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Research article

How size and resource traits control species' biomass in monoculture and mixture and drive biodiversity–ecosystem functioning relationships

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Humans are driving unprecedented environmental change, causing the loss of species from local ecosystems. This local species loss is likely to result in declines in ecosystem functioning but understanding why these so-called biodiversity-ecosystem functioning relationships vary is crucial for conservation and sustainable land management. Previous studies have shown that variation among biodiversity–ecosystem functioning (BEF) relationships can be explained by a 'function-dominance correlation', i.e. the correlation of species' biomass in monoculture ('functioning') versus mixtures ('dominance'). One potential reason for the importance of the function–dominance correlation is its relationship to underlying plant traits. Here, we explore which traits control species' biomass in monoculture and mixture and thereby drive the function–dominance correlation, and hence BEF relationships. To do this, we perform a modeling experiment with six trait-based models of plant community dynamics and classify model traits as either 'size' or 'resource' traits. This approach allows us to better

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generalize across systems that differ in terms of their key traits and/or how a given trait affects individual performance and ecosystem functioning. We found that size traits, but not resource traits, predicted species' monoculture biomass in five out of the six models. However, in mixture, resource traits became more important and – in addition to size traits – explained substantial variation in species' biomass in four models. In models where size traits were consistently important predictors of biomass variance in monoculture and mixture, the function–dominance correlation was high, and BEF relationships were strongly positive. Our analysis shows how generalizable categories of functional traits allow predicting BEF relationships across systems, and thereby the potential effects of losing species on ecosystem functioning.

Keywords: ecosystem functioning, plant community dynamics, plant community models

Introduction

Humans are driving unprecedented environmental change (IPBES-IPCC 2021) that causes the loss of species across the globe (IPBES 2019) and many studies suggest that biodiversity loss will have adverse consequences for ecosystem functioning (Tilman et al. 2014). However, the relationship between biodiversity and ecosystem functioning (BEF) remains difficult to predict because it can vary across sites (Ratcliffe et al. 2017). This variability is often described as context-dependent; yet, key processes underlying the different effects of biodiversity, particularly species richness, on ecosystem functioning may also drive this variation. A classical explanation behind BEF relationships is the 'sampling effect' (Huston 1997, Hooper et al. 2005): communities with higher species richness are more likely to contain species that have a large impact on ecosystem functioning (Loreau and Hector 2001). This 'positive' sampling effect (Crawford et al. 2021) is not merely an outcome of community stochasticity but is realized through community dynamics, which are driven by the interaction between regional and local scale assembly mechanisms (Leibold et al. 2017).

Recently, it was shown that the impact of local species loss on ecosystem functioning depends on the degree to which the species providing the most 'function' in monoculture are the same species that are dominant in mixed communities (Crawford et al. 2021). This ecosystem property has been referred to as the 'function–dominance correlation' (Crawford et al. 2021). That is, in some systems, the most dominant species in the community (i.e. in mixture) are the same species that provide a high level of functioning (biomass, productivity or other ecosystem functions) when they grow alone (i.e. in monoculture). These systems are characterized by a strongly positive function–dominance correlation that generates a positive relationship between realized diversity and ecosystem functioning across levels of species richness in this modeling experiment (Crawford et al. 2021). In this modeling experiment, where the ability of a species to become dominant in mixtures is unrelated to its ability to provide function in monoculture, the function–dominance correlation is weak or non-existent and, consequently, the relationship between biodiversity and ecosystem functioning is weak, non-existent, or even slightly negative in this modeling experiment (Crawford et al. 2021). Finally, in this modeling experiment, systems where the most dominant species in mixtures provide the least function in monoculture would be characterized by a negative function–dominance correlation and a negative biodiversity–ecosystem functioning relationship in this modeling experiment (Crawford et al. 2021), although such systems may be rare. Thus, it is essential to understand how and when dominant species sustain ecosystem functions across these models. The degree to which a species can provide function in monoculture and reach dominance in mixture is likely driven by species' traits (Zheng et al. 2021). For example, in grassland ecosystems, dominant grass species with high photosynthetic rates can enhance primary productivity (Roscher et al. 2011), while in forest ecosystems, dominant tree species with extensive root systems can improve soil stability (Reubens et al. 2007).

Analyses of correlations among plant traits have often revealed generalizable categories of plant form and function. One key categorization relates to plant size versus plant resource acquisition and use (Reich 2014, Díaz et al. 2016, Joswig et al. 2022). We categorize plant traits that relate to the potential amount of resources that can be acquired through space use as 'size traits'. Larger individuals (and species) can access a larger volume of space and resources because they extend their organs higher up (leaves) and deeper down (roots) than smaller species. For example, plants with a large rooting volume can acquire more soil nutrients, and taller plants have better access to light. Alternatively, we categorize resource-related traits ('resource traits') as traits that relate to the rates (per unit time or mass) of resource uptake and use independent of size, or species' characteristics related to them, such as growth or survival rates (Reich 2014). For example, nitrogen use efficiency shows us how efficiently a plant is able to use soil nitrogen rather than where it is able to get nitrogen from. Similarly, though less intuitively, wood density tells us the rate at which resources can be processed through the vascular system of a tree (Wright et al. 2004, Chave et al. 2009).

