

LETTER

Biodiversity effects on ecosystem functioning respond unimodally to environmental stress

Jan M. Baert,^{1,2,3*}
Nico Eisenhauer,^{4,5}
Colin R. Janssen¹ and
Frederik De Laender⁶

Abstract

Understanding how biodiversity (B) affects ecosystem functioning (EF) is essential for assessing the consequences of ongoing biodiversity changes. An increasing number of studies, however, show that environmental conditions affect the shape of BEF relationships. Here, we first use a game-theoretic community model to reveal that a unimodal response of the BEF slope can be expected along environmental stress gradients, but also how the ecological mechanisms underlying this response may vary depending on how stress affects species interactions. Next, we analysed a global dataset of 44 experiments that crossed biodiversity with environmental conditions. Confirming our main model prediction, the effect of biodiversity on ecosystem functioning tends to be greater at intermediate levels of environmental stress, but varies among studies corresponding to differences in stress-effects on species interactions. Together, these results suggest that increases in stress from ongoing global environmental changes may amplify the consequences of biodiversity changes.

Keywords

Stress, biodiversity, community model, meta-analysis, plant communities.

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INTRODUCTION

Over the past 25 years, a compelling number of experiments has demonstrated that biodiversity affects ecosystem functioning (Chapin *et al.* 1997; Loreau *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2011, 2012). Since most studies support a positive biodiversity–ecosystem functioning (BEF) relationship, this has raised concerns that ecosystem function provisioning is at risk from ongoing global biodiversity changes (Hooper *et al.* 2005, 2012; Cardinale *et al.* 2012). However, evidence is also mounting that the consequences of biodiversity changes may not be predictable from a single, universal BEF relationship (Mittelbach *et al.* 2001; Pärtel *et al.* 2010; Tilman *et al.* 2014). Not only can the shape of BEF relationships differ among ecosystems (Cardinale *et al.* 2011, 2012), an increasing number of studies now demonstrates that changes in environmental conditions can also alter the shape of BEF relationships within a system (Pfisterer & Schmidtke 2002; Wardle & Zackrisson 2005; Li *et al.* 2010; Steudel *et al.* 2011, 2012; Isbell *et al.* 2015; Baert *et al.* 2016; Guerrero-Ramírez *et al.* 2017). How environmental changes alter the shape of the BEF relationship thereby appears to strongly depend on both the system and environmental change driver under study (Cowles *et al.* 2016; Ratcliffe *et al.* 2017). However, few studies have so far explored the processes underlying observed environmental change-induced alterations in BEF relationships (Rixen & Mulder 2005; Baert *et al.*

2016; Hodapp *et al.* 2016). Hence, it remains unstudied if differences among studies as to how environmental changes alter BEF relationships can be reconciled within a single mechanistic framework. This is a major knowledge gap as observations and predictions suggest rapid future changes in environmental conditions to go hand in hand with biodiversity change, which can cause the consequences of predicted biodiversity changes to deviate from the current expectations that are based on the present-day environmental conditions (Pereira *et al.* 2010; Sala *et al.* 2011; Hooper *et al.* 2012; Pimm *et al.* 2014).

Biodiversity research has thus far mostly focused on aggregated ecosystem functions (e.g. total biomass production) in single trophic level systems (Hooper *et al.* 2005; Tilman *et al.* 2014; Ratcliffe *et al.* 2017). Such ecosystem functions typically consist of the sum of the individual species' functional contributions. Biodiversity effects on aggregated ecosystem functions therefore result from differences in the relative strength of inter- and intraspecific interactions, which cause species to function differently in the presence of other species (Loreau & Hector 2001; Fox 2005). Two classes of biodiversity effects are thereby discerned: dominance and complementarity effects (Loreau & Hector 2001; Fox 2005). Dominance effects refer to changes in ecosystem functions through changes in species' functional contributions as a result of competitive replacement, and hence increase ecosystem functioning when functional and competitive abilities are correlated so that high-functioning

¹Laboratory of Environmental Toxicology and Applied Ecology, Ghent University, Coupure Links 653, 9000, Ghent, Belgium

²Behavioural Ecology and Ecophysiology Research Group, University of Antwerp, Universiteitsplein 1, 2610, Antwerp, Belgium

³Terrestrial Ecology Unit, Ghent University, K.L. Ledeganckstraat 35, 9000, Ghent, Belgium

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany

⁵Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103, Leipzig, Germany

⁶Institute of Life-Earth-Environment, Namur Institute of Complex Systems, Research Unit of Environmental and Evolutionary Biology, University of Namur, Rue de Bruxelles 61, 5000, Namur, Belgium

*Correspondence: E-mail: jan.baert@ugent.be

species replace low-functioning species. Complementarity effects, in contrast, refer to changes in species functional contributions by alterations in the intensity of competition through the presence of heterospecifics, but without resulting in competitive replacement. Niche complementarity and facilitation are hence two important drivers of positive complementarity effects, increasing species' functioning by reducing the amount of competition individuals experience in mixed communities compared to monocultures (Loreau & Hector 2001; Fox 2005). A distinction can thereby be made between trait-independent and trait-dependent complementarity effects. Trait-independent complementarity effects refer to the average complementarity effect across species as a result of all interactions in the system. Trait-dependent complementarity effects designate how species deviate from this average complementarity effect in relation to their functional traits, generally quantified as their monoculture yield, as a result of asymmetric or one-way interactions. Both classes of biodiversity effects can also be negative. Dominance of species with low functional abilities and antagonistic interactions that increase competition can accordingly result in negative dominance and complementarity effects, respectively, and thus in negative BEF relationships (Loreau & Hector 2001; Fox 2005).

