Environmental and trait variability constrain community structure and the biodiversity-productivity relationship

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Abstract. There is still considerable debate about which mechanisms drive the relationship between biodiversity and ecosystem function (BEF). Although most scientists agree on the existence of two underlying mechanisms, complementarity and selection, experimental studies keep producing contrasting results on the relative contributions of the two effects. We present a spatially explicit resource competition model and investigate how the strength of these effects is influenced by trait and environmental variability, resource distribution, and species pool size. Our results demonstrate that the increase of biomass production with increasing species numbers depends on the concurrence of environmental and trait variability: BEF relationships are stronger if functionally different species coexist in a landscape with heterogeneous resource supply. These large biodiversity effects arise from complementarity effects, whereas selection effects are maximized when broad trait ranges coincide with narrow ranges of resource supply ratios. Our results will therefore help to resolve the debate on complementarity and selection mechanisms.

Key words: ecosystem function; heterogeneity; metacommunities; productivity; resource competition; selection and complementarity; spatial resource; species biodiversity; species traits.

Introduction

After more than two decades of biodiversity-ecosystem functioning (BEF) research and initially controversial discussion, ecologists now widely agree on the existence of biodiversity effects on ecosystem functions and processes (Cardinale et al. 2012). Recent meta-analyses summarize the evidence from hundreds of experiments across a wide range of ecosystem and habitat types. These show that biodiversity enhances processes such as resource capture and productivity (Cardinale et al. 2006, 2012), with patterns being largely consistent across trophic levels (Griffin et al. 2013) and ecosystem types (Cardinale et al. 2006). Thus, the loss of biodiversity is expected to negatively affect stocks, process rates, and ecosystems depending thereon (Balvanera et al. 2006). In recent years, these experimentally observed patterns were also confirmed by a number of studies on natural communities (Cardinale et al. 2009, Hodapp et al. 2013, Filstrup et al. 2014).

Two mechanisms commonly used to explain biodiversity effects are the so called complementarity and selection effects (Loreau and Hector 2001). Complementarity effects comprise reduced niche overlap and broader coverage of environmental niche space with increasing species numbers due to tradeoffs in multiple traits and positive interactions between species

(facilitation) in more diverse communities. Selection effects refer to non-random correlations between the biomass of a single species in monoculture, and the relative yields of this species when grown in a mixture. Partitioning the net biomass increase into complementarity and selection effects accounts for the possibility that a species' impact on ecosystem functions might not be positively correlated with the species' performance in monoculture, a fact that has been commonly ignored in BEF studies (Hillebrand and Matthiessen 2009). Note that the selection effect should be distinguished from sampling effects, which are also often referred to in this context (Loreau and Hector 2001). The latter describe the increasing probability of sampling highly productive species or complementary species combinations with increasing species richness.

The combined effects of mechanisms regulating coexistence and the ones relating diversity to function have been studied by a small number of theoretical studies. For instance, Mouquet et al. (2002) showed that the application of different coexistence mechanisms within various habitat produces a wide range of BEF patterns. Another two theoretical approaches illustrated how ecosystem functionality across temporal and spatial variation can be promoted by coexistence of functionally diverse groups (Norberg et al. 2001) or by dispersal between meta-community patches (Loreau et al. 2003). However, none of these studies discussed the underlying diversity mechanisms in terms of the selection and complementarity framework.

At the same time, the partitioning of diversity mechanisms has been applied to numerous experimental data sets, but different studies have produced contradicting results regarding the importance or dominance of selection or complementarity effects and consequently did not allow to deduce any general pattern. The application of a meta-community modelling framework (Cardinale et al. 2004) showed that complementarity and selection effects could generate similar diversity-productivity patterns and that both grew stronger with time. For spatial scales, however, there was a distinct separation of diversity mechanisms, showing selection effects to dominate on the local scale and complementarity effects on the regional scale.

In an attempt to explain mechanistically under which conditions higher biodiversity begets higher ecosystem functioning, Ptacnik et al. (2010) introduced the concepts of environmental and trait dimensionality. Environmental dimensions are given by the number of conditions affecting growth and mortality, such as resource supply ratios, abundance, and diversity of consumers, fluctuating environmental conditions or disturbances. Trait dimensionality captures organisms' differences with regard to their resource acquisition traits, but also their tolerance to stressors and consumers. In short, Ptacnik et al. (2010) constructed a few limiting cases in their concept: If species are highly different but the environment provides only one niche, biodiversity will not or only weakly increase functioning, as only one trait combination will be best adapted and best performing. If species are highly similar in their traits but the environment provides a number of niches, a large part of the niche space is not covered by the trait space and BEF relationships will be weak. Only when a large environmental variability is met by a large variation in traits will there be strong positive relationships between trait diversity and resource use. This hypothesis is supported by an experimental study on artificial stream ecosystems, which revealed that ecosystems with higher numbers of available niches require according levels of trait complexity for an optimal use of the provided resources, and that less diverse communities leave certain niches unoccupied which results in lower productivity (Cardinale 2011). In accordance with these results, Loreau (2001) compared different scenarios of absolute resource use intensity, degree of generalization and resource-use similarity among species in a microbial community using a simple ecosystem model. He showed that nutrient decomposition and productivity were both positively affected by an increase in species number. In contrast, a more diverse set of resources had rather negative effects on productivity when the additional niches were not covered by any species.

In this study, we introduce a general framework for testing and extending the hypothesis formulated by Ptacnik et al. (2010) in order to identify the general mechanisms leading to the various empirically observed BEF patterns. Our model is the first to allow the independent variation in both trait diversity and environmental variability in a spatially explicit setting. Our model covers new ground compared to previous models (Loreau 2001, Loreau et al. 2003, Cardinale et al. 2004), because it explicitly analyzes the effects of spatial resource distributions on resource competition, species assembly, and the diversity-productivity relationship. Unlike typical BEF experiments, which test BEF on small spatial and temporal scales, our general set-up also allows to investigate how coexistence mechanisms and functional trait diversity interactively shape long-term BEF patterns in large-scale ecosystems. In addition to spatially explicit competition and different levels of trait and environmental variability, we analyze the influence of spatial heterogeneity in resource supply and species pool size. The model is set up in the style of a phytoplankton experiments in a network of connected chemostats; however, the basic underlying mechanisms of resource uptake, competition and production could be easily adjusted to many other consumer-resource meta-ecosystems.

