



Factors affecting functional diversity of grassland vegetations

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ABSTRACT

The functional diversity of local plant communities is considered to be an important driver of ecosystem resistance and resilience. Various landscape characteristics can influence local functional diversity, but their relative importance is poorly understood. We used a spatially explicit grassland model (TRANSPOP) to simulate competition between 19 functional plant strategies as defined by Grime's C-S-R framework, each with different affinities for levels of Nutrient availability (N) and Disturbance (D). First, we explore the effects of N and D levels on strategy preference. Subsequently, we studied functional diversity in patchy landscapes with various levels of heterogeneity, patch size, connectivity and environmental dynamics (with patches differing in N and D). We evaluated the relative importance of these factors in determining the functional diversity of permanent grasslands of the temperate climatic zone.

Simulated N and D optima for occurrence of strategies matched those of Grime. Perpendicular N and D gradients were twice as diverse as correlated configurations. The results show that heterogeneity in N and D was the most important factor determining strategy diversity, followed by environmental dynamics, connectivity and patch size. Grasslands with large heterogeneity and patch size have a high functional diversity, whereas high values for dynamics and connectivity had, in general, a negative impact on functional diversity. The frequent occurrence of significant interactions among characteristics suggests that the optimal spatial design of landscapes with respect to functional diversity is context dependent.

Contrary to expectations, connectivity generally had a negative effect on the diversity of plant strategies. This was attributed to the fact that connectivity intensifies competition between strategies. High connectivity and environmental dynamics, low patch size and low heterogeneity intensifies interspecies competition and causes rapid species loss, which strongly reduces resistance and resilience. This shows that high species diversity in itself does not protect against diversity loss, but that factors contributing to the maintenance of high diversity reduce the risk of species extinction and enable resistance and resilience.

1. Introduction

1.1. Functional diversity, resistance and resilience

The functional diversity of local grassland communities, the number of functionally disparate species within a community, is considered to be an important driver of ecosystem resistance and resilience, i.e. the ability of an ecosystem to deal with environmental change or to return to its former state after disturbances (Fischer et al., 2006; Holling, 1973; Isbell et al., 2015; Schweiger et al., 2019). Ecosystems with a high diversity of functional groups are better able to respond to disturbances and temporary environmental change because there is a greater probability of there being species tolerant of a certain disturbance or environmental change in the local species pool (Craven et al., 2018; Folke

et al., 2004; Loreau et al., 2001). Another factor that determines resistance and resilience at a larger spatial scale is the availability of such species in the regional species pool, a form of ecological memory (Bengtsson et al., 2003; Sterk et al., 2016). Species that have become less abundant or locally extinct can be recruited from elsewhere through dispersal or from the seedbank (Peterson, 2002; Wisnoski et al., 2019), enabling them to re-enter the ecosystem. Dispersal ability and seed longevity (dormancy) are therefore considered to be crucial traits of plant species enabling them to cope with disturbance and environmental change. There are various landscape characteristics that can influence the functional diversity of local plant communities, but their relative importance is still poorly understood (Leibold et al., 2017), which in turn might hamper conservation efforts (Chase et al., 2020).

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1.2. Extinction and colonisation

The local diversity of grassland communities is governed by two processes: colonisation by new species and the extinction of established species. Colonisation by new species is enhanced by high connectivity between habitat patches (Damschen et al., 2019; Ozinga et al., 2009), while extinction is governed by local environmental change, interspecies competition (Schippers et al., 2015a) and disturbances (Muller et al., 2014). Plants with dormant seeds, however, may recover from disturbances by reestablishment from the seedbank (Scott and Morgan, 2012; Shea et al., 2010). Interspecies competition is governed to a large extent by local nutrient availability (Roeling et al., 2018; Schippers et al., 1999). At low nutrient availability, plants with an efficient nutrient economy outcompete fast growing species, whereas at high nutrient availability, fast growing species outperform species with an efficient nutrient economy through resource pre-emption (Hetzer et al., 2021; Poorter et al., 1990; Schippers and Kropff, 2001). The diversity and species composition of local plant communities are thus determined both by processes that operate on a local scale (e.g. environmental filtering and biotic interactions) and by processes that operate on a higher spatial scale (e.g. connectivity and processes related to habitat heterogeneity) (Leibold et al., 2017, 2004). Traditionally, these two scales have been studied separately, but the emergence of meta-community models enables us to combine both scales because these models keep track of local and spatial processes simultaneously (Chase et al., 2020). However, although such scale-explicit approaches offer great potential for generalisations, often they do not incorporate information on functional diversity.

1.3. Grime's vegetation theory

Grime (Campbell and Grime, 1992; Grime, 1979, 2001) developed the C-S-R framework of three fundamental strategies of plant species in response to nutrient availability and disturbance (see also (Moulin et al., 2021)): competitors (C) dominate at low disturbance and high nutrients, stress tolerators (S) are abundant at low disturbance and low nutrients, while ruderals (R) survive at high disturbance and high nutrients. Grime's C-S-R framework assumes a three-way trade-off between competition for resources (C), endurance of resource limitation (S) and recovery after disturbance (R). From this he derived seven strategies (C, S, R, CS, CR, SR, CSR), in which CS, CR, SR and CSR strategies have intermediate characteristics of C, S and R. Subsequently he defined 12 crossover strategies to produce a total of 19 strategies adapted to specific disturbance and nutrient regimes. Grime (2001) predicted that a greater resilience in R and C strategies on the basis of their faster rates of resource capture and growth. On the other hand a greater resistance is expected for the S strategy due to their longevity and better tolerance of harsh conditions (e.g. low nutrient availability). Moreover he predicted that both resistance and resilience will be higher in communities with a higher functional diversity. This is consistent with experimental results in grasslands in the UK (Grime et al., 2000) and the results from a global meta-analysis of the results from we use data from 39 grassland biodiversity experiments (Craven et al., 2018).

1.4. Spatial vegetation modelling & diversity

Lattice-based models are frequently used to describe vegetation dynamics. These models include tree-based and plant-based gap modelling in which seed and seedlings compete for a gap in a mature vegetation cover (Coffin and Lauenroth, 1990; Elzein et al., 2020; Kellomäki and Väisänen, 1991; Morin et al., 2020; Peters, 2002; Reynolds et al., 2001). When these models are applied to multiple species, they may generate insight into the factors affecting species dominance and diversity. For instance, Schippers et al. (2001) used a lattice-based gap model (TRANSPOP) to simulate competition and coexistence between perennials and annuals with dormant and non-dormant seeds at various

disturbance levels. They found a stable coexistence between strategies with dormant and non-dormant seeds at intermediate levels of disturbance.

1.5. Approach

Various landscape characteristics can influence local functional diversity, but their relative importance is poorly understood. We studied the effects of connectivity, spatial heterogeneity, patch size and environmental dynamics on the functional diversity of permanent grasslands of the temperate climatic zone. We used the spatially explicit meta-community model TRANSPOP (Schippers, 2001) that enables us to study long-term species sorting in response to disturbance (D) as a starting point. We extended this model with routines allowing inter-plant competition affected by nutrients (N). This enabled us to study species response to both nutrients and disturbance. We parameterised 19 herbaceous grassland species according to the C-S-R framework of Grime. First we tested strategy preferences for N and disturbance D in homogeneous landscapes and gradients of N and D. Subsequently, we studied functional diversity in patchy landscapes with various levels of heterogeneity, patch size, connectivity and environmental dynamics. We define a patch as a group of adjacent cells having the same N and D level. We used the model to evaluate the relative importance of these factors in determining the functional diversity in grasslands using the Shannon diversity index. More specifically, we tested the following hypotheses.