Theoretically, the environmental dependency of BEF relationships should thus arise from changes in species functional contributions that alter dominance and complementarity effects (Baert *et al.* 2016). Environmental change can affect species functional contributions directly and indirectly. Interspecific differences in species' sensitivities to the environmental changes determine direct effects. Species interactions may cause additional indirect effects by changing the density of a species' competitors (Barton & Ives 2014). Opposing ecological theories exist, however, on the effect of environmental stress on these species interactions themselves, assuming that per-capita interaction do either remain unaffected, change in strength, or even shift from competitive to facilitation at high stress (Chesson & Huntly 1997; Maestre *et al.* 2009; Hart & Marshall 2013). The importance of environmental stress effects on species interactions for biodiversity effects on function remains unresolved at present (Baert *et al.* 2016).

Environmental stress invariably selects for tolerant species. We, therefore, hypothesise that the slope of BEF relationships should initially increase with environmental stress. Biodiversity increases the probability that a system will contain tolerant species that can replace sensitive species (in line with the insurance effect of biodiversity, Yachi & Loreau 1999). Hence, more diverse systems are less likely to experience severe reductions in function compared to less diverse systems, resulting in an increased slope of BEF relationships (Steudel *et al.* 2012; Hodapp *et al.* 2016). However, the BEF relationship should collapse to a horizontal line when stress is sufficiently high to inhibit the growth of all species. Thus, overall, the slope of a BEF relationship should respond to stress in a unimodal way. Moreover, stress inevitably induces a correlation between functional and competitive abilities, causing tolerant species that grow relatively well in monoculture to displace sensitive species as stress intensifies (Baert *et al.* 2016). Hence, we expect that the response of the dominance effect to stress will be a key driver of this unimodal response.

Here, we first used a game theoretic competition model to explore how increasing environmental stress alters BEF relationships for aggregated ecosystem functions and the underlying dominance and complementarity effects in competitive systems. We simulated four different scenarios of environmental stress effects on per-capita interactions: environmental stress had either no effect, increased, or decreased the strength of per-capita interactions without changing the type of species interactions, or reduced per-capita interactions with obligate shifts to facilitation at high levels of environmental stress as postulated by the stress gradient hypothesis (Chesson & Huntly 1997; Maestre *et al.* 2009; Hart & Marshall 2013). Direct effects of environmental stress on fitness were modelled as reductions in species per-capita growth rates in all scenarios. We tested if BEF-relationships and underlying biodiversity effects responded monotonically or unimodally to increasing environmental stress, by fitting second-order polynomials to the simulated data. To assess the generality of our findings, we performed this analysis for a wide range of BEF relationships that are theoretically possible under unstressed conditions, including negative, horizontal, and positive BEF relationships. Next, we confronted model predictions with observed changes in BEF relationships from a meta-analysis of 44 studies in primary producer systems that manipulated species richness under at least 3 different environmental conditions.

METHODS

Model structure

We used a stochastic game theoretic community model (Huang *et al.* 2015) to simulate a broad spectrum of theoretically possible BEF relationships. In this model, population dynamics are thereby assumed to be exclusively driven by birth, death, and inter- and intraspecific interaction processes, occurring at rates b , d and a , respectively. For every species i , the rates at which its density (N_i) may increase (T_i^+) or decrease (T_i^-) by one individual can be expressed as follows:

$$T_i^+ = b_i N_i, \quad (1)$$

$$T_i^- = d_i N_i + N_i \sum_{j=1}^n a_{i,j} N_j, \quad (2)$$

where n is the number of species in the community. In the absence of heterospecifics (i.e. $n = 1$), the equilibrium density of species i thereby equals $a_{i,i}^{-1} (b_i - d_i)$. Note that, as birth and death events are independent, stochastic demographic fluctuations will occur around the equilibrium population density in the system (Huang *et al.* 2015).

