectify errors. For model testing, we used species-specific parameters of the plant community described by Pfestorf et al. (2016) with some modifications (see Table S2.1 in Appendix S2). For simplicity and readability, we provide here only a general overview of the model. A full description of the model version used in this study is provided following the ODD protocol (Overview, Design concepts, Details; Grimm et al., 2010; Grimm et al., 2020) in Appendix S2.

2.4 | Overview of the IBC-Grass model

IBC-Grass is an individual-based spatially explicit model. It simulates the spatial and temporal dynamics of a plant community on a torus 2D-grid of 100×100 cells. Each grid cell was set to a spatial resolution of 1cm×1cm. These grid cells are characterized by a specific supply of above-ground resource (light) and below-ground resources (e.g., nutrients). Individual plants occupy spatially defined coordinates within the grid and are represented by their above- and below-ground circular Zones of Influence (ZOI; Weiner et al., 2001). The latter defines the space and, thus, the quantity of resources to which the plants have access. The accumulated resource uptake is allocated to the above- and below-ground biomass, as well as to reproductive biomass, in weekly time steps. The annual vegetation growth cycle was set at 30 weeks. The model describes the following key processes: inter- and intraspecific competition for above- and below-ground resources, individual plant growth, plant mortality, seed production, seed dispersal, seed mortality, germination, spacer growth and ramet establishment for clonal species, as well as plant dieback during the winter break.

The above-ground competition for light was modeled size-asymmetrically. Neighboring plants (specified by overlapping ZOIs) share resources proportional to their respective biomass and shoot geometry (May et al., 2009). In contrast, below-ground competition follows a size-symmetric mode (Weiner et al., 2001) in which competing plants share available resources equally in overlapping ZOI areas.

During weeks 16–20, plants allocate a specified proportion of the resources accrued to reproduction. Perennial and annual plants allocate 5% and 20% of their weekly resource uptake, respectively,

to seed production. Clonal plants use 5% of their resources for spacer growth (i.e., vegetative connection between the mother and possible daughter ramets) and ramet development during weeks other than weeks 16–20. Although only one spacer can grow at a time, this occurs throughout the year, except during the weeks of seed production. At week 21, seeds are dispersed over the grid cells, with a probability of 50% mortality. Seedlings can establish in vacant cells for up to four weeks after dispersal and in the first four weeks of the next year.

Plant mortality can result from three factors: resource stress, winter dieback, and a random background mortality of 21% per year. If resource uptake is below a fixed threshold fraction (e.g., 20% of the optimal uptake), plants suffer from resource stress, which linearly increases the probability of mortality each week. The plant dies when a species-specific survival time is exceeded. All ramets and annual plants die shortly before winter break. Perennial plants lose their total reproductive biomass and half of their above-ground biomass during the winter dieback.

2.5 | Simulated plant community

Simulation experiments for heterogeneity–diversity relationship scenarios were based on the described resource maps derived from empirical soil carbon-to-nitrogen data. We parameterized with empirical records in the TRY plant trait database (Kattge et al., 2020) and other scientific literature (see Table 1). The plant community described here comprised 10 grassland species ecologically adapted to sites with low to medium-high values of soil C/N ratio, characterizing the grassland in the Mallnow Nature Reserve. Species nomenclature follows Ristow et al. (2011). Based on the plant adaptive strategy scheme (Grime, 1988; Hunt et al., 2004), the selected species were distributed over three plant functional types along resource competition and stress adaptation dimensions. These are: (1) the competitor (adapted to high-resource pre-emption and higher establishment success under low stress); (2) the intermediate (possess average competitive to stress-tolerant traits and are more abundant at the intermediate resource range); and (3) the stress-tolerant (adapted to high-resource stress, with a high establishment success in extremely nutrient-poor soils). Each plant species was described by 26 trait parameters divided into 16 species-specific state variables and 10 common parameters, which were kept constant for all species.

