**Title:** The function-dominance correlation drives the direction and strength of biodiversity-ecosystem functioning relationships

**Running title:** Function-dominance correlation drives BEF

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**ABSTRACT**

Community composition is a primary determinant of how biodiversity change influences ecosystem functioning and leads to variation in relationships between biodiversity and ecosystem functioning across systems (BEF). The presence of dominant species, for example, can either enhance or inhibit functioning. We examine the consequences of these dynamics across six structurally-realistic plant community models. We find that a positive correlation between species’ functioning in monoculture vs. their dominance in mixture (the “function-dominance correlation”) generates positive BEF relationships across levels of species richness. However, because realised diversity declines when few species dominate, a positive function-dominance correlation also generates negative BEF relationships within any given species richness treatment. Removing external seed input strengthens function-dominance correlations across species richness treatments but weakens it within them. These results suggest that changes in the identity of species in a local species pool may more strongly decrease or increase ecosystem functioning than changes in species richness alone.

**INTRODUCTION**

Humans are driving drastic environmental changes leading to global biodiversity loss (*Millenium Ecosystem Assessment Ecosystem and human well-being: synthesis* 2005; Tittensor *et al.* 2014; Newbold *et al.* 2015; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). The rate of this biodiversity loss will likely accelerate in the coming decades (Pereira *et al.* 2010; Pimm *et al.* 2014; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). Biodiversity experiments demonstrate that the loss of randomly selected species from controlled communities generally decreases local ecosystem functioning (Tilman *et al.* 2014). However, the response of ecosystem functioning to biodiversity change is also context-dependent. Even within a single ecosystem type such as grasslands, there is significant divergence in the direction (negative vs. positive, Meyer *et al.* 2018), strength (Guerrero-Ramírez *et al.* 2017), and drivers (Barry *et al.* 2019b) of biodiversity-ecosystem functioning (BEF) relationships. This variation in BEF relationships is even greater when multiple ecosystem types are considered (Duffy *et al.* 2017; van der Plas 2019). Understanding this variability is of critical importance to anticipating the impact of biodiversity change.

One cause of this variability is likely variation in local-scale processes, such as species interactions, which determine which species can coexist in a community and the extent to which facets of biodiversity may influence ecosystem functioning (Wright 2002; Holt 2013; Barry *et al.* 2019a). Interplay between these processes may result in variation in BEF relationships across ecosystems differ in the nature and strength of local and regional community assembly mechanisms (Leibold *et al.* 2017). Communities with more species are more likely to include species that produce high levels of ecosystem functioning (e.g. biomass) through a “sampling effect” (Huston 1997; Hooper *et al.* 2005). As a result of this sampling effect, communities with high planted species richness are higher functioning, while communities with low planted species richness are lower functioning on average. This leads to a characteristic positive BEF relationship across communities with different levels of species richness. Alternatively, within a community, the dominant species may contribute the most to functioning and outcompete other species. If this occurs, ***realised diversity*** may be negatively related to functioning across communities that are planted with similar numbers of species (Leibold *et al.* 2017, Fig. 1A). We refer to this characteristic pattern of contrasting BEF relationships across communities with very different versus similar numbers of species as a “counter-gradient” (Fig. 1). This type of counter-gradient is often associated with Simpson’s paradox which indicates that an underlying covariate may influence observed patterns (Simpson 1951).

We hypothesise that the covariate driving this paradox and, more importantly, the variation in BEF relationships across systems, is the correlation between a species’ ability to dominate in mixture (‘dominance’) vs. its baseline capacity to contribute to ecosystem functioning (‘functioning’). When this correlation is positive, we expect the counter-gradient to have a positive slope across communities that differ in species richness and a negative slope with realised diversity across communities with similar species richness (Fig. 1A). Alternatively, when this correlation is negative, we expect this counter-gradient to have a negative slope across communities that differ in species richness and a positive slope across communities that have similar species richness (Fig. 1B) because of a negative sampling effect. That is, in more diverse communities, the likelihood of including a dominant low-functioning species would be higher. Likewise, within communities of similar planted species richness, when the community is dominated by the low-functioning species, functioning is expected to be lower than in communities where species abundances are more evenly distributed (i.e. at higher realised diversity). We refer to this correlation between species dominance in mixture and their capacity to provide functioning as the “function-dominance correlation”.

In addition to these local processes related to the identity and dominance of species in local species pools, regional processes, such as seed dispersal, can affect coexistence by maintaining populations that would otherwise go extinct (Leibold & Chase 2018). These regional scale processes also influence ecosystem functioning (Leibold & Chase 2018). We hypothesise that reducing seed dispersal likely increases the importance of the function-dominance correlation for BEF relationships since seed dispersal may decrease the abundance of the dominant species. If the function-dominance correlation is positive, for example, this lower abundance of the dominant species will lead to a lower functioning of the community (Leibold *et al.* 2017). However, when the community is isolated from seed dispersal, the dominant species will outcompete other species leading to increased ecosystem functioning while reducing realised diversity.