1.6. Hypotheses

- (1) We expect that spatial heterogeneity, in terms of nutrients and disturbance, enhances diversity through species sorting across environmental gradients (Fournier et al., 2017; Gastauer et al., 2021). As environmental diversity increases, we expect more species will survive in these grasslands (Bergholz et al., 2017; Deák et al., 2021; Guo et al., 2018).
- (2) We expect that high connectivity across the landscape (enabling high dispersal distances) enhances species diversity in grasslands by shifting the balance between colonisation and local extinction towards colonisation (Wang and Altermatt, 2019). This enhanced colonisation stimulates plant species establishment in local communities, increasing diversity (Ozinga et al., 2009).
- (3) We expect that high environmental dynamics, involving changes in the nutrient availability and disturbance regime of grassland patches over time, will cause rapid species loss, because these changes disrupt the species sorting process (Fournier et al., 2017; Leibold and Loeuille, 2015). Therefore, we expect to find the highest functional diversity where the environmental dynamics is lowest.
- (4) The distribution of patches in a grassland is also determined by its patch size which determines the grain size of the configurations. Patch size, can be considered an important driver determining diversity and resilience (Schippers et al., 2015b). With increasing patch size we expect larger and therefore more robust local populations (Verboom et al., 2010). As patch sizes become smaller interpatch distances become shorter, which induces better colonisation (Debinski et al., 2001; Wang and Altermatt, 2019), in turn enhancing species persistence. Therefore, we hypothesise that diversity is highest at intermediate patch sizes because of the combination of good survival and high recolonisation.
- (5) We expect that the effects of heterogeneity, patch size, connectivity and environmental dynamics are not independent of each other (i.e. there are significant interactions between these factors). This would imply that these effects are context dependent. Complex interaction effects might be an emergent property of metacommunities because local community dynamics and spatial processes influence each other (Leibold et al., 2004).

2. Model description

2.1. Spatial structure

The population dynamics of grassland species in the temperate climatic zone were simulated using TRANSPOP, a spatially explicit population model (Schippers et al. 2001). In this model, space is represented by a lattice in which individual cells represent sites where plants can establish, die and reproduce. The cell size is such that it can accommodate a single adult of a species or strategy, but each cell has a seedbank that can contain seeds of all the grassland species. This means that the cell size must be related to the plant size in the vegetation. We assumed an area of 10×10 cm for an average adult plant. Adult plants produce seeds that are dispersed over all or part of the lattice. We used a lattice of 300×300 cells with periodic boundaries to mimic a continuous grassland.

2.2. Demographic structure

For herbaceous vegetation, the temperate climatic zone is characterised by strong seasonal changes which determine the transitions between states (Balzarolo et al., 2019). Our model contains the following state variables: the number of seeds of each species in each cell (Z), and the adult type (A) present in each cell (The abbreviations in brackets refer to Fig. 1 scheme). At the end of each growing season, adult plants produce seeds (F_{az}) which subsequently disperse (D_p). Seeds arriving in a cell are added to the species specific seedbank of that cell. In autumn or early spring, a fraction of the seeds germinate (P_{zj}) and become seedlings (J). These seedlings compete with each other, based on seedling quantity and competitive strength, to become an adult (P_{ja}). Seedlings can only become an adult in vegetation gaps where the old adult does not survive (P_{aa}) by natural mortality or external disturbance (D_t) (sensu Grime, 1979). Disturbances were applied at random and quantified as the fraction of cells where the adult plant is removed every year. Also neighbouring adults compete with each other, depending on their affinity for nutrients (P_v). This gives the model a simple dynamic structure governed by four plant traits: the seed production per adult F_{az} and the three transition probabilities: (1) the probability that an adult will survive P_{aa} , (2) the probability that a seed will survive P_{zz} and (3) the probability that a seed will germinate and become a seedling P_{zj} (Fig. 1). As the number of adults, seedlings or seeds present at any time in any

cell might be small, all calculations involving numbers and probabilities are done in a demographically stochastic way, resulting in discrete numbers of individuals present in each stage (Durrett and Levin, 1994). In the model one cell can contain only one adult, so a mechanism must be defined to describe the process of adult recruitment P_{ja} . This is usually modelled as a lottery process (Fagerström, 1988; Lavorel and Chesson, 1995) in which the probability that a seed of a species will become adult is determined by the proportion of germinating seeds.

To simulate the adult recruitment in a cell, first, for each species the number of seedlings (J) is calculated from the number of seeds (Z) and the germination probability P_{zj} (Fig. 1):

$$J = Z \cdot P_{zj} \quad (1)$$

This stochastic calculation results in integer numbers of seedlings between 0 and Z . The probability P_{ja} that a certain species i will become an adult is proportional to the number of seedlings of this species and its competitive strength K_i :

$$P_{jai} = \frac{J_i \cdot K_i}{\sum_{x=1,n} J_x \cdot K_x} \quad (2)$$

where J_i is the number of seedlings of species i in a cell and n is the total number of species in the model (in our case $n=19$). Note that the competitive strength is a function of the nutrient level (see Table 1).

To account for vegetative competition, we also introduce direct competition between adults (Fig. 1). Adult species compete for light, nutrients and water and should have an overlap in their root zone and leaf area (Schippers and Joenje, 2002) therefore we let only the closest four neighbouring species interact. Each year we compare the competitive strength between an adult in a (central) cell K_c and the competitive strength of the adults of the four surrounding cells K_{1-4} . The probability that the adult in the central cell will be taken over by species i of the surrounding adults is:

$$P_{vi} = \frac{K_i}{4 \cdot K_c + \sum_{j=1,4} K_j} \quad (3)$$

assuming that the plant in the central cell is four times as powerful as its competitive strength, because it is already established. If surrounding species are equally competitive, the probability that the central cell is replaced is 0.5. So a strategy in the central cell with the same competitive power (K) as the surrounding cell has a 50% probability to be replaced by one of the surrounding cells and in 50% of the cases the central cell is not replaced (Eq. (3)).

2.3. Strategy parameterisation

The 19 plant strategies used in the model were permutations of Grime's C, S and R strategies (Table 1) and each strategy is represented by one 'species'. The demographic parameters are from Schippers et al. (2001). The competitors (C) and stress tolerators (S) received demographic parameters from perennials without a seedbank and the ruderals (R) received parameters from annuals with a seedbank. Important trade-offs between strategies are that ruderals produce more seeds with a long lifespan, which enables them to establish a seedbank, whereas stress tolerators and competitors produce fewer seeds, but these germinate on the first occasion. However, R adults are short-lived, whereas S and C adults are long-lived. The competitive power of the adults is derived from Grime's C-S-R classification. The C and R strategies have a competitive strength (K) of 1 at high nutrient levels and 0 at low nutrient levels whereas S has a competitive strength of 0 at high nutrients and 1 at low nutrient levels. We assumed that intermediate strategies have intermediate parameters for their demography and competitive strength. For example, strategy CS has the same demographic parameters as the C and S strategists, but their maximum competitive strength is reached at the mean nutrient values of C and S, which is 0.5. Strategy CR has the mean demographic parameters of the C

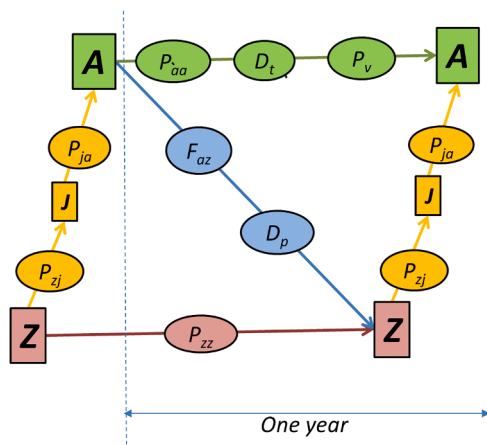


Fig. 1. Model scheme with state variables, transitions and processes over time in a cell: A = adult type, Z = number of seeds, J = number of seedlings, P_{aa} = adult survival probability, D_t = disturbance, P_v = probability that an adult is replaced by vegetative competition, P_{zj} = germination probability, P_{ja} = adult recruitment, F_{az} = seed production, D_p = dispersal, P_{zz} = seed survival probability, Colours: Green = adult pathway, Purple = seed pathway, Orange = adult recruitment pathway, Blue = seed production pathway.