We consider a one-dimensional environmental gradient (E) along which species functioning is altered through direct effects on the per-capita growth rate (Fig. 1). The species-specific functional response, $r_i(E)$, was modelled by a normalised gamma distribution to restrict values between 0 and 1 (i.e. maximal fitness; Fig. 1):

$$r_i(E) = \left[\frac{E}{\theta_i (k_i - 1)} \right]^{k_i - 1} e^{-\frac{E}{\theta_i} + (k_i - 1)} \quad (3)$$

The shape parameter k_i and scale parameter θ_i of the gamma distribution thus determine the width of the environmental niche ($-k_i \theta_i^2$) and the optimal environmental conditions ($k_i \theta_i$)

at which the maximal per-capita birth rate of species i is attained. We used a gamma distribution to allow for both symmetrical and asymmetrical niches. Note that values for the environmental gradient are hence restricted to positive values.

The per-capita growth rate of each species along the environmental gradients $b_i(E)$ can hence be written as follows:

$$b_i(E) = b_{0,i} r_i(E) \quad (4)$$

where $b_{0,i}$ is the maximal per-capita birth rate of species i at optimal environmental conditions (Fig. 1).

Since optimal conditions and functional responses may differ among species within a system, we quantify the stressfulness of environmental conditions (E) as the stress intensity (SI), which is the average species' fitness reduction at these environmental conditions (Steudel *et al.* 2012):

$$SI(E) = 1 - \sum_{k=1}^m \frac{r_k(E)}{m} \quad (5)$$

where m is the number of species within the experiment (see also model simulations). Hence, stress intensity ranged from 0 for on average optimal conditions to 1 for severely stressed conditions (Fig. 1).

We define four scenarios of environmental stress effects on per-capita interactions, and thus indirect effects of environmental stress, representing the main hypotheses commonly postulated (Hart & Marshall 2013). When the sign of species interactions is not altered by stress, stress effects on per-capita interactions are modelled as follows:

$$a_{i,j}(E) = a_{0,i,j} [1 + \beta_i SI(E)]^\gamma \quad (6)$$

The species-specific parameter β_i thereby denotes the strength by which increasing environmental stress affects per-capita interactions for a given species. The power γ defines whether per capita interactions are unaffected ($\gamma = 0$), increase ($\gamma = 1$) or decrease ($\gamma = -1$) with increasing stress. For the fourth scenario in which per capita interactions shift to facilitation by environmental stress, i.e. change sign as proposed by the stress gradient hypothesis (Maestre *et al.* 2009), stress effects on per-capita interactions are modelled as:

$$a_{i,j}(E) = a_{0,i,j} [c_i - SI(E)][1 + \beta_i SI(E)]^\gamma \quad (7)$$

where the species-specific parameter c_i indicates the stress intensity at which per capita interactions for species i become negative, and thus shift from competition to facilitation.

Along the one-dimensional environmental gradient, the transition rates of a system of n species under given environmental conditions (E) can thus be written as follows:

$$T_i^+ = b_i(E) N_i \quad (8)$$

$$T_i^- = d_i N_i + N_i \sum_{j=1}^n a_{i,j}(E) N_j \quad (9)$$

Scenarios and parameterisation

We simulated the model for four scenarios of environmental stress on per-capita interactions. In the first scenario, we assumed no effects of environmental stress on per-capita interactions. Hence, the parameter γ was set to zero for those model simulations (eqn 6). In the second and third scenario, we

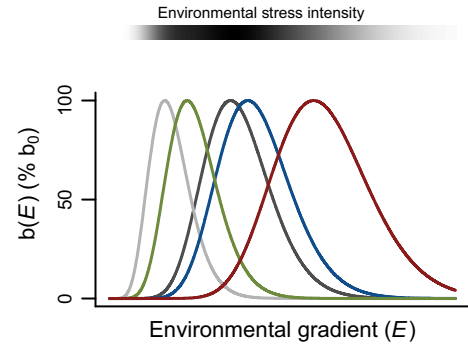


Figure 1 Species functional responses along and environmental gradient and the definition of environmental stress intensity as used by the model. Niches of five hypothetical species are depicted as the change in the per-capita birth rate (b) over an environmental gradient (E). Note that values have been normalised to the percentage reduction in the maximal per-capita birth rate, $b_{i,0}$. The stress intensity of an environmental condition is calculated as the average % reduction in the maximal per capita birth rate of the species. Lighter colours indicate higher environmental stress intensity.

assumed a continuous increase or decrease in per-capita interactions, and thus competition, but without changes in the type of interactions at high stress (eqn 6). In both scenarios, β_i was sampled from $U(0, 10)$ for each model simulation. The parameter γ was set to 1 (scenario 2) or -1 (scenario 3) to simulate a continuous increase or decrease strength of per-capita interactions, respectively. In the fourth scenario, we assumed a linear decrease in per-capita interactions with shifts to facilitation at high levels of environmental stress (eqn 7). Identical to scenario 3, β_i was sampled from $U(0, 10)$ and γ was set to -1 . The additional parameter c_i , denoting the stress intensity at which per-capita interactions shift from positive to negative, was sampled from $U(0.75, 1)$ for each model simulation.