2.6 | Model validation

The performance of the model in reproducing the empirical plant community was evaluated by comparing the differences in plant species richness and composition of indicator species between empirical observations and simulation results for 10 selected sample plots with soil C/N ratios ranging from 11.57 to 23.2. The simulation results represent 20 replicated model outcomes at the end of a 50-year seasonal cycle, which is considered a reasonable equilibrium



TABLE 1 Plant functional types and species-specific trait parameters of the simulated plant community.

Parameter	Description (unit)	Plant functional type/Species name											
		Competitor			Intermediate			Stress-tolerator					
		<i>Festuca brevipila</i>	<i>Festuca psammophila</i>	<i>Rumex acetosella</i>	<i>Arrhenatherum elatius</i>	<i>Koeleria macrantha</i>	<i>Carex humilis</i>	<i>Cerastium semidecandrum</i>	<i>Galium verum</i>	<i>Arenaria serpyllifolia</i>	<i>Artemisia campestris</i>		
f_{leaf}	Leaf mass ratio (mg/mg)	0.785	0.788	0.695	1.000	0.970	0.703	0.605	0.692	0.575	0.697		
C_{shoot}	Above-ground ZOI area per leaf mass (cm^2/mg)	0.615	0.619	0.705	0.920	0.752	0.595	0.550	0.739	0.665	0.644		
ru_{max}	Maximal resource use in ZOI area per time (Resource units/ cm^2/week)	60	60	60	60	40	40	40	20	20	20		
$surv_{\text{max}}$	Maximal survival time during resource stress (weeks)	2	2	2	2	2	4	4	6	6	6		
$m_{\text{max shoot}}$	Maximum shoot mass (mg)	2411	1931	2099	2119	2376	1301	1315	1125	1000	1375		
$m_{\text{max root}}$	Maximum root mass (mg)	1917	1914	1551	2113	2035	1205	690	315	361	551		
Res_{share}	Resource sharing between ramets (Boolean)	1	1	1	0	1	0	0	1	1	1		
$Alloc_{\text{spacer}}$	Resource allocation to spacer growth (%)	5	5	5	5	5	5	5	5	5	5		
m_{spacerL}	Spacer length (cm)	11.15	10.20	10.20	12.75	12.75	10.50	9.52	6.20	7.95	13		
SD_{spacerL}	Standard dev. of spacer length (cm)	11.05	10.10	10.10	12.35	12.00	10.15	9.52	6.11	7.95	12		
$Alloc_{\text{seed}}$	Resource allocation to seed (%)	5	5	5	5	5	5	5	5	5	5		
m_{seed}	Seed mass (mg)	0.269	0.21	0.371	2.19	0.265	1.14	0.05	0.3	0.15	0.103		
$mean_{\text{disp}}$	Mean dispersal distance (m)	0.35	0.60	0.30	0.04	0.38	0.10	0.60	0.30	0.88	0.60		
SD_{disp}	Standard dev. of dispersal distance (m)	0.35	0.60	0.30	0.04	0.38	0.10	0.60	0.30	0.88	0.60		

point, following which no appreciable changes in the species richness and Simpson reciprocal diversity index were recorded. We used the published vegetation and soil properties data of Horn et al. (2015) as a reference. Using the medians and median absolute deviations of species richness from the simulated plots, we conducted a pairwise Mann–Whitney U test to identify significant differences between the model output and empirical observations. Spearman's Rho coefficient was computed to infer the strength of the relationship between the variables.

2.7 | Simulation experiments

We performed two batches of simulation experiments. The first batch explored whether landscape patchiness, as a measure of configurational heterogeneity, increases species diversity equally under different mean below-ground resource (C/N ratio) conditions. For this, we compared the temporal dynamics of local communities grown under a fixed mean C/N ratio (i.e., “no heterogeneity”) and a high patchy mosaic (patchiness=0.06, standard deviation (SD) of mean C/N ratio=10 units per cm²) under mean below-ground resources of low (14) and high (36) C/N ratios over a 50-year simulation period.