Table 1

Parameterisation of Grime (1979) strategies used in the model: C (competitor), S (stress tolerator) and R (ruderal) population dynamical parameters according to Schippers et al. (2001), competitive power (*K*) according to expected dominance in relation to Nutrients (*N*) level. Note that combined strategies are parameterised as an average of pure strategy parameters. Scores are used to characterize a vegetation in terms of C, S and R components.

| Number | Grime strategies | Adult survival | Seed survival | Seed germination | Seed production at low N | Seed production at high N | maximum Kat N level | C score | S score | R score |
|--------|------------------|----------------|---------------|------------------|--------------------------|---------------------------|---------------------|---------|---------|---------|
| 1 | C | 0.800 | 0.000 | 0.900 | 0 | 1000 | 1 | 1.00 | 0.00 | 0.00 |
| 2 | S | 0.800 | 0.000 | 0.900 | 0 | 1000 | 0 | 0.00 | 1.00 | 0.00 |
| 3 | R | 0.000 | 0.800 | 0.100 | 0 | 3000 | 1 | 0.00 | 0.00 | 1.00 |
| 4 | CS | 0.800 | 0.000 | 0.900 | 0 | 1000 | 0.50 | 0.50 | 0.50 | 0.00 |
| 5 | CR | 0.400 | 0.400 | 0.500 | 0 | 2000 | 1.00 | 0.50 | 0.00 | 0.50 |
| 6 | SR | 0.400 | 0.400 | 0.500 | 0 | 2000 | 0.50 | 0.00 | 0.50 | 0.50 |
| 7 | CSR | 0.533 | 0.267 | 0.633 | 0 | 1667 | 0.67 | 0.33 | 0.33 | 0.33 |
| 8 | C/CR | 0.600 | 0.200 | 0.700 | 0 | 1500 | 1.00 | 0.75 | 0.00 | 0.25 |
| 9 | C/CSR | 0.667 | 0.133 | 0.767 | 0 | 1333 | 0.83 | 0.67 | 0.17 | 0.17 |
| 10 | C/CS | 0.800 | 0.000 | 0.900 | 0 | 1000 | 0.75 | 0.75 | 0.25 | 0.00 |
| 11 | CR/CSR | 0.467 | 0.333 | 0.567 | 0 | 1833 | 0.83 | 0.42 | 0.17 | 0.42 |
| 12 | R/CR | 0.200 | 0.600 | 0.300 | 0 | 2500 | 1.00 | 0.25 | 0.00 | 0.75 |
| 13 | R/CSR | 0.267 | 0.533 | 0.367 | 0 | 2333 | 0.83 | 0.17 | 0.17 | 0.67 |
| 14 | R/SR | 0.200 | 0.600 | 0.300 | 0 | 2500 | 0.75 | 0.00 | 0.25 | 0.75 |
| 15 | S/CSR | 0.667 | 0.133 | 0.767 | 0 | 1333 | 0.33 | 0.17 | 0.67 | 0.17 |
| 16 | S/CS | 0.800 | 0.000 | 0.900 | 0 | 1000 | 0.25 | 0.25 | 0.75 | 0.00 |
| 17 | S/SR | 0.600 | 0.200 | 0.700 | 0 | 1500 | 0.25 | 0.00 | 0.75 | 0.25 |
| 18 | CS/CSR | 0.667 | 0.133 | 0.767 | 0 | 1333 | 0.58 | 0.42 | 0.42 | 0.17 |
| 19 | SR/CSR | 0.467 | 0.333 | 0.567 | 0 | 1833 | 0.58 | 0.17 | 0.42 | 0.42 |

and R strategies, but their maximum competitive strength is reached at the same nutrient level as C and R (Table 1).

2.4. Connectivity

We assumed homogeneous dispersal within a certain distance, expressed as the number of cells. At a connectivity of 1, the mother plants dispersed their seeds to a block of 3 × 3 cells; at a connectivity of 100, the mother plants dispersed their seeds to a block of 201 × 201 cells around the central mother cell. Since dispersal is very variable within a strategy (Grime, 2001), we made connectivity a site property, the accessibility of the patch being determined by the frequency and effectiveness of dispersal vectors, assuming equal dispersal in all strategies.

3. Simulations and results

The model was initialised with the 19 strategies randomly distributed over an area of 300 × 300 cells, in which each cell had a probability of 1/19 of being occupied by one adult of each of the 19 strategies. To obtain near equilibrium values, we evaluated the effects of heterogeneity, patch size, connectivity and environmental dynamics on the functional diversity after 500 years.

3.1. Simulations in homogeneous grasslands

To compare the simulations with Grime’s strategy preferences, we performed a series of simulations in a homogeneous grassland of 300 × 300 cells with periodic boundaries (column *x* = 1 is connected to column *x* = 300, row *y* = 1 is connected to row *y* = 300). We performed 2100 simulations at 20 nutrient levels between 0.05 and 1.0 and 21 disturbance levels between 0 and 1.0 at five connectivity levels: 1, 3, 10, 30 and 100 (all strategies had equal connectivity). We started all simulations with the 19 strategies equally randomly distributed. To obtain the simulated strategy preference in terms of nutrients and disturbance we calculated the weighted average of nutrients and disturbance of each strategy in the final coverage. We performed linear regression between the Nutrients (*N*) and Disturbance (*D*) preferences of Grime and the simulated preferences.

The simulations show that connectivity had no effect on the competitive outcome. The results show that 18 of the 19 strategies were able to dominate at various *N* and *D* values in the simulations (Fig. 2).

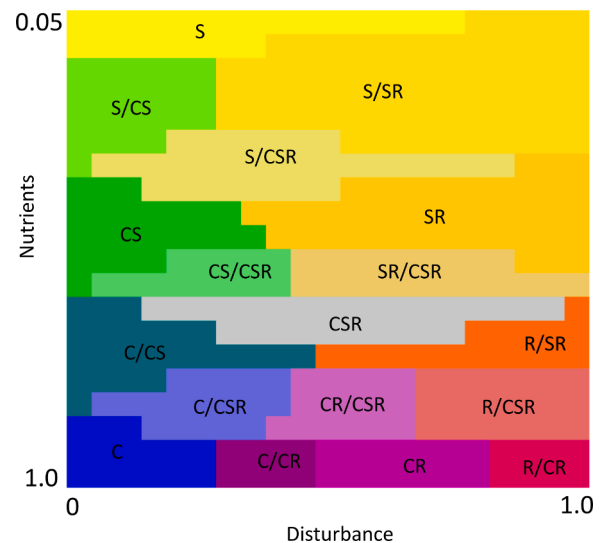


Fig. 2. Simulated strategy dominance of C-S-R strategies (Grime, 1979) in homogeneous grasslands at various levels of nutrients and disturbance. The colour of each grid represents the most abundant strategy present in a simulation after 500 years.

Only the R strategy did not survive the full 500 years. It survived for about 100 years at high nutrient and disturbance levels, but was then outcompeted by the R/CR strategy. Linear regression shows that the *N* and *D* preference in the model was significantly related to the preference for *D* (Coef.=1.003, $R^2=0.888$, $P<1.0E-7$) and *N* (Coef.=1.025, $R^2=0.998$, $P<1.0E-17$) coordinates as used in Grime’s C-S-R classification (Grime, 1979). The species diversity of the homogeneous simulations after 500 years varied between 1–4 strategies and was on average 1.4 strategy per simulation.