METHODS

Model

We modeled spatial competition of n species for two limiting resources on a two-dimensional grid (Fig. 1a). We assumed a spatially heterogeneous resource distribution and that organisms are able to move randomly between adjacent grid cells. The description of biomass growth follows a standard multispecies resource competition model, where the growth rate is defined by a combination of the Monod kinetics of resource uptake and Liebig's law of the minimum (León and Tumpson 1975, Grover 1997, Huisman and Weissing 2001). Thus, species-specific growth depended on the availability of a species' most limiting resource

$$g_i\left(R_1, R_2\right) = g_{max} \min\left\{\frac{R_1}{K_{i1} + R_1}, \frac{R_2}{K_{i2} + R_2}\right\} \quad (1)$$
$$\text{with } i = 1{:}n,$$

where g_{max} is the maximum growth rate, R_1 and R_2 are the local concentrations of the two resources, and K_{i1}, respectively K_{i2}, are the corresponding half-saturation constants of species i.

To model meta-community dynamics, we allowed for dispersal between adjacent grid cells with the same dispersal rate d for all species. At the grid boundaries we assumed no flux boundary conditions. Let $N_{x,y}^i$ denote the local biomass of species $i = 1 \ldots n$ and $R_{x,y}^j$ the local concentration of resource $j = 1,2$ in cell (x,y). The biomass dynamics of species i then follow the equation

$$\frac{dN_{xy}^i}{dt} = \left[g_i\left(R_{xy}^1, R_{xy}^2\right) - m\right] N_{xy}^i + d\,\Delta N_{x,y}^i, \quad (2)$$

where the first term describes local growth and loss processes (with mortality m), and the second term is the discrete Laplace operator
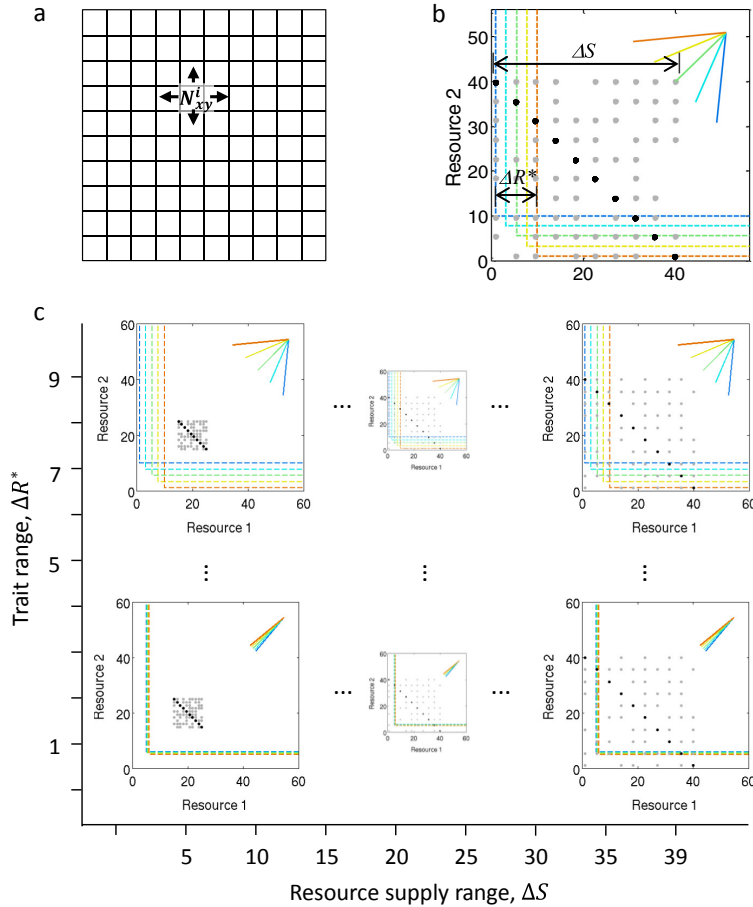
FIG. 1.   Model framework to capture meta-community dynamics, determined by resource distribution, species dispersal, and species characteristics. (a) Species are able to move across a model grid by constant dispersal to neighboring cells. (b) Competitor tradeoff in resource requirements (dashed lines show the zero-net-growth-isoclines); the consumption vectors (solid lines) follow "Optimal Foraging Theory". The resource supply points either lie along a tradeoff line (black dots represent "Gradients" and "Random locations" scenario) or within a square (grey dots represent "Random supplies" scenario). The range of R^*values covered by the species community, defines trait variability, ΔR^*, and the difference between the highest and lowest concentrations of resource supply defines the resource variability, ΔS. (c) Community characteristics (biomass production, effective species numbers) were calculated for different combinations of trait (ΔR^* = [1, 5, 7, 9]) and environmental (ΔS = [5, 10, 15, 20, 25, 30, 35, 39]) variability.

$$\Delta N_{x,y}^i = \frac{N_{x,y+1}^i + N_{x,y-1}^i + N_{x+1,y}^i + N_{x-1,y}^i - 4N_{x,y}^i}{h^2} \quad (3)$$

which describes diffusion of organisms on a lattice with cell size h. Resource dynamics were given by the difference between resource inflow and resource consumption (for simplicity, we neglect the diffusion of resources)

$$\frac{dR_{xy}^j}{dt} = D\left(S_{xy}^j - R_{xy}^j\right) - \sum_i c_{ij} N_{xy}^i g_i\left(R_{xy}^1, R_{xy}^2\right) \quad (4)$$

with $j = 1, 2$,

where c_{ij} is the consumption rate of resource j for the production of one unit of biomass of species i, D is the dilution rate, and S_{xy}^j is the local equilibrium concentration of resource j in the absence of consumers (resource supply point sensu Tilman). To model resource heterogeneity, we assumed that the resource supplies, S_{xy}^j, differ between cells, but are constant over time.

PARAMETERS

We used dimensionless units for length, time, and resource concentrations. The grid consisted of 20 × 20 cells, where one unit of length was defined to be the size of a grid cell, h. The time units were defined to allow for a maximum growth rate $g_{max} = 1$ per unit of time, implying that the biomass can maximally increase by the factor of $e \approx 2.72$ per unit of time. One unit of resource was defined to be the minimum resource requirement of the most competitive species for this resource. The dispersal of

TABLE 1.   Model parameters.