In order to test these hypotheses and identify general, broadly conserved links between function-dominance correlations and BEF relationships, we considered six independently derived and validated plant community models. We subjected these six models of plant community dynamics to a common experimental design. This experiment mirrors a traditional BEF experiment except that it also includes a treatment in which the simulated communities are completely isolated from seed dispersal. Further, these models represent a variety of systems and community assembly processes, such as negative density dependence and resource partitioning, so the outcomes of this exercise are unlikely to be limited to a specific system or set of processes.

We found that, across models and ecosystem types, the function-dominance correlation determines the strength and the direction of BEF relationships. When the dominant species in mixture are large producers of ecosystem functioning in monocultures (i.e., positive function-dominance correlation), BEF relationships tend to be positive across communities of contrasting species richness and negative across communities of similar species richness. Alternatively, BEF relationships tend to be weak, or lead to a “negative counter-gradient”, when this correlation is weak or negative, respectively. Further, the importance of the function-dominance correlation for BEF relationships across communities is higher in the absence of external seed input. With the function-dominance correlation, we provide an ecologically grounded metric that explains the variability among BEF relationships. This work has major implications for how to apply BEF research to the problem of biodiversity change. A major trend of biodiversity change in local communities appears to be changes in the identities of the species (Dornelas *et al.* 2014; McGill *et al.* 2015; Blowes *et al.* 2019). If BEF relationships are determined by the function-dominance correlation, then this change in the identity of species in the local community may have larger or smaller impacts on ecosystem functioning than declines in species richness *per se*. If the species that are dominant and high functioning are lost, we expect that their loss will cause declines in ecosystem functioning unless they are replaced by species that perform similarly well. Alternatively, if the species lost are dominant but contribute little to ecosystem functioning, the effect of losing these species in a local community on ecosystem functioning may even increase functioning.

**MATERIALS AND METHODS**

*Model descriptions*

We included six published plant community models that cover a diverse array of ecosystems and model types, ranging from forests to succulent communities, and from systems of differential equations to fully individual-based simulation models (Table 1). This diversity of models enabled us to identify broadly conserved interactions between systems’ function-dominance correlations and their emergent BEF relationships, while reducing any bias that would otherwise be introduced by focusing on one study system or class of models. The models capture key elements of their target systems and have been extensively analysed and documented in published literature. They support realistic levels of biodiversity, and the mechanisms driving coexistence between their species is known.

*Grass1* (Clark *et al.* 2018) explores the effects of trade-offs between the ability of species to take up and retain resources vs. their ability to prevent other species from accessing resources. Species must excel at one of these types of behaviours in order to persist in mixture. The model is designed to portray dynamics in a Minnesota tallgrass prairie, and was parameterised from observations of three plant traits measured in experimental monocultures. Model dynamics are deterministic, and allow for an arbitrarily large number of species to stably coexist, provided that their traits all fall within the correct regions of trade-off space.

*Grass2* (Turnbull *et al.* 2013) is also designed to mimic dynamics in grassland plant communities, and focuses on a classic trade-off between the relative growth rate of a species and its carrying capacity. The model explicitly considers the effects of seasonal cycles. Fast-growing species can coexist with slower-growing species with higher carrying capacities because their faster growth rates allow them to rapidly exploit resources early in the growing season, which they cannot subsequently lose. The model is deterministic, and, given the right distribution of trait values, allows arbitrarily large numbers of species to stably coexist.

*Grass3* (IBC-grass, May *et al.* 2009; Weiss *et al.* 2014) explores the trade-off between asymmetric competition for light and susceptibility to grazing within central European managed grasslands. Competition is individual-based and spatially-explicit. Given adequate belowground resources, larger, faster-growing species dominate competition for light, but are also subject to more frequent grazing relative to their shorter, more stress-tolerant competitors. In *Grass3*, the trade-off between growth rate and stress-tolerance equalises fitness among competing species, but stable coexistence is realised through conspecific negative density dependence that reduces the fitness of individuals when surrounded by conspecific neighbours.

*Forest1* (PPA, Rüger *et al.* 2020) is designed to simulate the dynamics of a diverse tropical rainforest at Barro Colorado Island, Panama, based on a small set of demographic rates (growth, survival, and recruitment). It accounts for height-structured competition for light by distinguishing four canopy layers. Canopy gaps are filled by the tallest trees from lower canopy layers, without regard for their horizontal position within one hectare (perfect plasticity approximation; Purves et al. 2008). Tree species fall along two demographic trade-offs: a growth-survival trade-off and a stature-recruitment trade-off (Rüger et al. 2018). The model is deterministic, and stable coexistence relies on external seed rain (Lichstein & Pacala 2011).