How traits relate to the ability of species to provide ecosystem function likely depends on the function of interest. Here, we focus on aboveground biomass, because it is a good indicator for many other functions and services, such as carbon storage, harvestable volume for forests, and ecosystem productivity and stability in grasslands (Allan et al. 2013). We expect the size- and resource-traits to drive function and dominance in two ways.

First, size traits may be largely important in monoculture. For example, in a 60-species pool of a grassland biodiversity experiment, plant height (a size trait) strongly predicted monoculture biomass across all functional groups except small herbs, similarly, individual biomass also predicted monoculture biomass in non-legumes and legumes (Roscher et al. 2011). LAI (a more resource-related trait) alternatively was important for all functional groups in grasslands (Roscher et al. 2011). In forests, biomass is often well predicted by the size of the largest trees alone (Bastin et al. 2018, Lutz et al. 2018). We expect that (H1) size traits drive function (i.e. biomass) in monoculture, but this may especially be the case in forests because species with larger individuals can access a larger ecosystem volume and associated resources and accumulate past productivity in their biomass (Violle et al. 2009, Garnier and Navas 2012).

Second, in grasslands, dominant species in mixed communities are thought to be large and resource acquisitive, while subordinate species are thought to be smaller and resource conservative (Mariotte 2014). Additionally, evidence from the Jena Experiment suggests that a diverse array of size and resource-related attributes explain species performance in mixture (Roscher et al. 2011). For mixed natural forests, shade-tolerant species (i.e. species with conservative resource use strategy and slow demographic strategy) attain higher basal area than light-demanding species (i.e. species with acquisitive resource use strategy; Koike 2001, Schulze et al. 2005, Purves et al. 2008). Additionally, in temperate and subtropical forests in Japan, tall-statured species were found to contribute more basal area than short-statured species (Koike 2001). Alternatively, in a restinga scrub community in Brazil, the most dominant species were those that best tolerated the low water availability (i.e. species with a conservative resource use strategy; Rosado and De Mattos 2010). We, therefore, expect that (H2) size or resource traits, or both, can drive dominance (i.e. biomass) in diverse communities.

Finally, plant communities where species function in monoculture and dominance in mixture are driven by the same traits (and in the same direction) should be characterized by a strongly positive function–dominance correlation (Fig. 1). In contrast, communities where species function in monoculture and dominance in mixture are driven by different traits (or are unrelated to traits) should be characterized by a weak function–dominance correlation. If function in monoculture and dominance in mixture were driven by the same traits but in opposite directions, we would expect the function–dominance correlation to be negative. However, we consider this to be an unlikely situation and omit it from Fig. 1. As we expect that size traits drive biomass in monoculture (H1), we expect that (H3) communities where size traits explain a large proportion of species' biomass in monoculture and in mixture will be characterized by a strong function–dominance correlation.

To test these hypotheses, we use a modeling experiment with six models of plant community dynamics. For brevity, we use the general term 'trait' to describe parameter values from our models that can be estimated directly from field measurements of individuals or populations, i.e. as opposed to values that need to be fitted through optimization (e.g. community dynamics). Note that these values therefore include both 'classic' traits that can be measured at the level of individual plants, and more complex 'attributes', such as monoculture biomass (see Table 1 for further discussion of these traits). The models allow us to mimic biodiversity experiments and to quantify the effect of size and resource traits on the biomass in monoculture and mixture, and to assess the strength of the function–dominance correlation. The models cover a variety of systems (grasslands, forests and drylands). Unlike in real ecosystems, the community assembly mechanisms are well understood, the relationships between traits and biomass are clear, and we have complete information on all traits. Understanding how traits drive the function–dominance correlation, and consequently BEF relationships, enables us to better predict the impact of species loss on ecosystem functioning across ecosystems that vary in species composition, coexistence mechanisms, or resource availability.