Parameter	Symbol	Value
Local biomass density of species i	N_{xy}^i	
Local concentration of resource j	R_{xy}^j	
Maximal growth rate	g_{max}	1
Mortality	m	0.25
Species dispersal rate	d	0.1
Minimal resource requirement of species i for resource j	$R_{i,j}^*$	1–10
Half-saturation constant	$K_{i,j}$	$R_{i,j}^* \frac{g_{max}-m}{m}$
Consumption rate of resource j by species i	c_{ij}	$0.05\,R_{ij}^*$
Number of species	n	1–25
Resource dilution rate	D	0.25
Local equilibrium concentration of resource j	S_{xy}^j	1–40
Variability of species traits	ΔR^*	1–9
Variability of resource supplies	ΔS	5–39

organisms was determined by the coefficient $d = 0.1$. For a two dimensional random walk with step size h and time step τ, the dispersal coefficient $d = h^2/4\tau$ (see e.g., Kiørboe 2008). Thus, the dispersal rate of 0.1 implies that organisms move to an adjacent grid cell every 2.5 units of time on average. This is enough to allow for source-sink or mass effects (Shmida and Wilson 1985) between local communities, but also to restrain species exchange to avoid homogenization across the entire grid. See other model parameters in Table 1.

For simplicity, we assigned the same maximal growth rate g_{max} and mortality m to all species. The minimal resource requirements (trait related to species coexistence) of species i for positive net growth, the so-called R_{ij}^* value, was

$$R_{i,j}^* = K_{i,j}\frac{m}{g_{max}-m}. \qquad (5)$$

These values define species-specific zero net growth isoclines (ZNGI) in the resource space. We assumed a linear tradeoff in resource requirements, locating the R_{ij}^* values of all species on a linear equidistant gradient within a specified range ΔR^* (see below). The ZNGIs for the case of five competing species are shown in Fig. 1b, colored dashed lines.

In addition to the R^* values, consumption rates c_{ij} (trait related to functioning) also differed between species. To simplify the model settings we defined the species-specific consumption rates according to "Optimal Foraging Theory" (Tilman 1982), which specifies that a species consumes resources in the proportion of its minimal requirements for these resources, i.e., $c_{i1}/c_{i2} = R_{i1}^*/R_{i2}^*$, or $c_{ij} = \alpha R_{ij}^*$ where α is a constant. Then the slope of a consumption vector is parallel to the line connecting the origin with the species' R^* value in the resource plane (Fig. 1b). This definition ensured that each species consumed more of its most limiting resource,

providing an opportunity for stable coexistence of any two competitors at equilibrium conditions in a uniform environment.

We varied trait and environmental (i.e., resource supply) variability to assess their effects on the relationship between biodiversity and productivity. The trait variability is defined as the range, ΔR^*, covered by the R^* values of the species community. The resource variability, ΔS, is defined as the difference between the highest and lowest concentration of resource supply across the grid (Fig. 1b). These two ranges of trait and resource supply variability were manipulated independently (Fig. 1c and Table 1). For a given ΔR^* value, the consumer resource requirements varied from $5.5 - \Delta R^*/2$ to $5.5 + \Delta R^*/2$. For a given ΔS value, the resource supplies were combinations of 20 equidistantly distributed resource concentrations across its range ($20.5 - \Delta S/2$ to $20.5 + \Delta S/2$). Note, that although we considered different ranges of resource supplies and different spatial resource distributions, the total amount of resources supplied over the whole grid $\sum_{x,y} S_{xy}^j$ remained the same.

To simulate varying degrees of heterogeneity in resource supply, we investigated three different spatial scenarios. (1) "Gradients": Inverse spatial resource gradients of the two resources along the x-direction, independent from y (i.e., across the grid from left to right, as schematically shown by the blue and orange colored squares in Fig. 2a). This scenario implements a linear tradeoff in resource supply (indicated in simplified form by the black dots in Fig. 1b) and leads to spatial sorting of competitors according to the tradeoff in their resource requirements. (2) "Random locations": In this scenario, the concentrations of supplied resources show the same local tradeoff as in the first scenario. However, this time resource combinations are randomly distributed across the grid cells (Fig. 2b), so spatial correlations in resource supply and spatial species sorting is lost. (3) "Random supplies": The supplied resource concentrations varied randomly and independently across the grid (indicated in simplified form by grey dots in Fig. 1b and by different colors in Fig. 2c). In this scenario both the spatial and between-resource correlations vanish.

Finally, to mimic the empirical approach of different levels of species richness in biodiversity manipulation experiments, we varied the initial number of species based on an overall pool of 30 species. The model was run both for monocultures of each species and for 30 randomly assembled mixtures of 2, 3, 4, 5, 10, 15, 20, or 25 species.

The system of the ordinary differential equations was solved in Matlab 2011 with Euler method. The code used for modeling is provided as online Data S1. To provide the stability of the numerical scheme, the time step was equal to min $\{0.1; 0.5\ h^2/4D\}$, where h^2 is the cell size. The initial density of all species was 1 across the whole grid, the initial resource concentrations equaled S_{xy}^j.

The model was run for 5000 units of time, which ensured convergence to equilibrium conditions. Only for very small trait ranges ($\Delta R^* = 1$) considerably longer

a Gradients

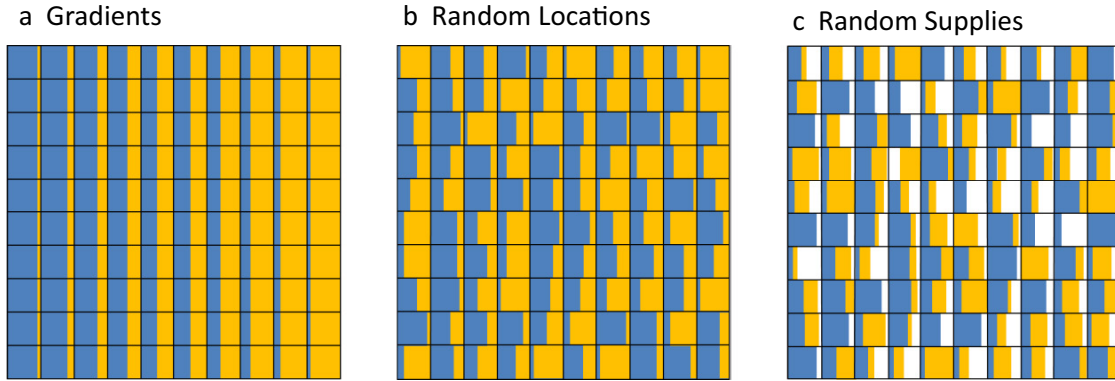## b Random Locations

c Random Supplies

FIG. 2. Three scenarios of spatial resource distribution. The blue and orange shadings indicate the relative concentration of the two resources. Gradients: Two opposing gradients of resources in horizontal direction. The resource concentrations linearly change within the resource range, ΔR. Random Locations: The same resource supply ratios as in the Gradients case, but randomly allocated across the grid. Random Supplies: Resource ratios as well as allocation across the grid are random. The total amount of resources supplied over the whole grid is the same in all scenarios.

run times (50 000 time units) were necessary as in that case competition is nearly even and time to competitive exclusion is long.