The second batch of experiments aimed to decipher how changes in compositional heterogeneity (i.e., the range of variability in fine-scale resource levels, as defined by the standard deviation of a specific mean resource value) and configurational heterogeneity (i.e., patchiness in spatial distribution) determine the magnitude and direction of heterogeneity–diversity relationships. This experiment was arranged in a full factorial design with four levels of mean below-ground resource availability (C/N ratios: 14, 18.4, 22.8, and 36), eight levels of SD of the mean C/N ratio (i.e., 0.00, 1.25, 2.50, 3.75, 5.00, 6.25, 7.50, 8.75, and 10.00) and seven levels of patchiness (i.e., 0.46, 0.39, 0.26, 0.20, 0.13, 0.06, and 0.00; higher patchiness values indicate higher levels of fragmentation) (see Figure 2). We

initialized model runs for these resource heterogeneity variables, using the above-stated species-specific parameters and 10 seedlings for each of the 10 species. Each model run lasted for 50 simulated years, and was repeated 20 times. This runtime sufficiently yielded stable population and community dynamics. At week 20 of each year (directly before seed dispersal), we recorded the number of surviving individuals of all species, as well as the estimates of species richness and the Simpson's reciprocal diversity index (hereafter cited as Simpson's diversity; *sensu* Pallmann et al., 2012) of the simulated grid.

3 | RESULTS

By comparing the simulation results and empirical observations obtained from the selected soil carbon-to-nitrogen ratio of the Mallnow site (between 11.57 and 23.2), we found no significant differences in species richness (Mann–Whitney U test: $W=33$, $p=0.202$). Against the empirical median species richness of 5 (median absolute deviation [MAD]=1.48, interquartile range [IQR]=2.75), from the simulations, a median species richness of 6 (MAD=2.22, IQR=3) was obtained, with an overestimation and/or underestimation of 8% deviation across the board (Spearman's $\rho=0.92$). As shown in Figure 3, the simulation results typify stochasticity in species richness within each mean C/N ratio value, when considering a standard deviation of 2.346 recorded in the sample plots. The model reproduced the dominance of *Festuca brevipila* and *F. psammophila* grasses in the plant cover of plots with C/N ratios in the low to medium-high range. Similarly, species with high stress tolerance traits, such as *Arrhenatherum elatius*, *Carex humilis*, and *Rumex acetosella*, were the most abundant species in plots characterized by low soil C/N ratios.

From the first simulation experiment, analyses of the temporal trajectories of the simulated grassland community indicated that under low below-ground conditions (mean C/N ratio=14), small-scale heterogeneity in a derivative high patchy soil C/N ratio mosaic

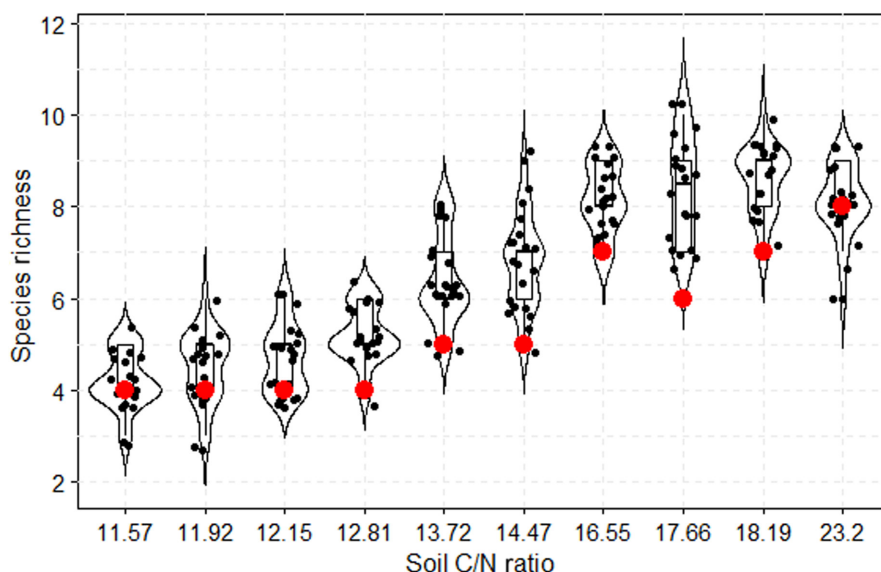


FIGURE 3 Species richness of selected plots across a range of low to medium-high soil carbon-to-nitrogen ratios in the Mallnow Reserve. The violin plots and black dots distributed therein represent the simulation results, whereas the red dots are the corresponding empirical observations.