*Forest2* (TROLL, Maréchaux & Chave 2017) is an individual-based and spatially-explicit model of tropical forest dynamics. It uses species-specific functional traits to parameterise tree physiological function and demographic processes, according to relationships and trade-offs taken from the literature. Individual trees compete for light within a 1 m3 voxel grid, in which tree death and gap formation create horizontal and vertical heterogeneity of light availability. Seed dispersal is spatially explicit and includes both local sources (fertile trees) and external seed rain. Here, we used a model version without additional Janzen-Connell type conspecific negative density dependence, and stable coexistence relies on external seed rain.

*Dryland* (Reineking 2006) is an individual-based, stochastic model, designed to analyse coexistence mechanisms based on allocation trade-offs and environmental heterogeneity. The model is parameterised for succulent communities in the Richtersveld, South Africa. Plants compete for water, and biomass allocation to leaves, roots, water storage and seeds affects plant growth, survival, and reproduction. At high water supply rates, species not investing in water storage outcompete species investing in storage, which in turn persist longer during drought periods. Long-term coexistence of a small number of species is maintained by spatio-temporal heterogeneity in water supply. In the present study, higher levels of local diversity were maintained via external seed rain. Within the Dryland model, our experimental design necessitated a modification to the species pool of the original model, to increase chances of simulating high-diversity communities (see Appendix S1: Model preparation).

*Experimental design*

For each model, a set of 64 species was selected by sampling a functionally diverse assemblage from its original species pool. Depending on the model, this was achieved through either sampling species at regular intervals from the underlying trade-off surface (*Grass1*, *Grass2*, *Dryland*), or by running k-means clustering (k = 64) on the species pool (*Grass3*, *Forest1*, *Forest2*). For each model, we then implemented an experimental design typical of BEF experiments (*sensu* Tilman *et al.* 1996; Roscher *et al.* 2004). The design included seven planted species richness treatments (1, 2, 4, 8, 16, 32 or 64 species) with 64 replicates each (except for the 64-species treatment with only one replicate). The 1-species treatment consisted of monocultures of the 64 species, and the 2- to 32-species treatments were implemented by randomly sampling (without replacement) from the 64-species pool of each model.

For each model, the 385 (6\*64+1) experimental communities were initialised with equal abundances of seeds or seedlings for each planted species (depending on each model’s default settings) and run until a stable abundance distribution was achieved (hereafter “equilibrium”) (see Appendix S1: Experimental Design). Therefore, the forest models were run for significantly longer than the grassland and succulent models, because their dynamics occur over longer time horizons.

During this stage, external seed rain from the initial species pool of the community took place (*“with seed rain”*). The amount of external seed rain for each species and time step was constant and corresponded to the average internal seed production per time step of all equilibrium monocultures divided by the number of species. To explore the effect of isolating the communities from their respective metacommunities, in a second stage of the same duration, external seed rain stopped (*“without seed rain”*). We measured diversity and ecosystem functioning on the last time steps of the seed rain and without seed rain stages.

*BEF relationships within models*

We used the Shannon diversity index to quantify community diversity because in addition to including richness, Shannon diversity includes the evenness component of diversity and therefore changes with species abundance. In several of the simulations, species abundances declined to very low levels rather than to zero. While these species became functionally extinct, realised species richness remained unchanged. However, our results were qualitatively similar for both indices (see Appendix S2). We present the results for three important but related ecosystem functions: 1. Aboveground biomass (main results), 2. Net primary productivity (Appendix S3), and 3. Overyielding in aboveground biomass, i.e. the capacity of a mixture to outperform monocultures of its component species (Relative Yield, Loreau & Hector 2001, Appendix S4). We apply the same methodology to each ecosystem function contained within the supplemental materials, but for clarity focus on biomass within this manuscript from this point forward. To enable comparison between models with very different amounts of total biomass, we scaled the community biomass across all simulated communities from 0 to 100 for each model by dividing by the maximum biomass achieved and multiplying by 100. We quantified the effect of realised Shannon diversity on biomass across and within species richness treatments, fitting realised Shannon diversity as a continuous fixed effect for each plant community model and seed rain stage.

Our analyses consisted of two steps. In the first step, for each plant community model and seed rain stage, we first fit a Bayesian linear regression between realised Shannon diversity and biomass across species richness levels to estimate the *“across species richness treatment”* BEF slope (black line in Fig. 1, see Appendix S1: Statistical Methods). In the second step, we fit independent Bayesian linear regressions within species richness treatments to quantify *“within species richness treatment”* BEF slopes (coloured lines in Fig. 1) for each plant community model and seed rain stage (see Appendix S1: Statistical Methods).