Analysis of the model results

Species diversity was calculated as the inverse Simpson index $n_{\text{eff}} = 1/\sum_i p_i^2$, where $p_i = N_i/\sum_k N_k$ is the relative regional or local species biomass (Simpson 1949, Jost 2006). The diversity index, n_{eff}, represents an "effective" number of species, which is equivalent to the number of equally common species required to yield an according Simpson index value. We present results for the regional diversity and the mean local diversity. For estimating the regional diversity, we used the regional species biomass (i.e., $N_{\text{reg}}^i = \sum_{x,y} N_{x,y}^i$), summed for every species over the entire grid, whereas the mean local diversity was obtained by averaging local diversity indices over all grid cells.

In the case of highly uneven species abundances, species richness can be considerably higher than the diversity index, n_{eff}, because low degrees of evenness reduce its value, despite possibly high species numbers. To understand how community evenness depends on the trait and environmental variability, we also calculated Pielou's evenness index (Pielou 1966). The results revealed that evenness slightly increased with decreasing resource range for high-trait variability and slightly decreased for very low resource and trait variability, but that its effect on the diversity index was unlikely to influence the overall pattern (Appendix S1: Fig. S1).

To estimate the functional diversity of the final community, we calculated Rao's entropy (Botta-Dukát 2005)

$$Q = \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} d_{ij} p_i p_j,$$

where the dissimilarity $d_{ij} = \frac{1}{2} \sum_{k=1\ldots2} \left| R_{ik}^* - R_{jk}^* \right| / \max(R_k^*)$ expresses the relative difference between the resource requirements of species i and species j.

To quantify the effect of biodiversity on system productivity, we calculated the average biomasses per grid cells produced by species i in monoculture, M^i, and in mixture, N^i. Both the mixture and monoculture biomass depend on resource heterogeneity. To estimate the relative diversity effects, we calculated the normalized mixture biomass as the ratio of the total biomass in mixture to the average monoculture biomass of a given species assemblage, $\sum_i N^i/\overline{M}$, where $\overline{M} = \sum_i M^i/n$. If this ratio was greater than one, then the mixture was more productive than its average species.

We estimated the absolute net diversity effect as the difference between the observed biomass of a species mixture and the biomass, which would be expected under the null hypothesis that all intraspecific and interspecific interactions are identical,

$$\Delta N_{\text{net}} = N_O - N_E.$$

According to the null model, the expected mixture biomass equals the average of the monoculture biomasses weighted by the initial relative density of the competitors. In our model, all species have the same initial density, therefore $N_E = \sum M_i/n$, and the expected biomass of each species $N_{Ei} = M_i/n$.

To partition the net diversity effect, ΔN_{net}, into a sum of ecologically interpretable terms, we follow Loreau and Hector (2001) and introduce the relative expected and observed species biomasses, as $\text{RN}_{Ei} = N_{Ei}/M_i = 1/n$ and $\text{RN}_{oi} = N_{oi}/M_i$, where N_{oi} is the observed biomass of species i in the mixture. Then the net diversity effect can be presented as

$$\Delta N_{\text{net}} = \sum_i \left(\text{RN}_{Oi} - \text{RN}_{Ei} \right) M_i$$
$$= n\overline{\Delta\text{RN}} \cdot \overline{M} + n \, \text{cov}(\Delta\text{RN}_i, M_i)$$

where $\Delta\text{RN}_i = \text{RN}_{Oi} - \text{RN}_{Ei}$ is the difference between the expected and observed relative species biomasses. The first term in this partitioning is positive if the species'

relative biomasses in a mixture are on average greater than expected from the null model, i.e., interspecific competition becomes weaker than intraspecific competition due to reduced niche overlap (complementarity effects). The second term is positive if there is a positive correlation between the monoculture biomass of a species and its performance in the mixture (selection effects).

RESULTS

With increasing initial species richness (from 1 to 25 species randomly chosen from the initial pool) the average normalized biomass continuously increased and leveled off at a richness of about 10–20 species, illustrating the effects of biodiversity on productivity (Fig. 6). By contrast, the variance of normalized biomass decreased with increasing diversity, indicating decreasing effects of species identity. The strength of BEF relationships was highly dependent on the combination of trait and environmental variability levels. The increase in normalized biomass with increasing initial species richness was greatest when the highest variation in traits coincided with an according variability in environmental niches. Under these conditions, biomass was around 1.5–2 times higher in species-rich mixtures

than in monocultures. If trait-variation was low and environmental variability high, mixtures outperformed monocultures by a maximum of 3–10% only, whereas at low environmental variability but high trait-diversity, mixtures were up to 1.5 times more productive than monocultures. Thus, increases in trait variability had relatively stronger impacts than increases in environmental variability.

These patterns were consistent across different modes of resource supply heterogeneity, although the spatial distribution of resources affected the results quantitatively. There was no BEF effect when ΔR^* was small. When ΔR^* was big we observed different responses: The system with opposing resource gradients ("Gradients" scenario) resulted in stronger BEF relationships than the scenarios with more heterogeneous resource distributions; The "Random Locations" and "Random supplies" scenarios led to comparable biomass increases when ΔS was small; whereas for big ΔS "Random locations" yielded higher increases in biomass in comparison with "Random Supplies" (Appendix S1: Fig S2, right column).