(patchiness=0.06, and SD=10.0), resulted in higher Simpson's diversity and species richness than in a "no-heterogeneity" landscape (Figure 4). Both Simpson's diversity and species richness declined sharply under "no-heterogeneity" conditions, earlier than in a heterogeneous patch mosaic where a steep decline in species richness of the simulated community only set in after 11 years. By the final simulation year, median Simpson's diversity and species richness in patchy mosaic diverged from the "no-heterogeneity" scenario by $1.6 (\pm 0.497 \text{ MAD})$ and $2 (\pm 1.480 \text{ MAD})$, respectively. The response to fine-scale heterogeneity in the low-resource scenario conveyed a beta diversity of 4. Under high below-ground resource availability (mean C/N ratio=36), the Simpson's diversity and species richness in the "no-heterogeneity" and heterogeneous conditions maintained comparable values throughout the simulation period. The final respective Simpson's diversity and species richness of the two high-resource scenarios converged at median values of $2.62 (\pm 0.156 \text{ MAD})$ and 4, which are equivalents of their values in the "no-heterogeneity" low-resource condition.

Subsequent analyses proceeded to further systematically evaluate the interactions of configurational (i.e., patchiness) and compositional heterogeneity (i.e., the extent of variability defined by the standard deviation, SD) of below-ground resources (mean resource level C/N ratio) on species diversity (Figure 4). At a low resource level (mean C/N ratio=14, left panel of Figure 5), the spatial configuration and composition of resource distribution both strongly influenced

Simpson's diversity. Although a sizable increase in Simpson's diversity was apparent along the compositional heterogeneity gradient, distinctive patterns emerged in response to the configurational patchiness at different levels of compositional heterogeneity. With compositional variability at SD between 0 and 1.25, a hump-shaped Simpson's diversity emerged when intermediate configurational patchiness only marginally increased the plant diversity. At medium compositional heterogeneity a U-shaped effect of configurational patchiness (i.e., least Simpson's diversity at the intermediate patchiness) was apparent. A further increase in compositional heterogeneity yielded mixed responses of Simpson's diversity to configurational patchiness, leading to a moderate reverse-J shape at the SD value of 10. In contrast, under high below-ground resource conditions (mean C/N ratio=36, right panel of Figure 5), the interaction of configurational and compositional heterogeneity of resource distribution yielded no distinct effect on Shannon diversity. Similar to the no-heterogeneity scenario, only competitive, fast-growing species dominated the community. A similar trend was observed for the species richness (see Figure S3.1 in Appendix S3).

The slopes of the relationship between species diversity metrics and compositional heterogeneity (i.e., $\Delta\text{-diversity}/\Delta\text{-SD}$ of the mean C/N ratio) synthesize effect levels along the gradient of configurational patchiness under contrasting mean carbon-to-nitrogen resource levels (Figure 6). Slope estimates were positive only at the low resource level (mean C/N ratio=14) across all the tested