Regressions were fit using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017) through the ‘brms’ package (Bürkner 2017) in R (R Core Team 2019) using 4 chains, 2000 iterations (1000 as warm up) and Gaussian distributions for all models. We used weakly regularising default priors, and inspection of the HMC chains for each model showed excellent convergence, with R-hat values of 1.0 for all estimates. We used posterior predictive checks to visually inspect how well the statistical models reproduced the data (see Appendix S5).

*Comparison across models*

To test for an effect of the correlation between the capacity of a species to provide ecosystem functioning in monoculture and its dominance in mixture (*“function- dominance correlation”*) on BEF relationships (Fig. 1), we quantified the baseline capacity of a species to provide ecosystem functioning by its monoculture biomass, and its dominance in mixture by its biomass in mixture. This metric is related to, but distinct from, the classic "selection effect" of Loreau and Hector (2001). The selection effect of Loreau and Hector (2001) is quantified using the correlation between monoculture biomass and the ratio of mixture biomass relative to monoculture biomasses. To avoid potential statistical problems related to this ratio distribution (Clark *et al.* 2019), we instead focus on absolute biomass here.

We quantified the function-dominance correlation for each seed rain stage separately. For each stage, we nonparametrically bootstrapped the species’ biomasses (n = 2500, with replacement) within the 32-species mixtures. We then calculated the Pearson’s correlation between the biomasses of these species in the mixtures and their respective biomasses in monoculture. We focused on the 32-species communities because they encompass the highest initial diversity of any treatment level excluding the 64-species treatment, which is unreplicated because our species pool contains 64 species. We then drew 2500 samples from the posterior distributions of the within-treatment and across-treatment BEF slopes of each model and regressed them against the function-dominance correlations. Since both metrics are estimated and thus incorporate error, we used Standard Major Axis regression (lmodel2, Legendre 2018).

**RESULTS**

*Communities with seed rain*

In communities with external seed rain, community biomass was positively correlated with realised Shannon diversity across species richness treatments in five of the six models (all except *Forest2*). The most pronounced positive relationships emerged from *Grass1*, *Grass2*, and *Forest1* (Fig. 2). Within-treatment BEF slopes were negative in four out of the six models. This pattern was most pronounced in *Grass1* and *Forest2*. In *Grass2* and *Forest1*, the within-treatment BEF slopes were negative for low species richness and became positive with increasing species richness. In *Grass3* and *Dryland*, within-treatment BEF slopes tended to be positive.

Consistent with our hypothesis, the effect of realised diversity on community biomass was more positive across species richness treatments (Fig. 3) and more negative within species richness treatments (Fig. 4) in models that display a strong function-dominance correlation (cf. Fig. 1). This relationship was also present in both supplemental ecosystem functions, productivity (Appendix S3) and Relative Yield (Appendix S4).

*Communities without seed rain*

After local communities were isolated from their metacommunity (by eliminating external seed rain), there was no consistent pattern in how the across-treatment BEF slopes changed across models (Fig. 2). Within-treatment BEF slopes often became more positive, either changing from negative to positive (*Grass2*, *Forest2*), becoming less negative (*Grass1*), or becoming more positive (*Dryland*) than in communities with seed rain.

The elimination of external seed rain did not substantially alter the function-dominance correlation, except for *Forest2*, where this correlation changed from positive to negative (see Appendix S5). As a consequence, the relationship between the function-dominance correlation and across-treatment BEF slopes became even more strongly positive (Fig. 3). In contrast, the relationship between function-dominance correlation and within-treatment BEF slopes tended to become weaker (Fig. 4). Both supplemental ecosystem functions, productivity (Appendix S3) and Relative Yield (Appendix S4), were again consistent with this result.

**DISCUSSION**

Biodiversity experiments have convincingly demonstrated the importance of biodiversity for ecosystem functioning. However, applying these findings to naturally assembled systems has proven complex because even in experimental settings, BEF relationships are variable (Guerrero-Ramírez *et al.* 2017; Ratcliffe *et al.* 2017; Barry *et al.* 2020). This variability hinders generalizable predictions for how global biodiversity change is likely to affect ecosystem functioning. The results of our model intercomparison suggest that differences in BEF relationships are driven by the function-dominance correlation. When dominant species have a high capacity to provide ecosystem functioning, diversity and functioning are positively related across communities with different species richness due to the sampling effect, but negatively related across communities with similar species richness – or within a species richness treatment in an experiment – because the dominant species outcompete those species that contribute less to ecosystem functioning. Further, removing external seed input strengthens the importance of the function-dominance correlation across species richness treatments, but weakens it within them. Our model intercomparison shows that these results are consistent for three ecosystem functions (biomass, productivity, overyielding) and across models that have previously been shown to accurately represent the dynamics of grasslands, tropical forests, and a dryland succulent community.