We used a Monte-Carlo simulation procedure to generate 100 BEF relationships, and simulated changes in each of those BEF relationships by increasing environmental stress, for each of the four scenarios of environmental stress effects on per-capita interactions. The generated set of BEF relationships represented an exhaustive set of ecologically relevant BEF relationships under unstressed conditions, ranging from negative to strongly positive relationships (Fig. 2). Per capita birth rates under optimal conditions, $b_{0,i}$, and per capita mortality rates, d_i , were randomly sampled from $U(0, 1)$ and $U(0, 0.01b_{0,i})$, respectively. The means of the gamma distributions (i.e. the optimal environmental conditions for every species), were sampled from $U(95, 105)$, and the variances were sampled from $U(10, 50)$. The strength of intraspecific interactions $a_{i,i}$, which is the main determinant of differences among species monoculture yields, was sampled from $U(10^{-4}, 10^{-3})$. The strength of interspecific interactions was subsequently sampled from $U(-0.01 a_{i,i}, 2 a_{i,i})$. A sensitivity analysis of the parameters distributions revealed that the model results did not depend on the parameter distributions: using different sets of ecologically relevant parameter distributions did not alter our results (Fig. S1).

Model simulations

For each simulation, we first generated a pool of 20 species by randomly drawing values for $b_{0,i}$, k_i , θ_i , d_i , $\alpha_{i,i}$ and $\alpha_{i,j}$ for all

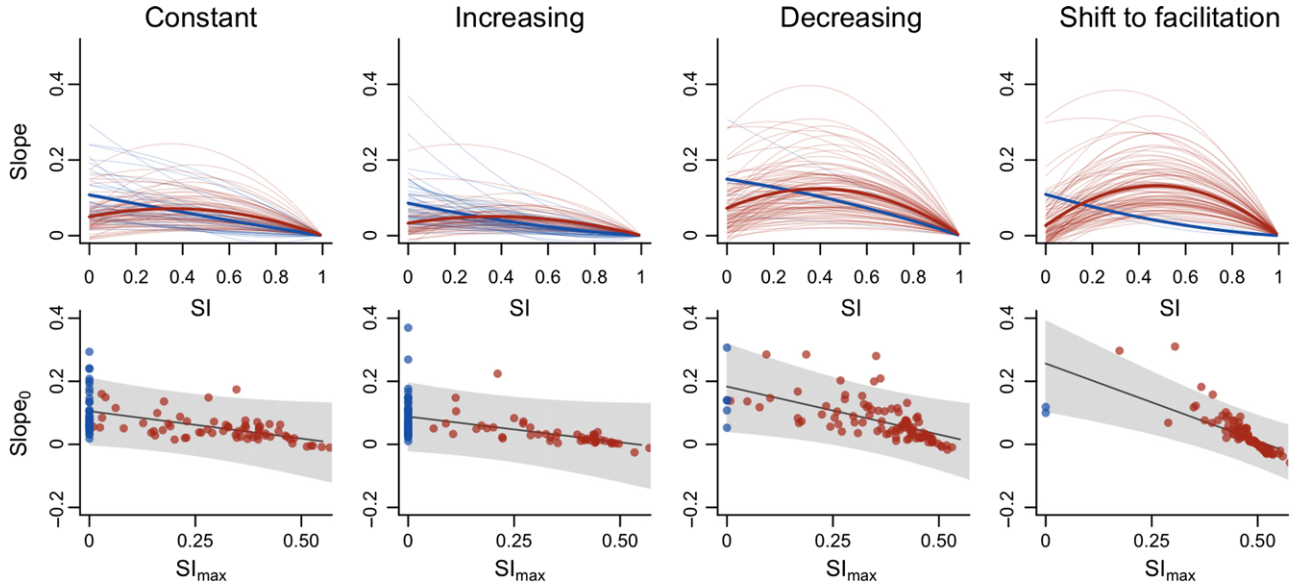


Figure 2 Upper panels: simulated changes in slopes of BEF relationships with increasing environmental stress intensity (SI) for constant, increasing, decreasing, and shifts from competitive to facilitative per-capita interactions under increasing environmental stress intensity. Lower panels: simulated relationship between the slope of the BEF relationship under unstressed environmental conditions ($Slope_0$) and the stress intensity at which a maximal slope is attained (SI_{max}). Red lines and dots indicate unimodal relationships, blue lines and dots indicate monotonic relationships. Thick lines represent the model predictions for unimodal and monotonic relationships. The grey shaded area corresponds to the 95% prediction interval.

species (Fig. S2). Next, 10 communities of 2, 4, 8, and 16 species were randomly assembled from this species pool, representing a standard design used in BEF studies (Cardinale *et al.* 2011). Community dynamics were then simulated under unstressed conditions and under nine conditions of environmental stress ($SI = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9$; Fig. S2). Community dynamics were simulated using the Gillespie algorithm to shorten simulation times by optimising the length of the time-steps used (Gillespie 1976). Initial ($t = 0$) densities were set to 100 for all species. Population densities always reached their stationary distribution at $t \leq 30$. Simulations were run till $t = 50$. Mean species densities were calculated from the species densities between $t = 40$ and $t = 50$. Each simulation was reiterated 12 times to ensure convergence of the stationary distribution (Fig. S3).