3.2. Simulations in gradients

We study competition and functional diversity in spatially explicit gradients of Nutrients (*N*) and Disturbance (*D*) with an orthogonal configuration: *N* gradient perpendicular to the *D* gradient. Because gradients are not always fully independent, e.g. large disturbances

induce litter and the decomposition of litter generate plant-available nutrients (Schippers, 2002), we also study the effects of a N gradient positively correlated with the D gradient and a N gradient negatively correlated with the D gradient. Both gradients run linearly from 0 to 1 in 300 equal steps. As in the preceding simulations, we also varied the connectivity (1, 3, 10, 30 and 100 cells). We applied linear regression to evaluate the effects of connectivity and gradient orientation on strategy diversity.

The results show that the lattice with perpendicular gradients had a significantly higher diversity of strategies than the lattices with the correlated gradients ($P < 2E-6$). At low connectivity (e.g. 3) the N and D preferences of the various strategies resemble those of the homogeneous cases (compare Figs. 2 and 3a), from which we conclude that strategies are able to ‘find’ and stay in their optimal N and D environments. Connectivity had a strong negative effect on diversity in the tested gradients (Fig. 3, $P < 1E-4$), probably because seeds from elsewhere invade suboptimal areas and may outcompete strategies in their optimal areas because of the high seed rain (Fig. 3).

3.3. Simulations in patchy grasslands

To investigate the role of spatial heterogeneity, environmental dynamics, patch size and connectivity on the functional diversity we introduce patches being a squared group of adjacent cells with the same values for nutrients (N) and disturbance (D). So in a single configuration the whole area is covered with patches of the same size. In different configurations these patches may have different sizes, longevity (environmental dynamics), connectivity and spatial variation in N and D values (heterogeneity). Spatial heterogeneity was applied as a patch of equally parameterised cells for N and D with a certain dimension (patch size), expressed as allowed random deviation from $N = 0.5$ and $D = 0.5$. For example, when the patch size was 10, the lattice of 300×300 cells was subdivided into 30×30 blocks (patches) of 10×10 cells and each patch received randomly drawn values for nutrient availability and disturbance fraction per year. At high heterogeneity (e.g. 0.5) these values were randomly drawn from the range 0 to 1; at low heterogeneity (e.g. 0.125) these values were drawn from the range 0.375 to 0.625.

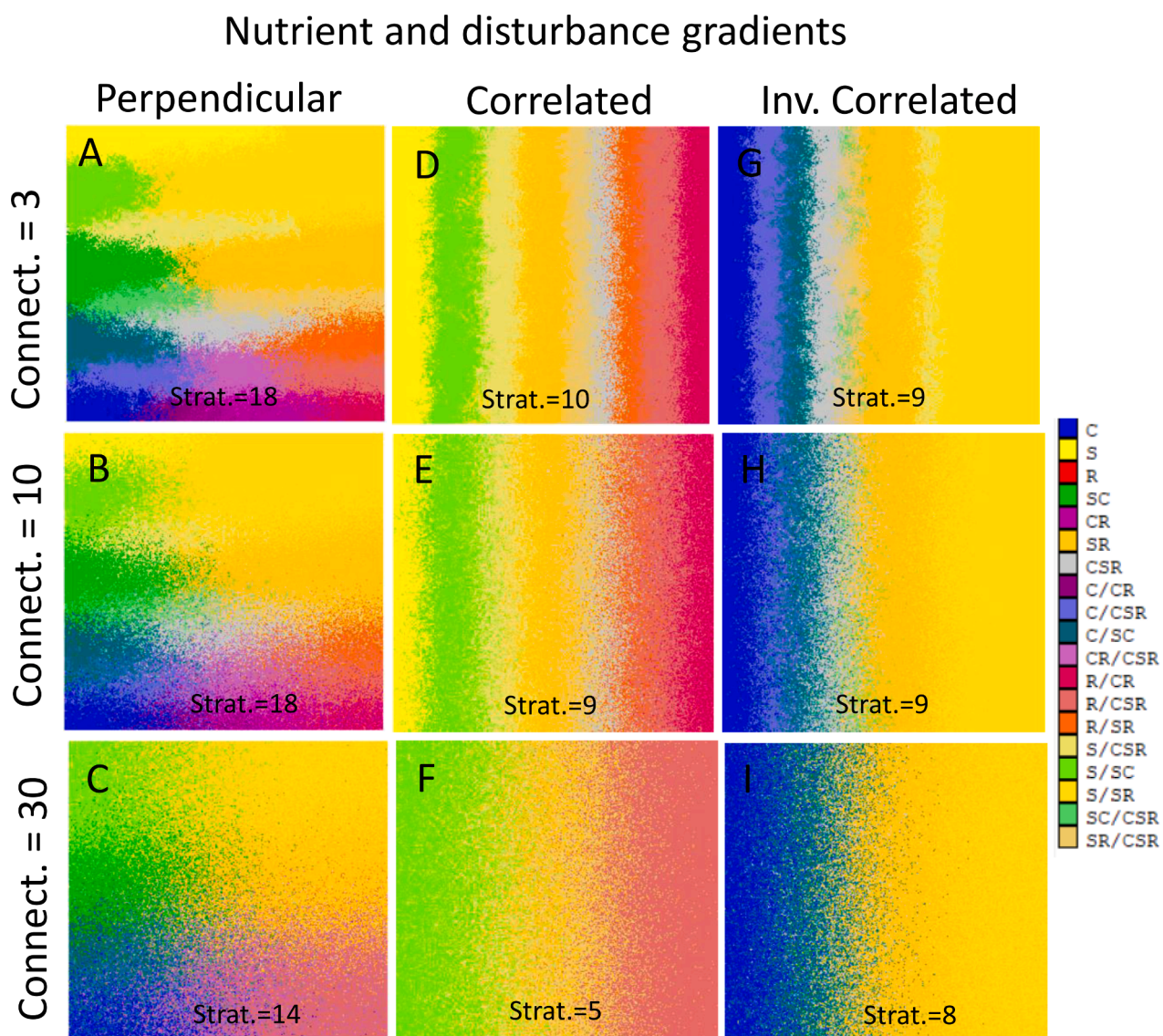


Fig. 3. Simulated effects of connectivity and gradient configuration of nutrient availability (N) and disturbance (D) on strategy survival (Strat.) and distribution of Grime's C-S-R strategies. Each graph is a spatially explicit end point of a simulation after 500 years that started with equally presence of all (19) strategies. Each dot represents a plant of a certain strategy. Gradients were applied with respect to Nutrient availability and Disturbance: first column, (A-C), D and N gradient perpendicular with high N and D in the lower right corner, second column, (D-F), N and D are correlated with high N and D values at the right side of the graph, third column, (G-I), N and D are inverse correlated, N is low, and D is high at the right side of the graphs.

Environmental dynamics in this framework was applied as the frequency of recalculation of N and D in a patch. If environmental dynamics is 1, the model recalculates all grassland patches (with new N and D values) with the same heterogeneity and size every year without changing the strategy and seed presence. If environmental dynamics is 0.1, the model recalculates new grassland patches in terms of N and D every 10 years, which means that the community has 10 years to adapt to the new configuration. We ran the model for various heterogeneity levels (0, 0.125, 0.25, 0.375, 0.5), patch size (1, 3, 10, 30 cells, being 1×1 , 3×3 , 10×10 , 30×30 cells), environmental dynamics (0, 0.01, 0.033, 0.1, 0.33, 1.0 year^{-1}) and connectivity (1, 3, 10, 30, 100 cells) combinations, yielding 500 simulations in total. To filter out the strategies that belong to a certain condition we use standardized values of the Shannon index of the functional diversity of the adult plants after 500 years to perform a linear regression. The Shannon index was chosen because it keeps track of strategy presence and abundance.