*The function-dominance correlation mediates BEF relationships*

In general, the relationship between realised Shannon diversity and biomass was positive across communities that differ in their species richness in our model experiment (5 out of 6 models). This result is consistent with results from many biodiversity experiments (reviewed by Tilman *et al.* 2014). Where the positive relationship between realised diversity and ecosystem functioning was strongest across species richness treatments (*i.e.* *Grass1*, *Grass2*, *Forest1*), the relationship between realised diversity and biomass was negative within species richness treatments. This negative BEF relationship within species richness treatments is also consistent with results from the Jena Experiment (Rychtecká *et al.* 2014; Leibold *et al.* 2017) but has not, to our knowledge, been tested in other BEF experiments. These contrasting patterns across and within species richness treatments suggest that an underlying latent variable may interact with both of these patterns (*i.e.* Simpson’s paradox, Simpson 1951).

Our results suggest that this “counter-gradient” is likely driven by the correlation between species’ dominance in mixture and their capacity to provide ecosystem functioning. Where this correlation is strong and positive (*Grass1, Grass2, Forest1*), BEF relationships across species richness treatments were most positive and BEF relationships within species richness treatments were most negative. This is because communities with more species are more likely to include dominant species that produce high levels of ecosystem functioning through a “sampling effect” (Huston 1997; Hooper *et al.* 2005). However, across species richness treatments, the dominant and high-functioning species may outcompete other species, and thus causing the negative within species richness treatment slopes. Alternatively, where the function-dominance correlation is weak (*Grass3*, *Forest2*, *Dryland*), the relationship between realised Shannon diversity and biomass is weak or insignificant across communities with contrasting or similar species richness.

This clear link between the function-dominance correlation and BEF relationships emerged despite the diversity of coexistence mechanisms and systems represented by our models. Interestingly, the strength of the function-dominance correlation was not related to the type of mechanisms that allowed for coexistence in the models, i.e. resource partitioning (*Grass1*, *Grass2, Dryland*), seed addition (*Forest1*, *Forest2*), or conspecific negative density dependence (*Grass3*). However, strong local coexistence mechanisms like resource partitioning (*Dryland*) and conspecific negative density dependence (*Grass3*) increased the positive impact of diversity on ecosystem functioning acrosscommunities with similar species richness. *Grass3*, for example, is spatially explicit and incorporates conspecific negative density dependence. Individuals that are surrounded by conspecifics perform more poorly than individuals that are surrounded by heterospecifics (May *et al.* 2009) Because individuals are more likely to be surrounded by heterospecifics in communities with more even species abundances (i.e. at higher Shannon diversity), these more diverse communities are higher functioning. This effect disappears at higher species richness levels because the effect of conspecific negative density dependence is strongest in low diversity communities. Similarly, in *Forest1*, BEF relationships within species richness treatments are negative at low initial species richness but become positive at high initial species richness. In this model, more diverse communities are likely to include several species of similar competitive ability that are able to coexist. These species include ‘tall’ species and ‘slow’ species, two complementary strategies. Tall species maximise biomass in upper canopy layers while slow species maximise biomass in lower layers. Thus, these species partition the vertical canopy gradient, leading to positive BEF relationships within species richness treatments at higher species richness levels. Further, because these six models are so different but lead to a common conclusion, we expect that the function-dominance correlation is relevant across a wide variety of terrestrial systems.

*The effect of removing seed rain*

One benefit of our modelling approach is our ability to eliminate external seed dispersal. In BEF experiments, although plots are weeded, it is usually not possible to distinguish whether new recruits of planted species result from seeding treatments, dispersal from within the plot, or external seed dispersal. Thus, it is impossible to fully isolate the effect of dispersal, and this weeding artifact is thought to be influential in producing BEF relationships (Roscher *et al.* 2004; Hooper *et al.* 2005). Yet, despite the likely importance of dispersal, we found that completely removing seed rain had little effect on across species richness treatment BEF relationships, which are the most commonly reported BEF relationships in the literature.

However, BEF relationships within species richness treatments often became more positive when external seed rain stopped *(Grass1, Grass2, Forest1, Forest2, Dryland*). For example, in *Grass2*, within species richness treatment slopes changed from negative to positive. In this model, species are dominant in mixture by having either a high carrying capacity or a high growth rate (Turnbull *et al.* 2013). Under seed rain, low-biomass species with high growth rates temporarily prevent their slower but higher functioning competitors from accessing soil resources. Consequently, higher functioning, slower-growing species are unable to reach their maximum size. Without external seed rain, these high growth rate-low functioning species decrease in their relative abundance and the remaining species are better able to fully utilise available resources, resulting in a positive within species richness treatment BEF relationship.