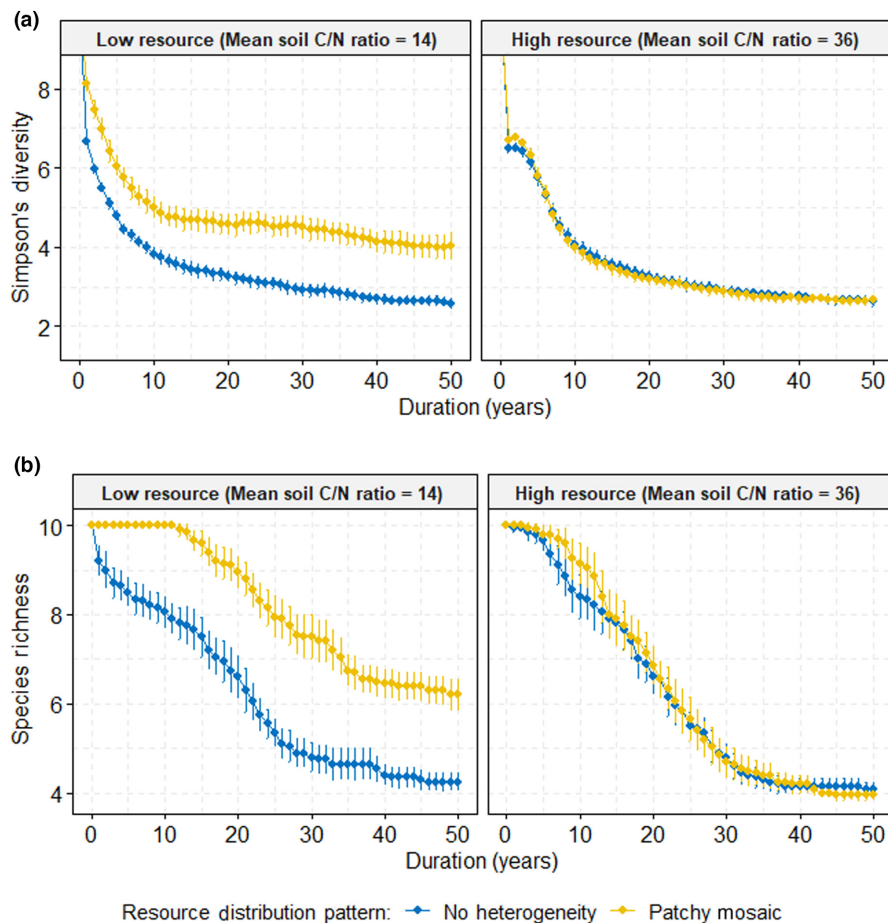


FIGURE 4 Temporal changes in Simpson's diversity (a) and species richness (b) of the simulated grassland community in the "no heterogeneity" and heterogeneous resource configurations under low (mean C/N ratio=14) and high (mean C/N ratio=36) below-ground resource conditions. Each experimental setting was initialized with 100 seedlings for each of the 10 species and run for 50 simulated years, with 20 repetitions. Data on the number of surviving individuals and estimates of Simpson's diversity and species richness were recorded at week 20 of each year.

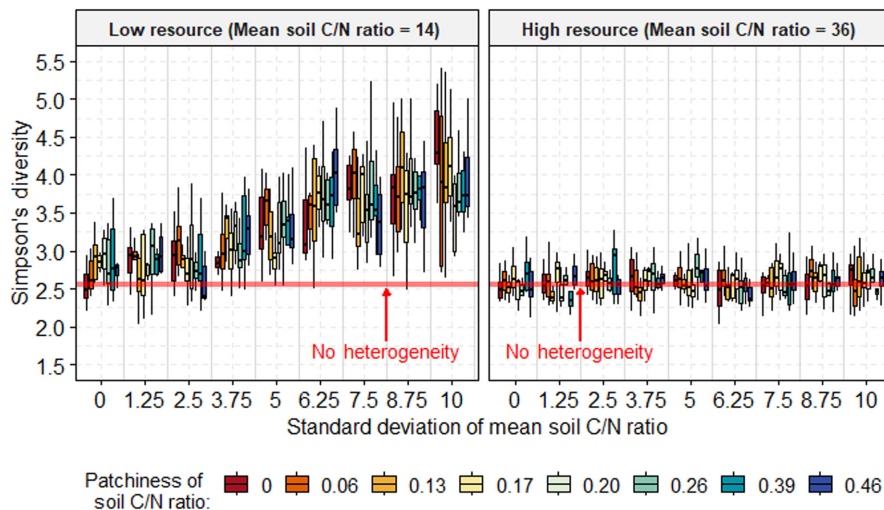


FIGURE 5 The response of Simpson's diversity to the interacting effects of compositional heterogeneity (defined by the standard deviation of the mean C/N ratio) and configurational heterogeneity (i.e., patchiness pattern) under contrasting below-ground resource availability (higher patchiness values indicate higher levels of fragmentation; see Figure 2). Each experimental setting was initialized with 100 seedlings for each of the 10 species and run for 50 simulated years, with 20 repetitions. Data on the number of surviving individuals, and estimates of Simpson's diversity and species richness were recorded at week 20 of each year.