Fig. 3 shows an overview of the overall patterns obtained for mixtures of 25 species for different combinations of ΔS and ΔR^* in the "Gradients" scenario (other scenarios resulted in similar patterns). The monoculture
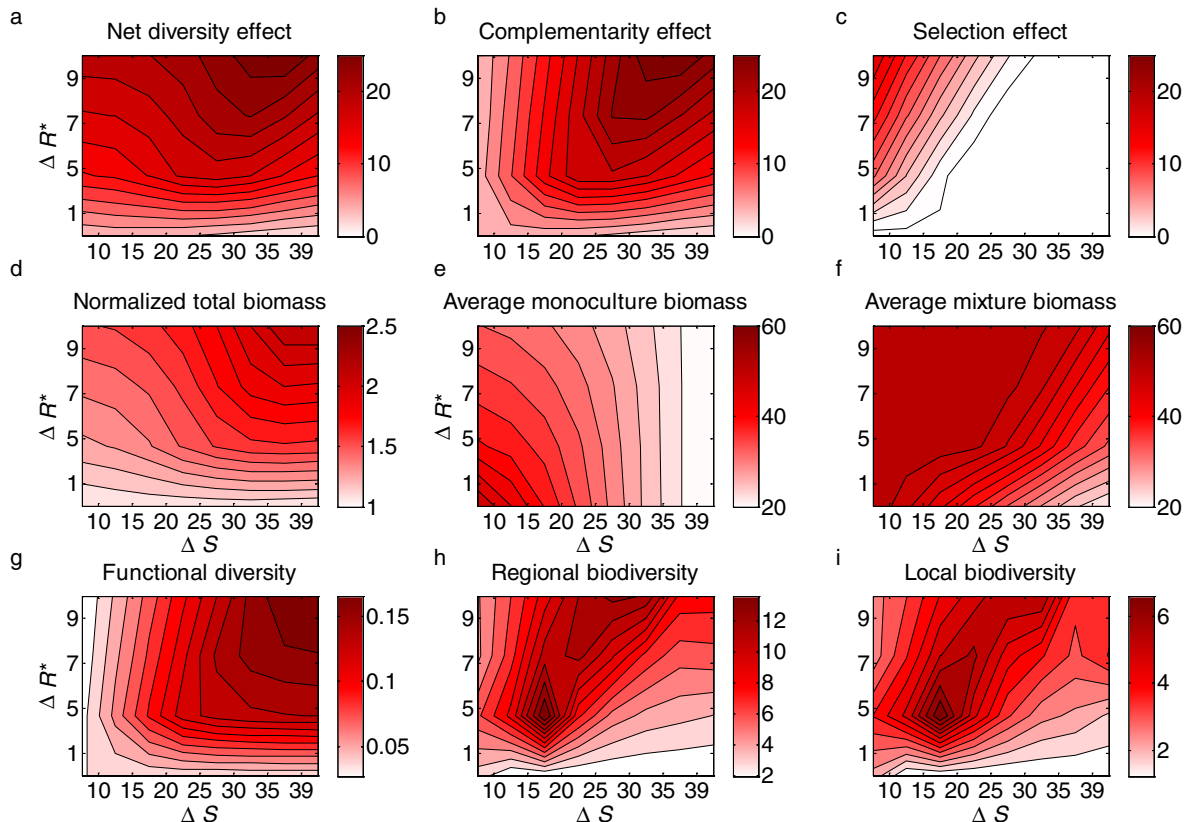

FIG. 3. Influence of trait and environmental variability on (a) net biomass increase, (b) complementarity effect, (c) selection effect, (d) normalized biomass, (e) average monoculture biomass, (f) average mixture biomass, (g) functional diversity (Rao's entropy), (h) regional effective species number, (i) local effective species number. The figure shows the results averaged across 30 mixtures of 25 randomly selected species in the Gradients scenario of resource distribution.

and mixture biomass both decreased with increasing ΔS, because organisms experienced more imbalanced resource supply ratios with strong limitation by one or the other resource, thereby decreasing overall resource use efficiency (Figs. 3e,f and Appendix S1: Fig. S2). However, the average monoculture and mixture biomass followed opposite patterns along the ΔR^* axis. The average monoculture biomass decreased with increasing ΔR^* and was maximal when both ΔS and ΔR^*were small, because then the resource supply ratio perfectly matched the species resource requirements. By contrast, the mixture biomass increased with ΔR^* and reached some saturation level in the upper left part of the parameter space (Fig. 3f), since only a functionally diverse community can result in the maximal diversity effects. Finally, the net biomass increase (Fig. 3a) and the normalized mixture biomass (Fig. 3d) had a weak dependence on ΔS, but they always increased with increasing resource range and trait ranges. Thus, our model shows that the conditions promoting the highest net diversity effects are not the same as the ones leading to highest overall biomass yield. Similarly, the conditions resulting in maximum mixture biomass differed to those leading to the highest monoculture biomass production.

Separating the net diversity effect into complementarity and selection effects yielded novel mechanistic insights into their interdependent constraints (Figs. 3b,c and Fig. 4, middle and right column for the three scenarios of resource distributions). Both effects increased with increasing trait variability. As a function of environmental variability (ΔS), selection effects decreased with

ΔS and complementarity effects were hump-shaped with a maximum when environmental niche space matched the trait-diversity range. We found strong impacts of selection effects under conditions combining wide trait ranges with narrow resource ranges, as these allow for greater differences in growth performance of individual species (Appendix S1: Fig. S3). As a consequence, the biomass yield of a mixture depended on the identity of the species in the assemblage. On the other hand, if the environment was too heterogeneous (high variability in resource supply), an optimal combination of traits to select for did not exist, which mitigated selection effects.

The strength of complementarity and selection effects depended also on the spatial distribution of resources. The strongest complementarity effects occurred when the resource supply was arranged along spatially opposed gradients (Fig. 4), when the difference between adjacent cells was minimal. The weakest complementarity effects occurred in the "Random supplies" scenario, when the supply intensities of both resources were randomly allocated in space, and both the spatial (similar resource ratios in neighboring cells) and local (a tradeoff in local resource supplies) correlations between resource availability were lost. This configuration, by contrast, promoted selection effects, which were the strongest in the "Random supplies" scenario and the weakest, or even negative, in the "Random locations" scenario. Note, however, that for very low and very high variation in resource supply (small or large ΔS) selection effects showed similar values across all supply modes.
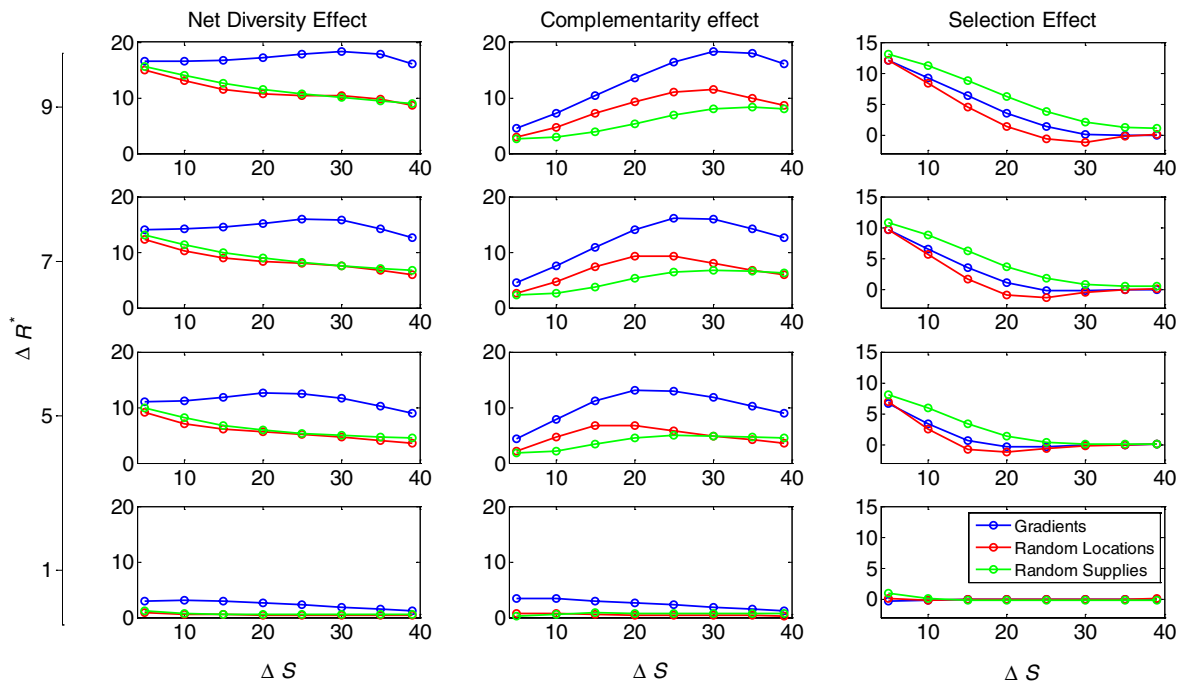