Ecosystem functioning was calculated as the sum of the mean species' densities. BEF relationships at each level of environmental stress were subsequently calculated by linearly regressing functioning against the initial species richness of the system. Biodiversity effects for all environmental conditions were calculated according to the additive partitioning approach by Fox (Fox 2005):

$$\begin{aligned} \Delta Y &= \sum_i^n Y_{o,i} - Y_{e,i} = \sum_i^n (RY_{o,i} - RY_{e,i}) M_i \\ &= n \operatorname{cov} \left(\frac{RY_{o,i}}{RYT} - RY_{e,i}, M_i \right) + \operatorname{cov} \left(RY_{o,i} - \frac{RY_{o,i}}{RYT}, M_i \right) \\ &\quad + n E(\Delta RY) E(M) \end{aligned} \quad (10)$$

where ΔY is the deviation between the expected and observed yield, which is the sum of the individual species deviations between observed ($Y_{o,i}$) and expected yields ($Y_{e,i}$). RY denotes the relative yield, i.e. the fraction of the monoculture yield.

The expected relative yield ($RY_{e,i}$) thereby equals the species initial proportion in the mixture (i.e. n^{-1}), whereas the observed relative yield is the mean value of each species stationary distribution divided by its monoculture yield under the same environmental conditions ($M_i = a_{i,i} [b_i(Env) - d_i]$). RYT is the relative yield total (i.e. $\sum_i^n RY_{o,i}$).

Review of literature data

We searched Thomas Reuters Web of Knowledge (www.webofknowledge.com) and Google Scholar (www.scholar.google.com) in February 2018 for experiments that manipulated species richness under at least three environmental conditions, and reported the species monoculture functions for all environmental conditions were considered, as this is a prerequisite to calculate the intensity of environmental stress and discriminate between monotonic and unimodal changes in BEF relationships (see Data normalisation and analysis). We used the search terms 'biodiversity', 'ecosystem', 'function', 'productivity', 'stress', 'temperature', 'nutrient', 'precipitation', 'chemical', 'salinity', 'environment' in various combinations. We additionally checked the cited literature for further original studies. Data were available as text, excel files or were digitised from the figures in the original publications. Digitised data did not differ by more than 1% among different applications (e.g. Engauge, WebPlot, ExtractGraph digitiser). This yielded a total of 44 studies (Fig. S4, Table S1), all of which used primary producer systems. Environmental gradients comprised drought ($n = 37$), temperature ($n = 3$), pollutants ($n = 2$), salt ($n = 1$), nutrients ($n = 1$) and shade ($n = 1$).

Data normalisation

Literature and simulated data were normalised prior to analysis. The severity of the environmental stress was calculated

according to eqn 5, as the ratio between the average observed monoculture under stress and unstressed conditions for all species. Unstressed conditions were defined as those environmental conditions under which species attained the highest mean monoculture functions. Since the units in which aggregated ecosystem functions are measured varied among studies, slopes were normalised by dividing the linear regression coefficient of the BEF relationship by the average monoculture function under unstressed conditions. Thus, normalised slopes all had species⁻¹ as a unit.

Analysis of simulated and empirical data

We carried out the same analyses on the simulated data (including all four scenarios of environmental effects on per-capita interactions) as on the empirical data. First, we tested how the slope of BEF relationships changed along environmental stress gradients, using second-order polynomials. Next, we tested how the effect on the BEF slope varied among the range of unstressed BEF relationships considered by the model or present in the empirical data. To do so, we regressed the slope under unstressed conditions against the stress intensity at which the BEF slope peaked. The dataset ID (i.e. simulated scenario 1, 2, 3, and 4 or empirical data) was included as an additional factorial fixed effect in the linear regression model to be able to compare among simulated scenarios and between simulations and empirical data. Residual diagnostics were assessed for deviations from normality and homoscedasticity (Fig. S5).

RESULTS

Model simulations

Model simulations revealed highly consistent changes in the slope of BEF relationships, irrespective of how environmental stress affected per-capita interactions (Fig. 2). In all four scenarios, most simulations confirmed a unimodal response of the slope of the BEF relationship to increasing environmental stress: biodiversity effects peaked at intermediate levels of environmental stress (Fig. 2). Only when initial BEF slopes were high, the model predicted a monotonic decrease in BEF relationships. When synthesising across the wide range of BEF relationships under unstressed conditions considered by our modelling, we found a negative relationship between the slope under unstressed conditions and the level of environmental stress where the BEF slope peaks (Fig. 2).