The results show that heterogeneity in terms of N and D was the most important factor determining strategy diversity, followed by environmental dynamics, connectivity and patch size (Table 2, Fig. 4). Grasslands with high heterogeneity and patch size had a high functional diversity (Fig. 4), while high values for dynamics and connectivity had, in general, a negative impact on the functional diversity. All interactions were significant, meaning that diversity responses change when predictor values changed. For example, at higher patch sizes (10, 30) and intermediate dynamics (0.1, 0.033) some connectivity even helped to increase diversity (Fig. 4. G, H, K, L) despite the generally negative effect of connectivity on diversity. Fig. 5 illustrates the effect of connectivity and grassland diversity on the final distribution of strategies. It shows how at low connectivity the strategies clustered in compact monocultures at roughly the patch size, whereas at higher connectivity the grassland heterogeneity block pattern was lost and accidental clusters of similar N and D determined local strategy dominance.

4. Discussion

4.1. Approach

We took a novel approach by using herbaceous plant strategies (based on Grime's C-S-R framework) in a metacommunity model allowing us to study local and spatial processes simultaneously (Leibold et al., 2004). The parameterised model was able to predict the strategy preferences for disturbance and nutrients published by Grime, 1979 (Grime, 1979) very well (Fig. 2, 3A), which shows the validity of our approach. Simulations in landscapes with N and D gradients showed that strategy survival is sorted along the N and D gradients, producing high vegetation diversity when N and D gradients are perpendicular to each other. This patchy survival pattern is enforced by relatively low rates of dispersal, which were apparently still sufficient to enable different strategies to sort for optimal N and D levels (Fig. 3A, B, C). We focus on the effects of various factors on strategy diversity after a long time period (500 years) to obtain near equilibrium values. The advantage of such an approach is that we allow the sorting process to select strategies

that survive over a long time but we miss the dynamics. A comparison of temporal patterns might reveal additional insights, for example on the succession and transient dynamics of strategies, but this was beyond the scope of this paper.

4.2. Main results

Simulations in patchy landscapes show that environmental heterogeneity in terms of N and D was the most important factor determining strategy survival, followed by environmental dynamics, connectivity and patch size (Table 2, Fig. 5). High grassland heterogeneity and patch size led to high functional diversity (Fig. 5), while high values for environmental dynamics and connectivity had, in general, a negative impact on the functional diversity of surviving strategies. All first order interactions between the predictor values were significant, indicating a change in response at different predictor levels.

4.3. Hypotheses

From our first hypothesis, we expect that spatial heterogeneity enhances functional diversity, that as a grassland becomes more diverse in terms of nutrients (N) and disturbance (D), the number of functional strategies that will be able to survive will increase. This is confirmed by our results. At high spatial heterogeneity the species sorting process governs strategy survival (Leibold et al., 2017): strategies survive in the patches where the environmental properties best fit their preferences for N and D.

Local heterogeneity is regarded to be an important factor determining diversity in grasslands (Hovick et al., 2015; Krauss et al., 2004; Scott and Baer, 2019). That heterogeneity is the most important factor determining functional diversity can be understood from the fact that spatial heterogeneity determines spatially explicit habitat variation in terms of nutrients and disturbance, a first requirement for the facilitation of strategies. For example, the diversity in the homogeneous simulation had on average 1.4 strategy per simulation (range 1 to 4) whereas the diversity of high heterogeneity can be 18 (Fig. 5). Other factors can only be of importance if they affect high diversity cases at high heterogeneity levels because they cannot generate diversity solely.

From our second hypothesis, we expect that high connectivity across the landscape (enabling high dispersal distances) enhances functional diversity in grasslands by shifting the balance between colonisation and local extinction in favour of the former. Our results, however, show the opposite: higher connectivity generally reduces diversity. This can be explained by the fact that increased connectivity increases not only the colonisation rate, but also the degree of competitive interactions between residence and colonising strategies, leading to a higher rate of competitive exclusion. At high connectivity, inducing a large seed rain, colonising strategies may replace residential strategies even when the latter are superior competitors locally. Therefore, colonising strategies can overcome local competitive exclusion in communities where they are poor competitors through immigration from communities where they are good competitors. This is called 'the mass effect paradigm' (Leibold et al., 2004). At lower connectivity, however, competition is more local, residential strategies are better at monopolising the resources in residential patches and the species sorting process predominates. The occurrence of strategies in each patch is not only determined by habitat suitability, but also by the accessibility of the patch within the landscape. For highly fragmented landscapes it has been shown that the degree to which strategies occur in suitable habitat patches was increased by a greater capacity for long-distance dispersal, greater adult longevity and the capacity to build a persistent seedbank (Ozinga et al., 2005; Van Der Veken et al., 2007). This indicates that the predictability of strategy composition from environmental conditions (due to species sorting) is reduced by both dispersal limitation and mass effects (Heino et al., 2015). For dispersal to be effective, a given strategy should still be present in other patches across the landscape, which act

Table 2
Standardised regression coefficients predicting Shannon plant strategy diversity

| Predictor | Coefficient | Pvalue |
|--|-------------|----------|
| Nutrient and disturbance heterogeneity (HET) | 0.232 | 5.93E-43 |
| Patch dynamics (DYN) | -0.167 | 1.06E-24 |
| Connectivity (CON) | -0.138 | 8.63E-18 |
| Patch size (PS) | 0.124 | 9.55E-15 |
| HET*DYN | -0.113 | 1.21E-18 |
| HET*CON | -0.104 | 5.83E-16 |
| DYN*CON | 0.104 | 5.87E-16 |
| PS*DYN | -0.094 | 1.86E-13 |
| HET*PS | 0.089 | 2.61E-12 |
| PS*CON | -0.060 | 2.25E-06 |