Fig. 4. The net biomass increase, complementarity and selection effects obtained for different combinations of trait (ΔR^*) and resource (ΔS) variability for mixtures of 25 species. Results are averaged across 30 mixtures of 25 randomly selected species. Line colors indicate the scenario of resource supply distribution (Gradients – blue, Random locations – red, Random supplies – green).
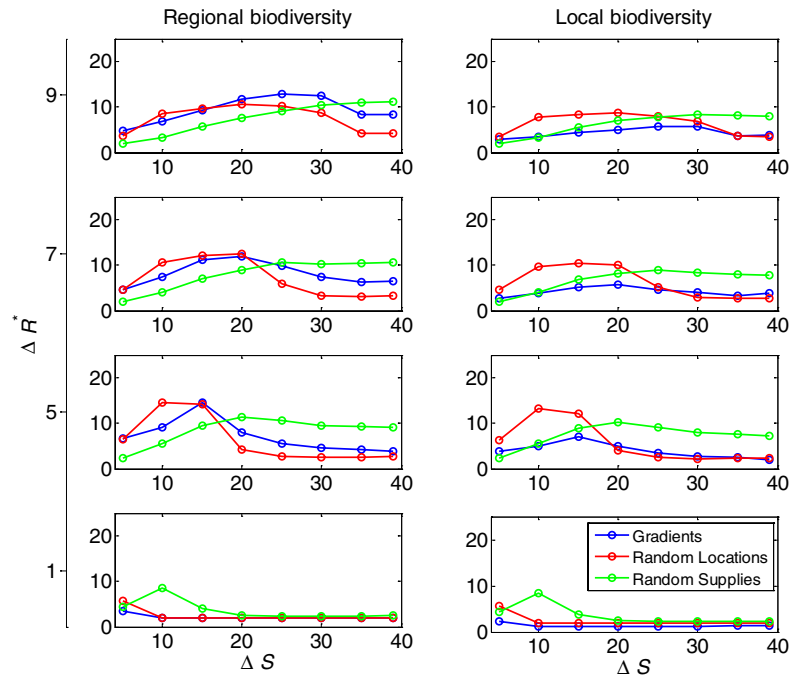
Fig. 5. Average local (cell-wise) and regional (grid-wise) biodiversity, measured by the inverse Simpson index, for different combinations of trait (ΔR^*) and resource (ΔS) variability, averaged over 30 mixtures of 25 species. Line colors indicate the three scenarios of resource supply distribution (Gradients – blue, Random locations – red, Random supplies – green).

In terms of diversity, we found similar patterns as for biomass production. Both the regional and local biodiversity increased with the initial species number for all range combinations and types of resource distribution. The highest effective species numbers were obtained when trait variability matched the range of available resource supply points (Fig. 5). A detailed analysis for mixtures of 25 randomly selected species revealed that both the local and regional biodiversity achieved a maximum at an optimum value of resource variation, and the location of this peak shifted to higher values of ΔS with increasing ΔR^* (Fig. 5). Species richness declined under low variability in resource supply across the grid, because in these cases, a small number of well adapted species dominated in each grid cell. Similarly, biodiversity decreased when the range of supplied resources was considerably higher than the range of species traits, because the species with the most unbalanced resource requirements benefitted and dominated most cells. Finally, note that the optimal range of resource variation depended on the type of resource distribution. The optimal range was broad in the "Random supplies" scenario and narrow in the "Random locations" scenario. Despite these differences in effective species numbers, functional diversity always peaked with high-trait and high-resource variability showing very similar patterns for all three resource supply scenarios for the 25 species mixtures (see Fig. 3g for the "Gradients" scenario).

To check the effect of species dispersal on the BEF effects, we ran the model without continuous immigration of species between neighboring cells. This strongly affected the local species biodiversity; however it did not essentially change the regional BEF relationships. Although locally only a maximum of two species were able to coexist, the global biodiversity was high when a wide range of resource supply conditions covered the range of species traits. Compared to the model with species dispersal, the regional biodiversity followed the same patterns but could reach greater maximal values (comp. Fig. 5 and Appendix S1: Fig. S6). Similarly, the reduction of dispersal led to a small change in the dependences of the regional BEF effects on the resource and trait ranges. In this setting, similar to the regional biodiversity, the net biomass increases, selection, and complementarity effects followed the same patterns but could attain greater values, as the source-sink dynamics and interspecific competition due to species emigration was reduced (Fig. 4 and Appendix S1: Fig. S5).

Finally, to test the robustness of our results, we performed a simulation assuming different boundary conditions and distinct maximal growth rates of the competitors. The modified model lead to similar dependences of productivity and species biodiversity on the ranges of trait and resource variability (comp. Figs. 3 and 5 with Appendix S1: Figs. S8 and S9, respectively).

DISCUSSION

We used a spatially explicit resource competition model to identify mechanisms underlying diversity effects on community productivity. Within this modeling framework,

we were able to incorporate two recently proposed extensions to current BEF research. First, Hillebrand and Matthiessen (2009) criticized the common practice of analyzing species coexistence separately from species traits regulating ecosystem function, which they suggested contributes to controversial results of BEF experiments. Second, Ptacnik et al. (2010) assumed that the strength of BEF relationships is likely to be influenced by matching variability in the environment and species traits.