While BEF relationships responded consistently to environmental stress across all simulations, the responses of the underlying biodiversity effects, however, depended strongly on how per-capita interactions were affected by environmental stress. In all four scenarios, environmental stress-induced changes in dominance effects drove the change in BEF relationships (Fig. 3). Unimodal changes in the complementarity effects, in contrast, only contributed to overall changes of the BEF relationship in scenarios 3 and 4, where the strength of per-capita interactions decreased with increasing environmental stress. When per-capita interactions remained constant or

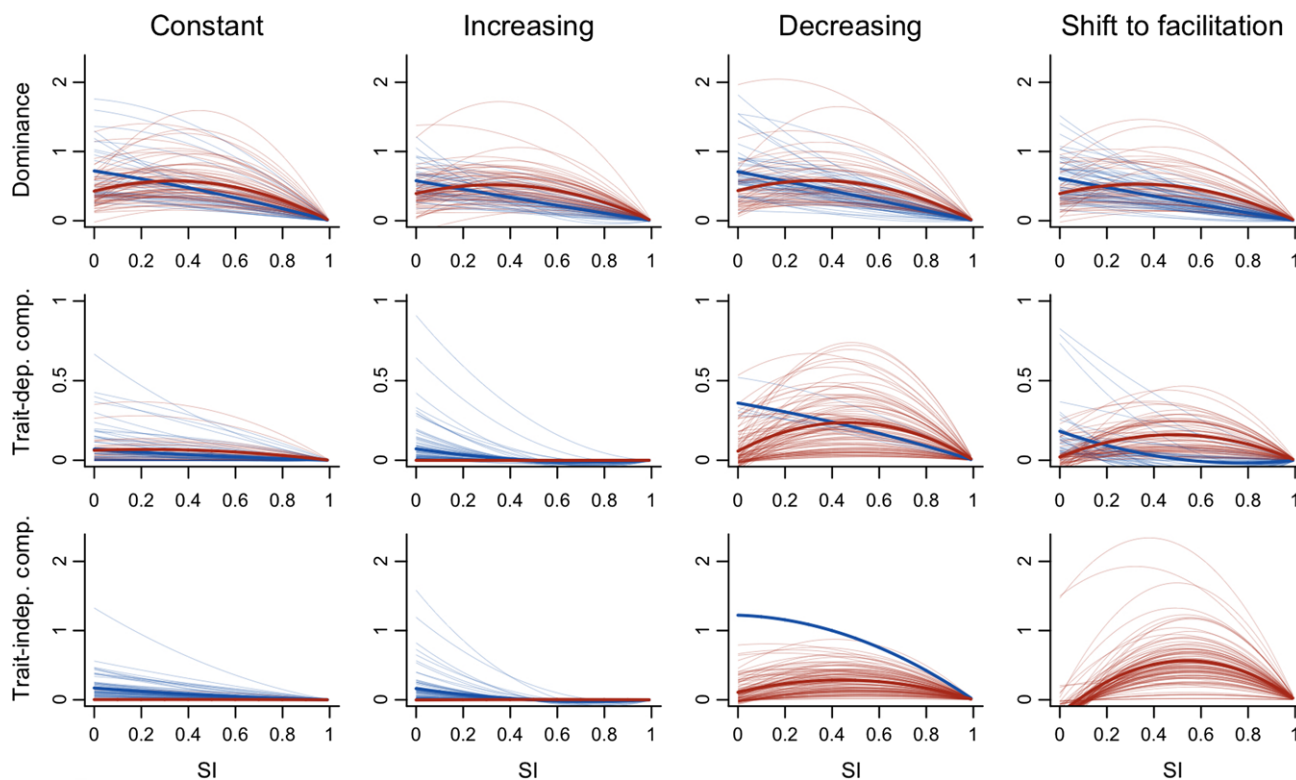


Figure 3 Simulated changes in dominance, trait-dependent and trait-independent complementarity effects with increasing environmental stress intensity (SI) for constant, increasing and decreasing per-capita interactions under increasing environmental stress intensity. Red lines indicate unimodal relationships, blue lines indicate monotonic relationships. Thick lines represent the mean model predictions for unimodal and monotonic relationships.

increased with environmental stress, complementarity effects instead on average decreased monotonically.

Meta-analysis of biodiversity experiments

Observed responses of the slope of BEF relationships to environmental stress, as reported in the 44 empirical studies, confirm predictions of a predominantly unimodal model response of BEF relationships to increasing environmental stress (Fig. 4). In the majority of these studies, fitted polynomials peaked at intermediate levels of environmental stress, while monotonically decreasing polynomials were only supported for studies where BEF slopes in unstressed conditions were strongly positive. Confirming model predictions, the environmental stress intensity where biodiversity effects peaked were indeed negatively related to the slope of the BEF-relationship under unstressed conditions (Fig. 4). This negative relationship was comparable between the simulated and empirical data for all the tested scenarios, and did not significantly differ between the simulated and empirical data for scenarios 3 and 4 in which per-capita interactions decreased with increasing stress (Table 1).