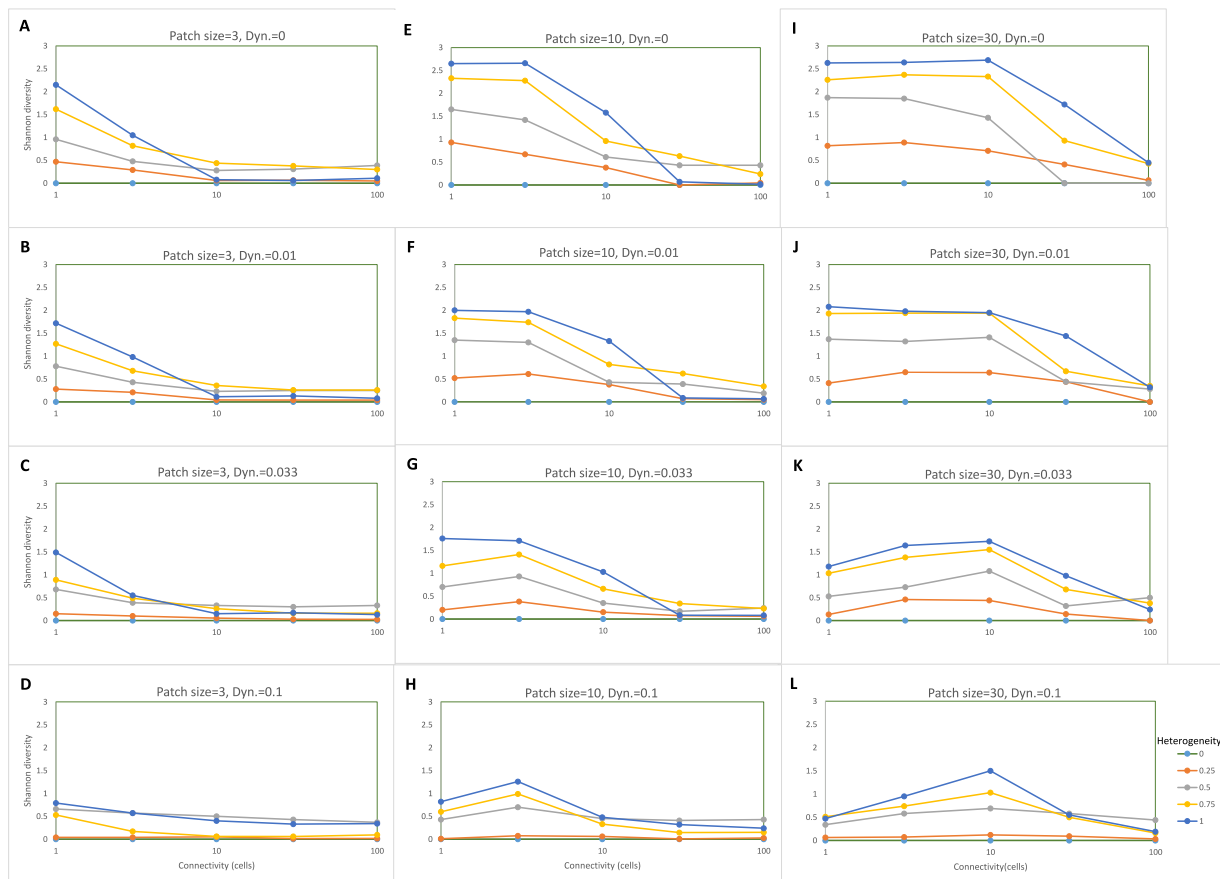


Fig. 4. Simulated effects of connectivity (x-axis), patch size (graph column), environmental dynamics (graph row) and heterogeneity (different lines) on the Shannon plant strategy diversity (y-axis).

like an external memory (Ogle et al., 2015). This is also dependent on other landscape characteristics, such as the availability of similar patches within the landscape. In addition, the effective dispersal of seeds depends on the availability and efficiency of dispersal vectors such as wind, water and animals. This aspect is not included in the model, but a reduced availability of dispersal vectors has been shown to be an important driver of species losses (Ozinga et al., 2009). When dispersal is limited, in highly fragmented landscapes we expect connectivity to have a positive effect on diversity. At intermediate connectivity, strategies that match the local environmental conditions survive and we expect the highest diversity resulting from the species sorting process when there is high spatial heterogeneity. But in landscapes with a high connectivity, where seed loads from elsewhere might be high, we expect a negative effect from connectivity on local diversity due to mass effects.

From our third hypothesis we expect that high environmental dynamics, the potential of a patch to change in terms of nutrient availability and disturbance, will cause rapid species loss because sorting strategies that select their matching patch have to start all over again after a change in conditions. This will shift the dynamic balance between rates of colonisation and local extinction, leading to a higher risk of regional extinction. This is consistent with metapopulation theory (Hanski, 1998). Our results confirm this: diversity was highest at lowest environmental dynamics. Environmental dynamics strongly disrupts the species sorting process, leading to low diversity values. Strategies should, after a reattribution event, try to find their optimal habitat again to secure long-term survival. This might be risky and lead to species extinction. We would expect ruderal strategies to be able to cope with the environmental dynamics because of their larger dispersal potential (more seeds) and their longer survival in the seedbank. In our simulations, at high environmental dynamics, the stress tolerating ruderal (SR)

is the dominant strategy, with moderately ruderal properties and maximum competitive strength at intermediate nutrient levels. Apparently, this intermediate strategy is superior here because its properties are adapted to the average N and D of dynamic grasslands, allowing it to outcompete other strategies.

According to our fourth hypothesis we expect grasslands with intermediate patch size to have the highest diversity because they combine high colonisation with a relatively low extinction rate. Our simulations show, however, higher diversity levels in coarse-grained landscapes, especially at low connectivity levels (Fig. 4, Table 2). When connectivity levels in the simulations were high (100), diversity was low. The good performance of a coarser grained landscape in combination with low connectivity can be explained by the fact that limited connectivity in combination with high patch sizes is responsible for seed dispersal within a patch already dominated by a single strategy. This consolidates strategy persistence in patches, but reduces interspecific competition that leads to strategy loss.

From our fifth hypotheses we expect that the effects of heterogeneity, patch size, connectivity and environmental dynamics are not independent of each other (i.e. there are significant interactions between these factors). This would imply that these effects are context dependant. Complex interactions might be an emergent property of meta-communities because local community dynamics and spatial processes affect each other (Leibold et al., 2004).

Patch heterogeneity showed strong negative interactions with both environmental dynamics and connectivity. This was caused by the fact that high spatial heterogeneity causes high strategy diversity, allowing a stronger negative response by environmental dynamics and connectivity. In contrast, patch size showed a positive interaction with heterogeneity, indicating a stronger positive response of patch size at higher

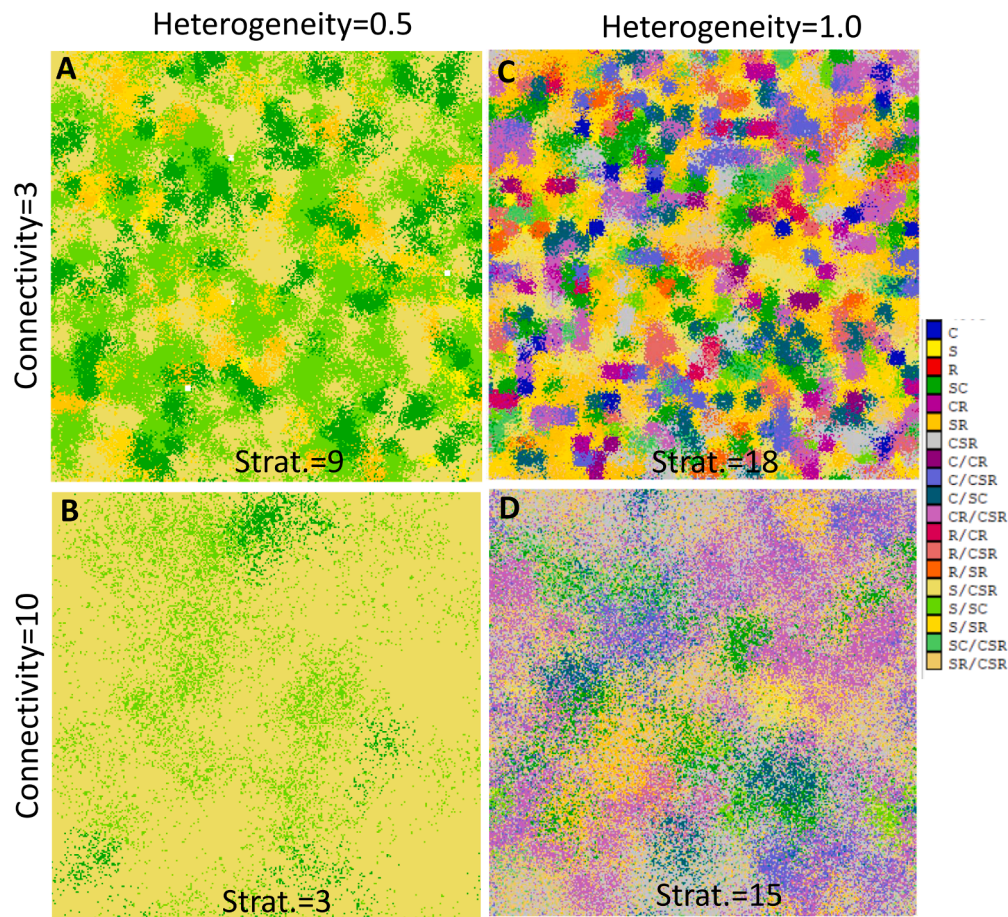


Fig. 5. Effects of connectivity and heterogeneity on the species spatial distribution and diversity of Grime's C-S-R strategies (Strat.) in patchy landscapes with a patch size of 10×10 cells and without any environmental dynamics.

heterogeneity levels.