By including both environmental and trait variability in the model, we were able to show that they both interactively affect biomass production and diversity effects (Fig. 6); however, most environmental conditions led to considerably higher complementarity than selection effects. Furthermore, conditions promoting selection effects (high-trait variation in combination with very little variation in environmental niches) are rather unlikely to occur in natural ecosystems.

Strong selection or complementarity effects always required a community with sufficiently broad range of species traits. The largest selection effects occurred if this community was placed into an environment with small resource variability, where the trait difference led to considerable differences in monoculture yields. Under the same conditions, complementarity effects were small, because additional species did not increase occupied niche

space further but instead replaced existing species as suggested by Roscher et al. (2005). By contrast, we observed the strongest complementarity effects when broad environmental niche space was covered by high-trait diversity, because in that case, many functionally different species can effectively utilize broad niche space. With further increase of the resource range, the complementarity effects decrease as the number of unfavorable sites increases.

In revealing that complementarity and selection effects are promoted by opposing sets of conditions (Fig. 3b,c), our model provides possible explanations for seemingly contradictory empirical results that indicate differing strengths in complementarity effects and a wide range of effect sizes from negative (Hooper and Dukes 2003) to highly positive (Roscher et al. 2005) selection effects. A failure to outperform the best performing monoculture (overyielding but no transgressive overyielding) has usually been taken as an argument for selection playing a more important role than complementarity effects (Bruno et al. 2005, Cardinale et al. 2006). Yet several recent studies have found complementarity effects to have higher impacts on diversity-productivity relationships than selection or species identity (Cardinale et al. 2007, Marquard et al. 2013) and have argued that contradictory results are mainly caused by insufficient study duration (Cardinale et al. 2007, Fargione et al. 2007). From our model, we can
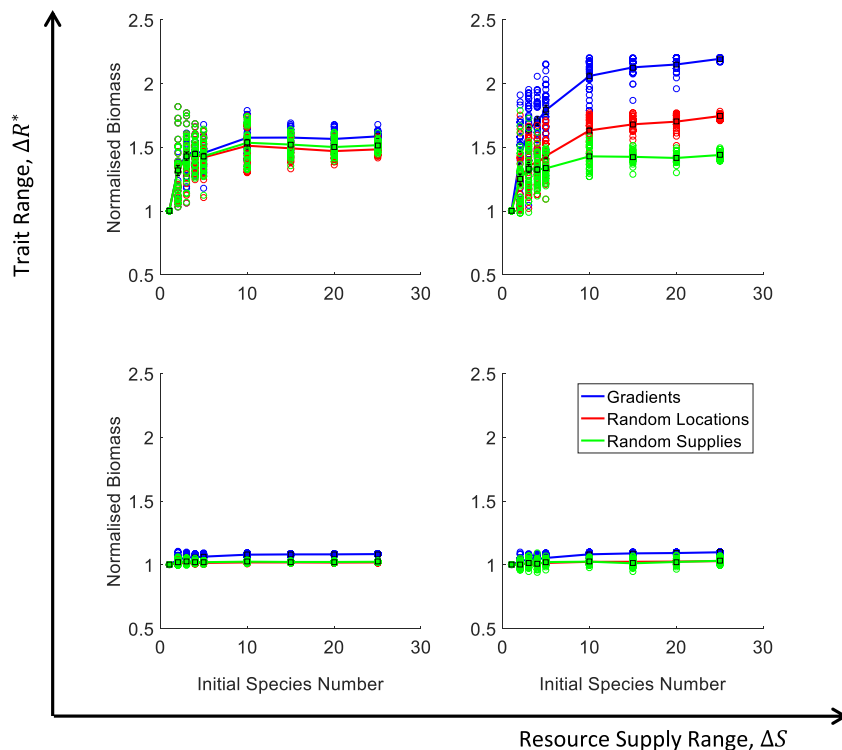

FIG. 6. The effects of initial species number on the normalized mixture biomass (relative diversity effect) for different combinations of the lowest and highest trait variability ($\Delta R^*_{min} = 1$, $\Delta R^*_{max} = 9$) and resource variability ($\Delta S_{min} = 5$, $\Delta S_{max} = 39$). Individual replicas (points) and mean values (black points connected by lines) for the three scenarios of resource distribution (Gradients – blue, Random Locations – red, Random Supplies – green) show increases in biomass with increasing species number if trait variability is large.

conclude that the spatial arrangement of resources as well as trait and environmental variability constrain both selection and complementarity effects and therefore provide arguments for the existence of both scenarios.

Unlike Cardinale et al. (2004), who suggested selection effects dominate on the local scale and complementarity effects on the regional scale, we found both complementarity and selection effects to operate on regional scales. These results are not in conflict, though, as the incorporation of different levels of trait and resource variability in our model represents an additional factor influencing diversity effects. Cardinale et al. assume either varying maximum carrying capacities for different patch types across species or limited niche overlap between species, which both lead to combinations of matching levels of trait and environmental variability on the regional scale. For that particular case, our model also shows mainly complementarity effects to drive the diversity-productivity relationship.

Another source of controversy around BEF results revolves around the measure of system productivity. Biodiversity can enhance the efficiency by which resources are transferred into biomass (realized productivity), whereas the so-called potential productivity is limited by the availability of resources (Cardinale et al. 2009). Consistent with this differentiation, the highest net biomass increase with diversity (Fig. 3a,f) did not coincide with the highest absolute total biomass in our model. In agreement with Mouquet et al. (2002), we found that total biomass values either stayed constant or decreased with increasing number of environmental niches. Over a range of ratios, community biomass was constant (the upper left part in Fig. 3f), and over this range either selection or complementarity resulted in positive net diversity effect. By contrast, in the range of high-resource variability and low-trait variability the total biomass decreased (the lower right part in Fig. 3f).

The decrease of the absolute species mixture biomass with broadening the range of resource availability is based on an increase in the number of sites with extremely imbalanced availability of the two resources, which reduced the number of potentially coexisting species (Harpole and Tilman 2007, Ptacnik et al. 2010) and provided resources in a ratio not efficiently transferable to biomass. The first mechanism is predicted by classic resource ratio theory, where highly imbalanced resource supplies reduce the potential for species coexistence (Tilman 1982). The latter mechanism reflects arguments from ecological stoichiometry, as resources supplied in large surplus compared to the limiting resource cannot be utilized (Sterner and Elser 2002). Thus, in agreement with empirical patterns (Cardinale et al. 2009) and conceptual statements (Hillebrand et al. 2014), stoichiometric effects constrain BEF patterns by affecting coexistence and multiple resource use efficiency.