Despite shifts of the within species richness treatment BEF relationships, the function-dominance correlation remained largely unchanged, except for *Forest2*, where the function-dominance correlation changed from positive to negative. In this model, small low-biomass species disproportionately benefited from the removal of external seed rain because they reach their reproductive size more rapidly than tall high-biomass species. Thus, they are able to colonise more empty sites and reach a higher biomass in mixture than tall species. This leads to a change in the function-dominance correlation from positive to slightly negative, which in turn caused a reversal of the counter-gradient (negative across, positive within species richness treatments) and reinforced the relationship between the function-dominance correlation and across species richness treatment BEF slopes. To our knowledge, this is the first example of a negative counter-gradient with a negative BEF relationship across species richness treatments, but positive BEF relationships within species richness treatments.

The results of removed seed rain in our modelling experiment may not be immediately applicable to naturally assembled communities. Seed rain in our modelling experiment is limited to the species in the original species pool and assumes constant seed input that is uniform across species. While this approach does not approximate natural seed dispersal, our results are consistent with findings from a recent meta-analysis of seed addition experiments (Ladouceur *et al.* 2020) which found that when dispersal limitation was alleviated by seed addition, species richness increased (also reviewed by Myers & Harms 2009) while biomass was largely unaffected. Our results similarly suggest that diversity is supported by dispersal. In all of our models, communities had generally higher realised diversity with seed rain than without it, but biomass remained largely unaffected in the majority of models (Appendix S6).

*Applying our results to other functions*

Here, we focus on the relationships between realised diversity and three closely related ecosystem functions: aboveground biomass, productivity, and overyielding. Aboveground biomass and productivity are good predictors for many functions, including several that are management and conservation relevant, such as root biomass, carbon storage/sequestration, harvestable volume for forests, and ecosystem stability (Allan *et al.* 2013; Ratcliffe *et al.* 2017). We expect that for this set of biomass- or productivity-related functions, our results here in terms of biomass/productivity will similarly predict BEF relationships. However, many functions such as above- and belowground decomposition, nutrient cycling, microbial biomass, resistance to climate extremes, and many others are not easily predicted by biomass or productivity. For this subset of functions – while the function-dominance correlation in terms of biomass is unlikely to predict these BEF relationships – the function-dominance correlation in terms of these other functions is likely to prove a useful predictor.

**CONCLUSIONS**

Global biodiversity loss and local and regional biodiversity change are among humanity’s most pressing concerns. The current consensus is that this change is likely to have devastating consequences on ecosystem functioning. However, our results suggest that diversity change will have the strongest impact on ecosystem functioning when the dominant species provide the most function. If this is also found to be true in experiments and naturally assembled systems, it has important implications for predictions based on biodiversity-ecosystem functioning research. Loss of – or change in – biodiversity may have smaller or larger effects on ecosystem functioning than currently predicted, depending on the species affected. If the species that are lost are dominant and high functioning, we expect that their loss will cause declines in ecosystem functioning unless they are replaced by species that perform similarly well. Alternatively, if the species lost dominated the community while contributing little to functioning, the effect of biodiversity loss on ecosystem functioning may be positive even while the other effects of losing these species could be negative. For example, recent research indicates that tall, high-biomass tree species may be more prone to extinction under higher temperatures or more arid conditions than those that are smaller and low-biomass (McDowell *et al.* 2020) with negative consequences for ecosystem functioning (Aubry-Kientz *et al.* 2019; Rüger *et al.* 2020). Our results suggest that within these systems, ecosystem functioning may be likely to decline even if it is not reliant on species richness *per se*. Our results also suggest that isolation from seed sources may amplify the importance of the identity of specific species. This is particularly relevant as land use change, and the habitat fragmentation that follows it, is currently regarded as the largest cause of biodiversity change globally (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). By comparing the outputs from six well-understood models that incorporate different community assembly mechanisms, we were able to identify an emergent community metric – the function-dominance correlation – that drives variation in BEF relationships. This synthesis provides key information about how changes in community composition rather than biodiversity loss *per se* are likely to influence ecosystem functioning under global change.

**AUTHOR CONTRIBUTIONS**

This study was devised as a product of a collaborative workshop attended by all authors. MC, NR, ATC, IM, FM, BR, and LAT designed the initial model intercomparison project with feedback from other authors. MC, ATC, IM, CF, and BR performed modelling experiments on individual models and provided data and feedback to MC. MC conducted model intercomparison analyses with input from NR, KEB, and ATC. MC, KEB, NR, and ATC wrote and revised initial drafts of the manuscript. All authors contributed to the revision of the manuscript.