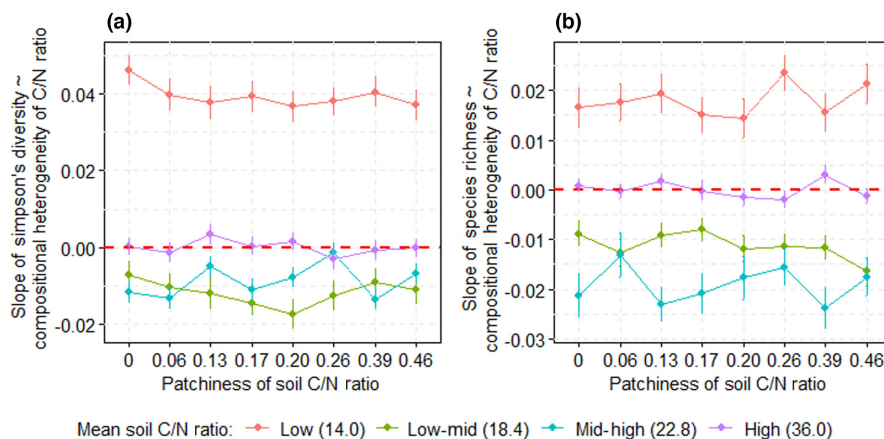


FIGURE 6 Slope estimates of the relationship between diversity and compositional heterogeneity (i.e., standard deviation of below-ground resources) at varying levels of patchiness and under contrasting below-ground resource availability (note: higher patchiness values indicate higher levels of fragmentation; see Figure 2). The bars represent standard errors of the slope estimates. Each experimental setting was initialized with 100 seedlings for each of the 10 species and run for 50 simulated years, with 20 repetitions. Data on the number of surviving individuals, and estimates of Simpson's diversity and species richness were recorded at week 20 of each year.

configurations. In contrast, we recorded negative slope estimates at mid-range resource levels (mean C/N ratio = 18.4–22.8). At a high resource level (mean C/N ratio = 36), the slopes teetered around zero, with no significant effect of configurational patchiness.

4 | DISCUSSION

In this study, we aimed to systematically explore how and under what conditions spatial resource heterogeneity affects plant co-existence and overall diversity at very fine scales. The heterogeneity–diversity relationship (HDR hypothesis of Williams and Houseman, 2013)

posits that increased spatial heterogeneity creates more ecological niches, which in turn promotes greater diversity. This study explores this relationship and sheds light on why previous empirical studies have generated non-convergent results. Specifically, we investigated the effect of below-ground resource heterogeneity generated by the patchiness of the resources (“configurational heterogeneity”) and the variability of available resources (“compositional heterogeneity”), as defined in previous studies (see e.g., Palmer, 1992; Fahrig et al., 2011; Ben-Hur & Kadmon, 2020). Furthermore, we considered levels of average resource availability (high vs low) as a third factor. Given the analyzed grassland community, our results suggest that the effect of heterogeneity on Simpson's diversity and species

richness strongly depends on resource limitations, with little to no effect of heterogeneity in high-resource habitats (Figures 4 and 5), whereas, under low-resource conditions, heterogeneity can strongly impact diversity depending on fine-scale variability of the resource composition and patchiness configuration (Figure 5). Thus, in low-resource habitats, both facets of heterogeneity, its configuration and its composition, interact in the magnitude and direction of the overall effect on diversity. While, above a certain threshold, an increase of compositional heterogeneity (i.e., resource variability, here measured as standard deviation of mean below-ground resources) leads to an increasing species co-existence, the strength of this effect is modulated by configurational heterogeneity (i.e., resource patchiness). While increasing patchiness showed a hump-shaped effect on diversity under low-resource conditions and minimal compositional heterogeneity, that is, co-existence is highest at intermediate patchiness (Figure 5), the effect is generally idiosyncratic along patchiness gradient. Disparate patterns emerged at the intermediate compositional heterogeneity and a reverse J-shape emerged at the highest level tested.