Interaction between connectivity and environmental dynamics was also strong at intermediate environmental dynamics levels and at larger patch sizes. Simulations even show that some connectivity causes higher diversity, indicating that connectivity at a certain level helps strategies to find suitable patches in changing grassland (Fig. 4. G, H, K, L). At higher connectivity levels, however, diversity is reduced by increased interspecific competition induced by species rich seedbanks. Here mass-produced offspring of accidental dominating strategies outperform other strategies in their optimal habitat (Bergholz et al., 2017; Schippers et al., 2015a). Therefore, we expect higher diversity at intermediate connectivity because dispersal is high enough to enable species to find suitable patches, but is low enough to prevent dominance across the landscape by a few species due to mass effects. Here the balanced presence of multiple species in the seedbank allows species to sort for their optimal habitat (Heino et al., 2015; Wirth et al., 2021).

Patch size negatively interacted with dynamics and connectivity, which indicates that at decreasing dynamics and connectivity species richness was more strongly affected by higher patch sizes. The large number of significant interactions suggests that the optimal spatial design of landscapes with respect to functional diversity is context dependent. For nature policy this implies that effectiveness of measures to increase diversity is affected by codetermining factors.

5. Conclusions

We found that strategy survival is affected by the orientation of the two gradients. The perpendicular orientation creates more diversity in Nutrients (N) and Disturbance (D) combinations, which provides more

room for the survival of strategies than the two configurations in which the gradients are correlated (run in the same direction). We expect that gradients at acute angles but significantly larger than zero will produce similar diversity in N and D and will therefore generate the same strategy diversity as the perpendicular orientation. Clearly, there are also other environmental gradients to consider, such as moisture, elevation, salinity and light (Jiang et al., 2012; Kadmon, 1995; Schmidt et al., 1996), that can also contribute to environmental and species diversity. This means that from the species conservation context, we should protect or create landscapes with multiple gradients because they are an important source of biodiversity.

The results of the patchy simulations show that grassland heterogeneity in terms of N and D was the most important factor determining strategy survival and diversity, followed by environmental dynamics, connectivity and patch size. We therefore expect that high grassland heterogeneity and patch size will lead to high functional diversity in the field. In contrast, high values for environmental dynamics and connectivity will, in general, negatively affect the functional diversity in the field. Because all predictor interactions were significant, we expect that diversity responds differently at different predictor levels. For nature policy this implies that effectiveness of measures to increase diversity is affected by codetermining factors.

The functional diversity of local grassland communities is considered to be an important ecosystem property determining its resistance and resilience (Fischer et al., 2006; Holling, 1973; Isbell et al., 2015). Ecosystems with a high diversity in functional groups are better able to respond to temporary change because there is a higher probability that there are species present in the local species pool that can cope with a certain disturbance or environmental change (Folke et al., 2004). In

diverse communities, sudden but temporary changes in nutrient availability and disturbance regime will select for species that can cope with these new environmental conditions at the cost of less appropriate strategies. If this competitive exclusion is slow, indicated by a large diversity at the end of the simulations, diversity will not decline quickly and the previous species composition can be restored because most species are still present in remnant populations. If competitive exclusion is fast, rapid species loss occurs and the vegetation cannot return to the previous state. High connectivity and environmental dynamics, low patch size and low heterogeneity intensifies interspecies competition and causes rapid species loss, which strongly reduces resistance and resilience. This shows that high species diversity in itself does not protect against diversity loss, but that factors contributing to the maintenance of high diversity reduce the risk of species extinction and foster resistance and resilience.

CRedit authorship contribution statement

Peter Schippers: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Wim A. Ozinga:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing. **Rogier Pouwels:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Published data were used for parameterization of the model

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References

- Balzarolo, M., Peñuelas, J., Veroustraete, F., 2019. Influence of landscape heterogeneity and spatial resolution in multi-temporal in situ and MODIS NDVI data proxies for seasonal GPP dynamics. *Remote Sens.* 11.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., Nystrom, M., 2003. Reserves, resilience and dynamic landscapes. *Ambio* 32, 389–396.
- Bergholz, K., May, F., Giladi, I., Ristow, M., Ziv, Y., Jeltsch, F., 2017. Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspect. Plant Ecol. Evol. Syst.* 24, 138–146.
- Campbell, B.D., Grime, J.P., 1992. An experimental test of plant strategy theory. *Ecology* 73, 15–29.
- Chase, J.M., Jeliakov, A., Ladouceur, E., Viana, D.S., 2020. Biodiversity Conservation Through the Lens of Metacommunity Ecology. *Annals of the New York Academy of Sciences*, pp. 86–104.
- Coffin, D.P., Lauenroth, W.K., 1990. A gap dynamics simulation model of succession in a semiarid grassland. *Ecol. Modell.* 49, 229–266.
- Craven, D., Eisenhauer, N., Pearse, W.D., Hautier, Y., Isbell, F., Roscher, C., Bahn, M., Beierkuhnlein, C., Bönisch, G., Buchmann, N., Byun, C., Catford, J.A., Cerabolini, B. E.L., Cornelissen, J.H.C., Craine, J.M., De Luca, E., Ebeling, A., Griffin, J.N., Hector, A., Hines, J., Jentsch, A., Kattge, J., Kreyling, J., Lanta, V., Lemoine, N., Meyer, S.T., Minden, V., Onipchenko, V., Polley, H.W., Reich, P.B., van Ruijven, J.,

- Schamp, B., Smith, M.D., Soudzilovskaia, N.A., Tilman, D., Weigelt, A., Wilsey, B., Manning, P., 2018. Multiple facets of biodiversity drive the diversity–stability relationship. *Nat. Ecol. Evol.* 2, 1579–1587.
- Damschen, E.I., Brudvig, L.A., Burt, M.A., Fletcher Jr, R.J., Haddad, N.M., Levey, D.J., Orrock, J.L., Resasco, J., Tewksbury, J.J., 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. *Science* 365, 1478–1480.
- Deák, B., Kovács, B., Rádai, Z., Apostolova, I., Kelemen, A., Kiss, R., Lukács, K., Palpurina, S., Sopotlieva, D., Báthori, F., Valkó, O., 2021. Linking environmental heterogeneity and plant diversity: the ecological role of small natural features in homogeneous landscapes. *Sci. Total Environ.* 763.
- Debinski, D.M., Ray, C., Saveraid, E.H., 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biol. Conserv.* 98, 179–190.
- Durrett, R., Levin, S.A., 1994. Stochastic spatial models: a user's guide to ecological applications. *Philosoph. Trans. R. Soc. B: Biol. Sci.* 343, 329–350.
- Elzein, T., Larocque, G.R., Sirois, L., Arseneault, D., 2020. Comparing the predictions of gap model with vegetation and disturbance data in south-eastern Canadian mixed forests. *For. Ecol. Manage.* 455.
- Fagerström, T., 1988. Lotteries in communities of sessile organisms. *Trends Ecol. Evol.* 3, 303–306.
- Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. *Front. Ecol. Environ.* 4, 80–86.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C. S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Ann. Rev. Ecol. Evol. Syst.* 35, 557–581.
- Fournier, B., Mouquet, N., Leibold, M.A., Gravel, D., 2017. An integrative framework of coexistence mechanisms in competitive metacommunities. *Ecography* 40, 630–641.
- Gastauer, M., Mitre, S.K., Carvalho, C.S., Trevelin, L.C., Sarmiento, P.S.M., Meira Neto, J. A.A., Caldeira, C.F., Ramos, S.J., Jaffé, R., 2021. Landscape heterogeneity and habitat amount drive plant diversity in Amazonian canga ecosystems. *Landscape Ecol.* 36, 393–406.
- Grime, J.P., 1979. *Plant Strategies & Vegetation Processes*. John Wiley & Sons, Chichester, p. 222.
- Grime, J.P., 2001. *Plant strategies, Vegetation processes, and Ecosystem Properties*. Wiley, Chichester.
- Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D., Kieley, J.P., 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289, 762–765.
- Guo, T., Weise, H., Fiedler, S., Lohmann, D., Tietjen, B., 2018. The role of landscape heterogeneity in regulating plant functional diversity under different precipitation and grazing regimes in semi-arid savannas. *Ecol. Modell.* 379, 1–9.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Heino, J., Melo, A.S., Siqueira, T., Soinenen, J., Valanko, S., Bini, L.M., 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.* 60, 845–869.
- Hetzer, J., Huth, A., Taubert, F., 2021. The importance of plant trait variability in grasslands: a modelling study. *Ecol. Modell.* 453.
- Holling, C.S., 1973. Resilience and the stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hovick, T.J., Elmore, R.D., Fuhlendorf, S.D., Engle, D.M., Hamilton, R.G., 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecol. Appl.* 25, 662–672.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., De Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., Van Der Putten, W.H., Van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577.
- Jiang, J., Gao, D.Z., DeAngelis, D.L., 2012. Towards a theory of ecotone resilience: coastal vegetation on a salinity gradient. *Theor. Popul. Biol.* 82, 29–37.
- Kadmon, R., 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *J. Ecol.* 83, 253–262.
- Kellomäki, S., Väisänen, H., 1991. Application of a gap model for the simulation of forest ground vegetation in boreal conditions. *For. Ecol. Manage.* 42, 35–47.
- Krauss, J., Klein, A.M., Steffan-Dewenter, I., Tschamtko, T., 2004. Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodivers. Conserv.* 13, 1427–1439.
- Lavorel, S., Chesson, P., 1995. How species with different regeneration niches coexist in patchy habitats with local disturbances. *Oikos* 74, 103–114.
- Leibold, M.A., Chase, J.M., Ernest, S.K.M., 2017. Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology* 98, 909–919.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* 7, 601–613.
- Leibold, M.A., Loeuille, N., 2015. Species sorting and patch dynamics in harlequin metacommunities affect the relative importance of environment and space. *Ecology* 96, 3227–3233.
- Loreau, M., Naem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology:

- biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294, 804–808.
- Morin, X., Damestoy, T., Toigo, M., Castagneyrol, B., Jactel, H., de Coligny, F., Meredieu, C., 2020. Using forest gap models and experimental data to explore long-term effects of tree diversity on the productivity of mixed planted forests. *Ann. For. Sci.* 77.
- Moulin, T., Perasso, A., Calanca, P., Gillet, F., 2021. DynaGram: a process-based model to simulate multi-species plant community dynamics in managed grasslands. *Ecol. Modell.* 439.
- Muller, J., Heinze, J., Joshi, J., Boch, S., Klaus, V.H., Fischer, M., Prati, D., 2014. Influence of experimental soil disturbances on the diversity of plants in agricultural grasslands. *J. Plant Ecol.* 7, 509–517.
- Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik, M.E., Tissue, D.T., 2015. Quantifying ecological memory in plant and ecosystem processes. *Ecol. Lett.* 18, 221–235.
- Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P., Van Groenendael, J.M., 2009. Dispersal failure contributes to plant losses in NW Europe. *Ecol. Lett.* 12, 66–74.
- Ozinga, W.A., Schaminée, J.H.J., Bekker, R.M., Bonn, S., Poschlod, P., Tackenberg, O., Bakker, J., Van Groenendael, J.M., 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108, 555–561.
- Peters, D.P.C., 2002. Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. *Ecol. Modell.* 152, 5–32.
- Peterson, G.D., 2002. Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5, 329–338.
- Poorter, H., Remkes, C., Lambers, H., 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.* 94, 621–627.
- Reynolds, J.F., Bugmann, H., Pitelka, L.F., 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. *Climatic Change* 51, 541–557.
- Roeling, I.S., Ozinga, W.A., van Dijk, J., Eppinga, M.B., Wassen, M.J., 2018. Plant species occurrence patterns in Eurasian grasslands reflect adaptation to nutrient ratios. *Oecologia* 186, 1055–1067.
- Schippers, P., Groenendael van, J., Vleeshouwers, L.M., Hunt, R., 2001. Herbaceous plant strategies in disturbed habitats. *Oikos* 95, 198–211.
- Schippers, P., Hemerik, L., Baveco, J.M., Verboom, J., 2015a. Rapid diversity loss of competing animal species in well-connected landscapes. *PLoS One* 10.
- Schippers, P., Joenje, W., 2002. Modelling the effect of fertiliser, mowing, disturbance and width on the biodiversity of plant communities of field boundaries. *Agric. Ecosyst. Environ.* 93, 351–365.
- Schippers, P., Kropff, M.J., 2001. Competition for light and nitrogen among grassland species: a simulation analysis. *Funct. Ecol.* 15, 155–164.
- Schippers, P., Snoeijs, I., Kropff, M.J., 1999. Competition under high and low nutrient levels among three grassland species occupying different positions in a successional sequence. *New Phytol.* 143, 547–559.
- Schippers, P., van der Heide, C.M., Koelewijn, H.P., Schouten, M.A.H., Smulders, R., Cobben, M.M.P., Sterk, M., Vos, C.C., Verboom, J., 2015b. Landscape diversity enhances the resilience of populations, ecosystems and local economy in rural areas. *Landsc. Ecol.* 30, 193–202.
- Schmidt, W., Weitemeier, M., Holzapfel, C., 1996. Vegetation dynamics in canopy gaps of a beech forest on limestone - the influence of the light gradient on species richness. *Verh. - Ges. Ökologie* 25, 253–260.
- Schweiger, A.H., Boulangéat, I., Conradi, T., Davis, M., Svenning, J.C., 2019. The importance of ecological memory for trophic rewilding as an ecosystem restoration approach. *Biol. Rev.* 94, 1–15.
- Scott, A.J., Morgan, J.W., 2012. Resilience, persistence and relationship to standing vegetation in soil seed banks of semi-arid Australian old fields. *Appl. Veg. Sci.* 15, 48–61.
- Scott, D.A., Baer, S.G., 2019. Diversity patterns from sequentially restored grasslands support the 'environmental heterogeneity hypothesis. *Oikos* 128, 1116–1122.
- Shea, K., Jongejans, E., Skarpaas, O., Kelly, D., Sheppard, A.W., 2010. Optimal management strategies to control local population growth or population spread may not be the same. *Ecol. Appl.* 20, 1148–1161.
- Sterk, M., Gort, G., De Lange, H., Ozinga, W., Sanders, M., Van Looy, K., Van Teeffelen, A., 2016. Plant trait composition as an indicator for the ecological memory of rehabilitated floodplains. *Basic Appl. Ecol.* 17, 479–488.
- Van Der Veken, S., Bellemare, J., Verheyen, K., Hermy, M., 2007. Life-history traits are correlated with geographical distribution patterns of western European forest herb species. *J. Biogeogr.* 34, 1723–1735.
- Verboom, J., Schippers, P., Cormont, A., Sterk, M., Vos, C.C., Opdam, P.F.M., 2010. Population dynamics under increasing environmental variability: implications of climate change for ecological network design criteria. *Landsc. Ecol.* 25, 1289–1298.
- Wang, S., Altermatt, F., 2019. Metapopulations revisited: the area-dependence of dispersal matters. *Ecology* 100.
- Wirth, S.B., Taubert, F., Tietjen, B., Müller, C., Rolinski, S., 2021. Do details matter? Disentangling the processes related to plant species interactions in two grassland models of different complexity. *Ecol. Modell.* 460.
- Wisnoski, N.I., Leibold, M.A., Lennon, J.T., 2019. Dormancy in metacommunities. *Am. Nat.* 194, 135–151.