The model also supported the argument brought forward by Hillebrand and Matthiessen (2009) that trait-based approaches, taking into account coexistence mechanisms as well as species-specific traits related to

ecosystem functions, will help to better explain the variety in BEF patterns. In modeling these two aspects simultaneously, we observed that highly productive species in monoculture did not necessarily dominate in mixtures but that both coexistence mechanisms and functional traits of individual species determined community productivity depending on the congruence of trait and environmental variability (Appendix S1: Fig. S4).

In addition to environmental and trait variability, our model detailed how spatial resource distribution affects biomass production, complementarity, and selection effects. For instance, the "Gradients" scenario led to much stronger complementarity effects compared to the other scenarios, as in this scenario, the neighboring cells had similar resource values and formed bigger favorable patches. By contrast, the selection effects reached maximum values in the "Random supplies" scenario, when both the local and spatial resource availabilities were uncorrelated. Here, the presence of patches where both resources were supplied at high rates increased the relative importance of species identity (i.e., certain species traits) and therefore the selection effect.

The maximum possible number of regionally coexisting species did not differ much between different levels of trait variability. With increasing trait variability, however, the location of the peak in diversity along the resource variability axis shifted to the right. For the "Gradients" and "Random Locations" scenarios, equal distributions of resource supply points along the tradeoff line were chosen, which led to close levels of regional biodiversity. By contrast, the local biodiversity levels were higher in the "Random Locations" than in the "Gradients" scenario, likely because of the higher level of environmental heterogeneity, which increases the biomass exchange between cells with sufficiently different environmental conditions. The supply points for the "Random supplies" scenario were sampled from a squared shape in the resource plane and therefore included relatively more points with intermediate resource ratios than in the other two scenarios. As a consequence in this scenario, species with intermediate resource requirements were more favored than species with extreme requirements, as shown in the monoculture performances (Appendix S1: Fig. S3). Consequently, the maximal biodiversity required larger resource ranges than in the other two scenarios.

The main modeling part included results for a metacommunity model with possibility of species dispersal between cells. However, our study shows that the dispersal and local coexistence of many species does not constitute the main prerequisites for the global BEF effects. Although the local coexistence of more than two species was only possible given dispersal between grid cells, the biomass production and regional BEF effects followed the same patterns across different combinations of trait and resource variability in the models with and without species dispersal (Fig. 4 and Appendix S1: Fig. S5). Furthermore, dispersal of species led to some reduction in BEF effects and species biomass, because of increasing source-sink effects between favorable and unfavorable patches.

According to resource-ratio theory (Tilman 1982) the number of locally coexisting species depends on the number of supplied resources. Therefore, in our model without species dispersal, maximally two species could coexist in a single grid cell. Being averaged across the grid, the local diversity showed values less than two, as some cells supported none or only one of the present species. By contrast, regional diversity did not drop but rather showed higher values for simulations without species exchange between grid cells (Appendix S1: Fig. S6), as the supplied resource ratio varied across the grid and the identity of locally surviving species varied accordingly. This result could be a consequence of the constant environmental conditions while under fluctuating conditions a minimum level of dispersal is probably necessary to prevent local species extinction from resource fluctuations and demographic stochasticity. Although the effects of dispersal on BEF requires further research, it is already clear that increasing dispersal should finally reduce the number of globally coexisting species and therefore reduce the potential effect of biodiversity on biomass productions.

We also found that very similar species assemblages (low-trait variability) at low environmental variability needed more time to reach equilibrium conditions. This phenomenon has already been discussed in conjunction with unstable coexistence mechanisms (Chesson 2000). The long-term dynamics in our model simulations emphasize the importance of conducting long-term studies in BEF research (Cardinale et al. 2007) and imply caution when discussing results derived from short-term BEF experiments.

Without a doubt we have omitted a number of biologically relevant aspects in the formulation of our model equations, such as species-specific mortality or dispersal rates. Despite these simplifications, we are confident that our results are robust. First, the model with and without dispersal and the model with various species specific growth rates show similar outcomes. Second, the local dynamics in the model without dispersal depend mainly on species $R*$ values, which in equilibrium conditions represents the overall differences in species traits (Grover 1997). Furthermore, our analyses illustrate that the main patterns supported by our model hold despite the application of different levels of resource heterogeneity and types of resource distributions. There are certainly mechanisms, such as diffusion and recycling of resources, that have been proven to affect spatial dynamics (Gravel et al. 2010, Loreau et al. 2013). As our main focus was the effect of different levels of spatial resource heterogeneity on community assembly and BEF patterns, however, we deliberately ignored these aspects in the current study. We consider the current set-up of the model as a basic framework open for extensions, which certainly include spatial as well as temporal resource dynamics. Another limitation with regard to applying this model to plant instead of plankton communities is that we currently only consider limitation in resources but not space. However, the space limitation occurs in the model without species

dispersal, as maximally two species can occupy a cell. As has been shown, this change does not lead to significant changes in the global characteristic. Finally, we also omitted effects of differing consumption rates, which might favor different species communities in different environments (Tilman 1982, Ryabov and Blasius 2011) and might have substantial effects on competition and community structures. Other possible extensions include different resource uptake mechanisms (storage effects), further trophic levels and tradeoffs in species characteristics (Edwards et al. 2013), and allometric aspects (Marañón et al. 2013).

Finally, our model is relevant to applied aspects of BEF research in a number of ways. First, biodiversity is often used as an indicator of ecosystem properties or processes – our model suggests that this is especially warranted in variable ecosystems exhibiting broad niche dimensionality in space or time. Second, the divergent conditions promoting the relative importance of selection or complementarity mechanisms can have consequences for ecosystem management. In an agricultural setting where environmental parameters can be controlled (fertilization, irrigation, etc.), a uniform environment which matches the requirements of the best performing species will provide the maximum possible yield. In such systems, selection effects can facilitate the growth of the species which is best adapted to the current conditions. By contrast, most natural systems exhibit high degrees of environmental heterogeneity and fluctuations where communities with greater species diversity are better able to buffer disturbances and environmental change, thus promoting system sustainability. Under such conditions, a single species is unable to exploit the available resources, such that the conservation of a broad trait variability that is able to cover the environmental niche space is necessary to ensure long-term ecosystem functionality via complementarity effects.

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