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**FIGURE LEGENDS**

*Figure 1.* We hypothesise that the strength and direction of the relationship between the diversity of a community and its total biomass will depend on the function-dominance correlation of its species (C). Communities with a positive function-dominance correlation (A) will tend to be dominated by species that also generate significant functioning. When included in a mixture, these species will decrease biodiversity as they increase total biomass. Across species richness treatments the likelihood of these species being incorporated into a community will increase, leading to a positive relationship between diversity and biomass. However, within species richness treatments, communities incorporating these dominant species will tend to have lower biodiversity – though more biomass – than communities in which they are absent. A negative function-dominance correlation (B) will lead to alternative diversity-biomass relationships, as they will tend to be dominated by species that provide little functioning. Across species richness treatments, this will lead to a negative relationship between diversity and biomass, as competitive – though low biomass – species are more likely to be incorporated into diverse mixtures. However, within species richness treatments, there will be a positive relationship between biomass and functioning as communities that lack these competitive species will subsequently contain higher diversity and biomass.

*Figure 2.* The relationship between realised Shannon diversity and total community biomass for six plant community models. Points represent individual plant communities. Coloured lines refer to the relationships within species richness treatments, while the black lines refer to the relationship across species richness treatments. Ribbons represent the 95% credibility intervals of the model fits. Significant relationships (95% CI does not include 0) are shown with solid lines. Insignificant relationships are shown with dashed lines.

*Figure 3.* The relationship between the function-dominance correlation and the slope of the BEF relationship across species richness treatments for six plant community models. Standard major axis regressions were run on each bootstrapped dataset (n = 2500), which each contained one function-dominance correlation paired with one posterior sample of the BEF slope per model. 95% confidence interval for the mean where derived through nonparametric bootstrapping of the slope parameter (n = 1000).

*Figure 4.* The relationship between the function-dominance correlation and the slope of the BEF relationships within species richness treatments for six plant community models. Standard major axis regressions were run on each bootstrapped dataset (n = 2500), which each contained one function-dominance correlation paired with one posterior sample of the BEF slope per model and species richness treatment. Intervals indicate 95% confidence of the mean, derived through nonparametric bootstrapping of the slope parameter (n = 1000).

**TABLES**

Table 1. Model descriptions.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Model ID** | **Study Area** | **Model Type** | **Spatial Extent** | **Parameterization** | **Coexistence Mechanisms** | **Literature** |
| Grass1 | Cedar Creek, Minnesota, USA | Ordinary differential equations | 1 m2 | Field data | Trade-off between competitive ability for soil nitrate and nitrogen-use efficiency | Clark et al. 2018 |
| Grass2 | Temperate grasslands | Ordinary differential equations | 1 m2 | Theoretical | Trade-off between rooting depth and resource uptake rate | Turnbull et al. 2013 |
| Grass3 | Central European grasslands | Individual-based, spatially-explicit model | 9 m2 | Field data (see Weiss et al. 2014) | Trait-driven niche and fitness differences defining competition above- and belowground; CNDD | May et al. 2009, Weiss et al. 2014 |
| Forest1 | Barro Colorado Island, Panama | Spatially-implicit demographic cohort model | 1 ha | Demographic trade-offs derived from forest inventory data | Demographic trade-offs; demography-driven niche differences within a vertical canopy gradient; external seed input | Rüger et al. 2020 |
| Forest2 | French Guiana | Individual-based, spatially-explicit model | 1 ha | Field data (functional traits) | Trait-driven among-species niche differences within a heterogeneous environment, both vertically (canopy gradient) and horizontally (gap dynamics); external seed input | Maréchaux & Chave 2017 |
| Dryland | Richtersveld, South Africa | Individual-based, spatially-explicit model | 25 m2 | Literature | Trade-offs between competition and storage ability for water, mediated through stochastic variation in water supply rate | Reineking et al. 2006 |

**FIGURES**

Figure 1.



Figure 2.