DISCUSSION

Our results demonstrate that environmental stress changes biodiversity effects on ecosystem functioning, and that the strength of these changes may vary considerably, yet predictably, among systems. We presented a model that, based on a minimal set of mechanisms, disentangles a general response driven by stress effects on dominance, from system-specific effects resulting from stress effects on complementarity (Figs. 2 and 3). While dominance effects and the BEF slope tend to respond in a unimodal way to increasing environmental stress, the response of complementarity effects to stress strongly depends on the per-capita species interactions and how these are affected by environmental stress (Fig. 3). Our meta-analysis of current biodiversity experiments confirms a key model prediction: the consequences of biodiversity changes for ecosystem functioning are likely to increase at low to intermediate levels of environmental stress (Fig. 4).

Model simulations suggest that the unimodal change in the BEF relationship to increasing environmental stress is

primarily driven by species differences in sensitivity to environmental stress through shifts of the dominance effect. As postulated, positive dominance effects were promoted by increasing fitness differences under increasing environmental stress, as species experiencing smaller fitness reductions will increasingly replace species experiencing severe fitness reductions. However, when levels of environmental stress became so high that fitness of most species is severely reduced, the strength of the dominance effect and the slope of the BEF relationship decrease again, because the potential for functional replacement is lost, even in more diverse systems. From this threshold stress level onward, the slope of the BEF relationship decreased until it reaches a flat line at extreme levels of environmental stress, where the functioning of all species is inhibited (Fig. 2). However, when dominant high-functioning species were also most sensitive to environmental stress, increasing stress is likely to replace these with low-functioning species, causing a loss of function and monotonic decrease in dominance effects with increasing environmental stress (Fig. 3).

Unlike the dominance effect, changes in complementarity effects were more system-specific and varied with the strength of, and environmental effects on, species interactions. Changes in complementarity effects strongly differed among model scenarios. Along an environmental stress gradient, the number of species that can significantly contribute to ecosystem functions was progressively reduced, which decreases the ratio between inter- and intraspecific interactions experienced by the remaining species. When per-capita interactions remained constant, this reduced both positive and negative complementarity effects at these elevated stress levels, causing a decrease in complementarity effects by increasing environmental stress (Fig. 3).

When stress increased the strength of per-capita interactions, i.e. increases interspecific competition, complementarity effects were likely to decrease even faster with increasing stress. In this case, stress additionally reduced the potential for positive complementarity effects. Although changes in complementarity effects did not drive the overall changes in BEF relationships in both scenarios, per-capita interactions can have a profound effect on the environmental stress level at which biodiversity effects peak. The slope of the BEF relationship may increase as long as decreases in complementarity

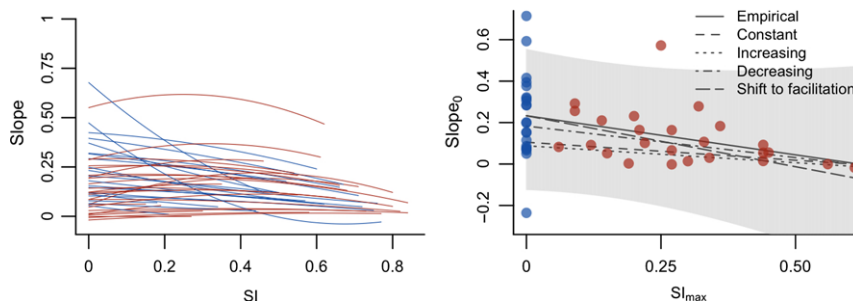


Figure 4 Left panel: Empirical observed changes in slopes of BEF relationships with increasing environmental stress intensity (SI). Right panel: Empirical and modelled relationship between the slope of the BEF relationship under unstressed environmental conditions (Slope₀) and the stress intensity at which a maximal slope is attained (SI_{max}). Red lines and dots indicate unimodal empirical relationships, blue lines and dots monotonic empirical relationships for the empirical data. The grey shaded area corresponds to the 95% prediction interval for the empirical data.

Table 1 Estimated relationship between the slope under unstressed conditions and the stress intensity at which maximal biodiversity effects are attained. Significances for model simulations are expressed against the value of the empirical regression

	Estimate	P-value
Intercept empirical data	0.233	< 0.001
Intercept constant interactions	0.105	< 0.001
Intercept increasing interactions	0.087	< 0.001
Intercept decreasing interactions	0.183	0.06
Intercept shift to facilitation	0.233	0.62
SI _{max} empirical data	−0.379	< 0.001
SI _{max} constant interactions	−0.174	0.009
SI _{max} increasing interactions	−0.163	0.008
SI _{max} decreasing interactions	−0.305	0.42
SI _{max} Shift to facilitation	−0.492	0.34

effects are offset by larger increases in dominance effects. Maximal biodiversity effects can therefore be expected to be attained at lower levels of environmental stress when systems are driven by highly positive complementarity effects under unstressed conditions (Fig. 3).