Testing the effects of resource heterogeneity under different mean resource availability revealed an overall positive effect of compositional heterogeneity on diversity. This pattern is consistent with the empirical observations of Williams and Houseman (2013). In contrast, for moderate resource availability, this effect turned negative, independent of the patchiness level. Under high resource availability, the effects of both compositional and configurational heterogeneity waned. Altogether, our results show that our initial two hypotheses that fine-scale patchiness (configurational heterogeneity) and resource variability (compositional heterogeneity) distinctively affect plant diversity hold only under low-resource conditions. Meanwhile, the third hypothesis, emphasizing the importance of the overall resource level for the magnitude and direction of fine-scale heterogeneity effects on diversity, was clearly confirmed. In the following, we discuss these findings with regard to the underlying causes and mechanisms.

The strikingly different effects of small-scale heterogeneity under different resource levels obtained in our simulation experiments could explain why previous empirical studies have shown positive, neutral, or negative results regarding the relationship between resource heterogeneity and diversity. A likely explanation for the marginal effect of below-ground resource heterogeneity under high-resource conditions is the general observation that increasing nutrient availability, for example, shifts competition from the below-ground compartment to the above-ground compartment, giving a disproportionate advantage to faster-growing tall species (Bobbink et al., 1998; Farrer & Suding, 2016; Hautier et al., 2018; Crawford et al., 2021). Under such conditions, when below-ground resources are not limiting, the niche-related processes facilitated by fine-scale heterogeneity are of no prime importance when dominated by neutral-type processes (Gravel et al., 2006), whereby the overall species richness is driven by a density-dominated competitive exclusion, for example. This may be the case for studies where empirical evidence suggests little or no effect of soil nutrient heterogeneity

on diversity relationships was recorded (e.g., Baer et al., 2004; Wijesinghe et al., 2005). The intermediate-resource settings provide more of an ecotone, providing a confluent range for highest species co-existence and diversity. Therein, resource variability may convey niche overlap while lending an additional advantage to some fast-growing species to preempt resources and outcompete others, culminating in a negative impact on local species assemblages and diversity (see Figure S3.3 in Appendix S3). In contrast, under low below-ground resource levels, small patches with higher nutrient availability can provide a microniche for individual plants, relating to how much the local resource levels differ from the grid average. Here, the variability of resource levels in different patches (i.e., the compositional heterogeneity) clearly plays an important role: the higher the variability, the higher the chance that there are at least some microhabitat patches that meet the required resource levels for individuals with high nutrient demand. In addition to such single-species effects, microniches also affect the outcome of plant-plant interactions, and hence local community dynamics and species co-existence (Crawford et al., 2019; Casper et al., 2000; Fitter et al., 2000; Wilson, 2000).

Interestingly, our results confirmed that the outcome of plant competition for heterogeneous below-ground resources depends greatly on specific resource patchiness and, correspondingly, on the species' ability to explore such resource patches (Wijesinghe et al., 2001; Day et al., 2003; Baer et al., 2004; Maestre et al., 2007; Rajaniemi, 2007; Gazol et al., 2013). The latter is mostly due to the differential abilities of plants to proliferate roots into nutrient-rich patches (Robinson, 1994 and references therein), and in the variable rates of nutrient uptake (Campbell et al., 1991; Robinson, 1994; Einsmann et al., 1999; Farley & Fitter, 1999; Fransen et al., 1999; Robinson et al., 1999; Hutchings et al., 2000; Wijesinghe et al., 2001). Regarding patchiness, our model revealed a hump-shaped response of Simpson's diversity to increasing patch sizes where compositional heterogeneity was inconsequential. On the one hand, the corresponding optimum diversity for medium patch sizes under low compositional heterogeneity can be explained by a minimum patch size that is needed to provide the required resources of a single plant. On the other hand, if resource patches become larger and are shared by several individuals, local competition increases, thus again amplifying competitive exclusion. Patches that reach a size that is much larger than individual plants might approach a homogeneous condition, leading to a lowered diversity, as obtained in "no-heterogeneity" scenarios.