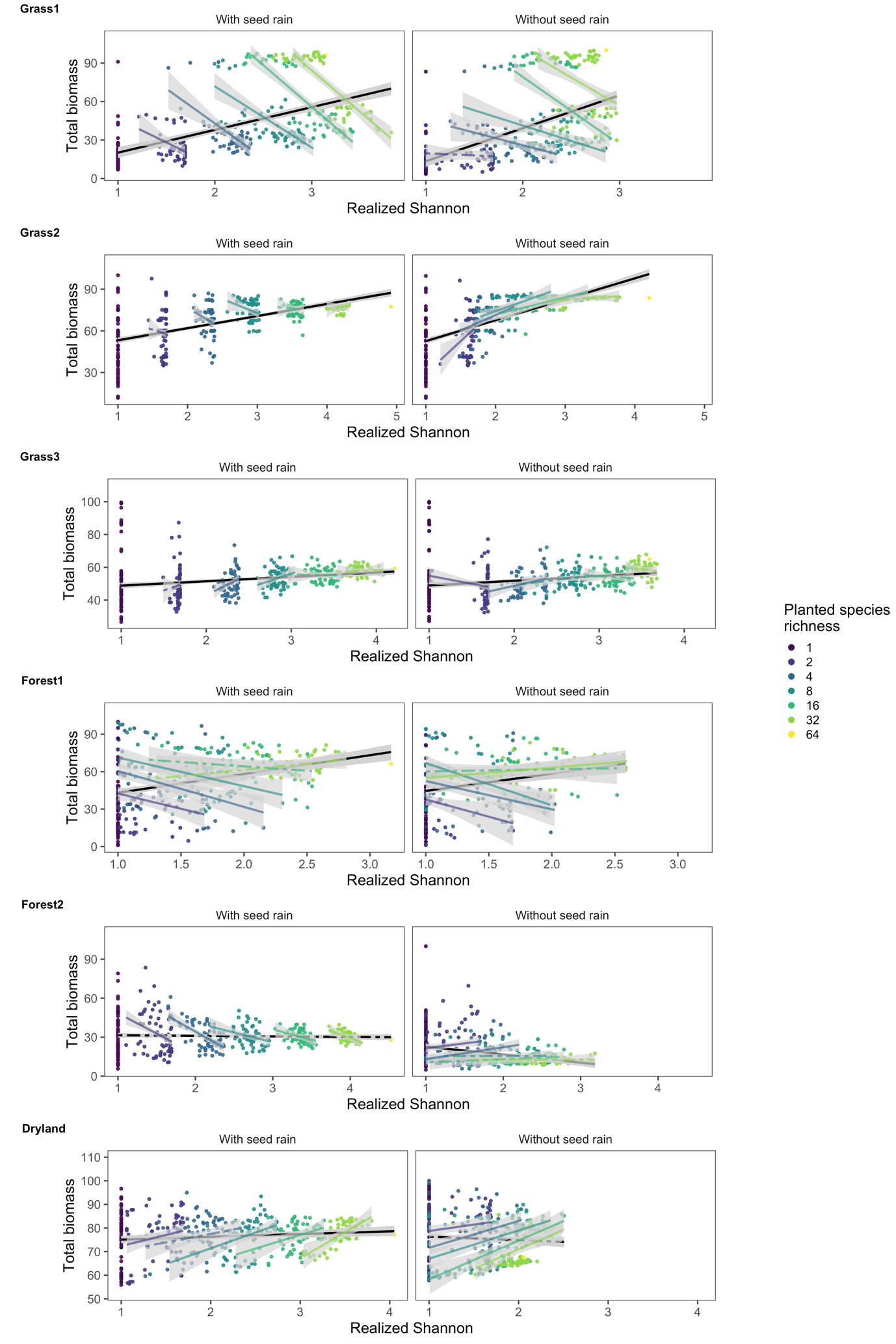


Figure 3.

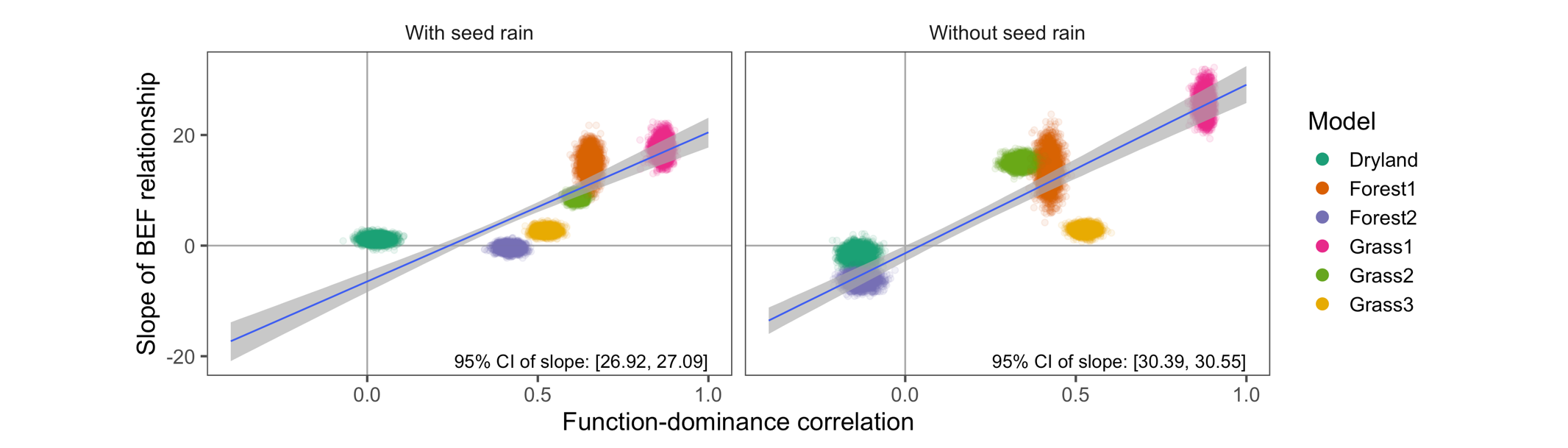


Figure 4.