When the strength of per-capita interactions decreased with increasing stress, the reduction in competition could however counteract negative direct effects of environmental stress by increasing complementarity effects under stress. Higher diversity thereby increased the potential for positive complementarity effects, increasing the slope of the BEF relationship. This increase in complementarity effects was even higher when interactions become positive under high environmental stress. At extreme stress levels, direct effects on fitness became so high that complementarity effects and BEF relationships start to decrease to reach a flat line (Figs. 2 and 3). In all four scenarios, the responses of trait-dependent complementarity effects were similar to those of trait-independent complementarity effects. This could be expected as both are driven by the same mechanisms and only express the extent by which complementarity effects are (a)symmetrical across all species in the system. Only their relative contribution to changes in BEF relationships is highly community-specific and depends on the asymmetry of the species interactions within the system (Fox 2005).

Our results reveal that separating a general from a system-specific response over an environmental gradient will be an important step in reconciling the apparent contradictions among the results reported by experiments manipulating biodiversity under different environmental conditions. While biodiversity experiments conducted over the past decades almost unequivocally yielded positive relationships (Hooper *et al.* 2005; Cardinale *et al.* 2012), changing environmental conditions have resulted in either increases (Fridley 2003; Boyer *et al.* 2009), decreases (Reich *et al.* 2001; Fridley 2002; Rixen & Mulder 2005; De Boeck *et al.* 2008; Wacker *et al.* 2009; Fernandes *et al.* 2011; Steudel *et al.* 2011, 2012), or no effects on the slope of the BEF relationship (Mulder *et al.* 2001). The theory presented in the present study allows these results to be interpreted within a single generalised framework, reflecting different system-specific realisations of a unimodal response of BEF relationships to environmental stress gradients. Monotonically decreasing relationships in both simulated

and empirical data may thereby in fact represent unimodal relationships that peak at extremely low levels of environmental stress, but which remained undetected by a too coarse resolution of the environmental gradient. Still, only few studies to date have manipulated species richness under a sufficiently broad range of environmental conditions to reveal such a unimodal response (Figs. 4 and S4) as many studies apply only two or three environmental stress levels.

Our model simulations revealed that shifts in per-capita interactions have important consequences for the mechanisms that can drive shifts in BEF relationships across environmental gradients. Increased niche complementarity and facilitation under environmental stress have been documented to increase in several plant systems (Rixen & Mulder 2005; Maestre *et al.* 2010; Hart & Marshall 2013; Wright *et al.* 2017). Hence, this may explain why the empirical relationship between the slope under unstressed conditions and the stress intensity under which maximal biodiversity effects were attained best corresponded to the model scenarios under which per-capita interactions and competition decreased with increasing stress (Table 1, Fig. 4). Still, only few studies have assessed the biodiversity effects underlying BEF relationships at different environmental conditions (De Boeck *et al.* 2008; Li *et al.* 2010; Steudel *et al.* 2011; Baert *et al.* 2016). As such, little empirical support exists for whether changes in BEF relationships are merely driven by dominance effects, or by a combination of dominance and complementarity effects. In addition, it should be noted that throughout this study we have focussed on equilibrium conditions. Environmental stress was assumed to affect species functional contributions through the per-capita growth rate, which caused the system to respond fast to any environmental change. In real primary systems, environmental stress can affect both somatic growth and reproduction. As produced seeds generally only germinate in the following growth season, species turnover can be much slower in real systems compared to our model simulations, and may lead to a reduced importance of shifts in dominance in real systems compared to our model simulations. Finally, in this study, we have restricted our model to first-order species interactions. Although there is a growing awareness that higher-order (including multi-trophic) interactions may significantly contribute to ecosystem functions (Soliveres *et al.* 2016; Grilli *et al.* 2017; Barnes *et al.* 2018; Wang & Brose 2018), we focussed on aggregated ecosystem functions within a single trophic level throughout this study. Our findings reveal that although they may be partly a consequence of higher order interactions, major patterns in primary producer systems, changes in the BEF relationship and underlying biodiversity effects primarily depend interactions within this single trophic level.

Environmental and biodiversity changes pose major threats to ecosystems worldwide (Hooper *et al.* 2012). Understanding how both processes are intertwined is therefore a major challenge to appropriately assess the consequences of ongoing and future biodiversity changes (Isbell *et al.* 2013, 2015; De Laender *et al.* 2016). The presented results provide a theoretical framework to meet this challenge, as they allow predicting the context-dependence of BEF relationships. Our model simulations revealed testable hypotheses on a consistent change in

BEF relationships in response to environmental stress, but also on how the underlying mechanisms and differences in the magnitude of changes in BEF relationships may differ between systems based on differences in the strength and environmental response of per-capita interactions. Moreover, while underlying mechanisms may be strongly system-dependent, our results suggest that the joint effects of forecasted biodiversity and environmental changes are likely to cause greater effects on ecosystem functions than previously anticipated.

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AUTHOR CONTRIBUTIONS

JMB and FDL conceived the idea. JMB implemented the model and analysed the data. All authors contributed to discussions and the writing of the manuscript.

DATA ACCESSIBILITY STATEMENT

References for all studies used in the meta-analyses with detailed descriptions of the source of the data are given in Table S1.

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

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