For grasslands, our findings confirmed that the effects of changes in compositional and configurational heterogeneity of below-ground resources at fine centimeter-size scales, as suggested by Schenk (2006), are indeed important. This aligns with recent studies by Crawford et al. (2019, 2021), indicating that plant-plant interactions at such scales can be crucial for local plant community dynamics. In addition, plant responses to the spatial distribution patterns of nutrients are species-specific. Depending on specific growth strategies, plants might struggle when trying to achieve the optimal distribution of roots under given levels of

resource heterogeneity, which might result in suboptimal growth and fitness (Wijesinghe & Hutchings, 1997; Wijesinghe et al., 2001, 2005). In contrast, clonal plants that spread vegetatively have an apparent advantage, as they can reach various resource patches simultaneously and dominate due to resource complementarity between patches (Hartnett & Bazzaz, 1983; Alpert & Mooney, 1986; Friedman & Alpert, 1991). This could then decrease the expected positive effect of small-scale soil nutrient heterogeneity, at least in certain settings (Eilts et al., 2011). However, this advantage may not increase the competitive ability in nutrient-rich habitats or in cases where resource patches are larger than individual plant root systems (Hutchings et al., 2003).

Although, in this study, we provide sufficient theoretical bases for all observed effects, the robustness and explicit application of the current model outcomes are subject to empirical evaluation. However, data suitable for such comprehensive evaluations are currently lacking. While our model assumed some temporal fractional loss and replenishment in the spatial composition and configuration of resources, plants themselves are modifying local resource availability, for example, by resource uptake but also by litter decomposition or by trapping organic material that is redistributed by wind or water, also depending on topography, soil parent material, etc. (Reynolds et al., 2007; Williams & Houseman, 2013). These additional feedbacks from plants back to resource availability, which are not explicitly described in this study, may limit a definitive prediction of competitive outcomes under spatially heterogeneous resource conditions.

5 | CONCLUSIONS

In this study, we made a first attempt to include empirical centimeter-scale data on soil carbon-to-nitrogen resource heterogeneity in a plant community model. Our findings show that both configurational and compositional below-ground heterogeneity in resources influence diversity patterns, but with a high dependence on the overall mean resource availability. These results confirm the view that under low-resource conditions, spatial heterogeneity in soil resources can be assumed to be a stronger driver of plant species' co-existence, and hence diversity, than light (*sensu* Tilman, 1982; Reynolds et al., 2007). In addition, they provide a mechanistic explanation for the observed interactive effects of configurational and compositional resource heterogeneity. This, we hope, will stimulate future research on small-scale heterogeneity, potentially of more than one resource, to better understand the role of fine-scale processes in promoting or counteracting co-existence in plant communities.

AUTHOR CONTRIBUTIONS

Adewole Olagoke, Florian Jeltsch, and Stefanie Maaß conceived the research idea; Stefanie Maaß conducted the field study; Adewole Olagoke performed the modeling, with inputs from Hagen Ritter, Britta Tietjen, Uta Berger, and Florian Jeltsch; Adewole Olagoke and

Stefanie Maaß led the writing of the paper; other authors contributed to the writing and discussion.

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DATA AVAILABILITY STATEMENT

The data and the description of the model supporting the findings of this study are openly available in the [Supporting Information](#). Model source codes are available upon request.

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SUPPORTING INFORMATION

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

Appendix S1. Description of the empirical field study and soil property data.

Appendix S2. Expanded IBC-Grass model description following the ODD protocol.

Appendix S3. Additional figures supporting some chapters of the main text.

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