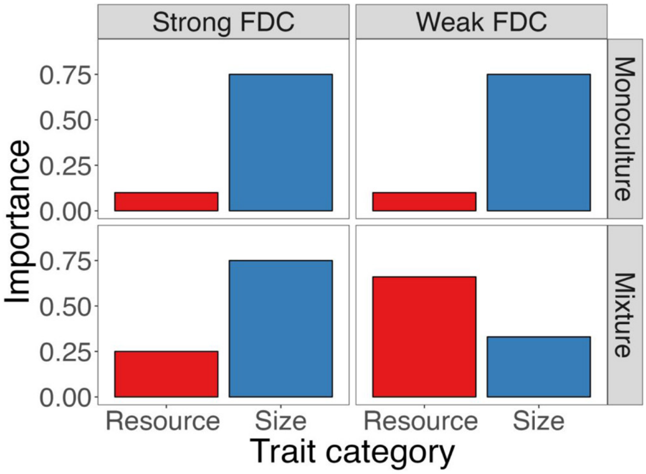

Figure 1. Hypotheses about the importance (% explained variation) of size and resource traits for biomass in monoculture (Function) and mixture (Dominance) for communities with strong and weak function–dominance correlations (FDC), respectively. We predict size traits to be the main drivers of biomass in monoculture (highest importance), and the resource traits to gain more importance in mixtures. We also predict that in systems with strong FDC the trends in trait importance will be similar between monoculture and mixture, in contrast to the systems with weak FDC, where a variation in trait importance is expected.

Material and methods

Our approach to understanding the function-dominance correlation relies on virtual biodiversity experiments conducted with six published plant community models. We selected these specific models because they meet five criteria. First, these models cover a variety of ecosystems, ranging from forests to succulent plants in drylands. Second, they represent the major model types, ranging from systems of differential equations to spatially explicit, individual-based models (Crawford et al. 2021). Third, the models support realistic levels of biodiversity. Fourth, coexistence between species in

Table 1. Categorization of traits used in this analysis and the corresponding descriptions in the original models. For composite traits derived from PCA analyses, multiple trait associations are indicated. Positive trait correlations along principal components are indicated by ‘and’, negative traits correlations by ‘versus’. To simplify across models, we use the general term ‘trait’ to describe parameter values from our models that can be estimated directly from field measurements of individuals or populations. Note that these values therefore include both ‘classic’ traits that can be measured at the level of individual plants (such as specific leaf area), and population-based measures like monoculture biomass. There is a history of measuring biomass as a ‘performance trait’ in the functional trait literature but this is often at the individual level (Violle et al. 2007) but also indicate that population level characteristics like biomass can also be considered traits (Weiher et al. 1999). [a]Low values refer to acquisitive strategies, high values refer to conservative strategies.

Model	Trait and description	Category and rationale
Grass1	MonoBiomass Monoculture aboveground biomass (abm)	Size; at fixed NUE, higher monoculture biomass indicates that species access a greater proportion of the total available nitrogen (Dybzinski and Tilman 2007, Tilman 1994)
	NUE1[a] Nitrogen use efficiency (1/pN)	Resource; species with higher NUE produce more biomass per unit of aboveground tissue nitrogen (Dybzinski and Tilman 2007)
Grass2	RootingVolume Volume of soil accessible (V)	Size; species with larger RootingVolume can access a greater amount of nitrogen
	NUE2[a] Nitrogen uptake efficiency (1/theta)	Resource; 1/nitrogen uptake rate per unit biomass (Turnbull et al. 2013)
Grass3	GrazingTolerance[a] PC1: tolerance to grazing: leaf to mass ratio (LMR) versus specific leaf area (SLA)	Resource; LMR is related to growth form (low LMA – erect, high LMR – rosette) and SLA indicates the palatability. Together both traits describe the tolerance to grazing with species with low values, i.e. low LMR and high SLA being least tolerant to grazing, i.e. resource acquisitive (Weiss et al. 2014)
	Size/Growth PC2: maximum resource utilization per time step (Gmax) and maximum size (MaxMass)	Mixed; Gmax is a Resource trait and MaxMass is a Size trait because species with larger maximum size can access a greater amount of light
	Spacing[a] PC3: specific leaf area (SLA) versus mean length of spacers (meanSpacerLength)	Resource; high SLA indicates higher rates of photosynthetic assimilation (Wright et al. 2004)
Forest1	GrowthSurvival[a] PC1: fast-slow continuum of lifestyles; annual diameter growth versus annual survival	Resource; a fast lifestyle with high growth and low survival rates is related to fast resource turnover. A slow lifestyle is conservative, with low growth but high survival rates.
	MaxHeight PC2: tree stature; annual diameter growth and survival versus recruitment	Size; tree stature is related to the amount of light that can be accessed
Forest2	LES[a] PC1: leaf economics spectrum; leaf N and P content per dry mass (leafN, leafP) versus leaf mass per area (LMA)	Resource; high leafN and low LMA indicate higher rates of photosynthetic capacity (Wright et al. 2004)
	MaxHeight PC2: tree stature (Hmax)	Size; tree stature is related to the amount of light that can be accessed
	WoodDensity[a] PC3: wood specific gravity (WD)	Resource; low wood density is related to faster growth and higher mortality rates and hence higher resource turnover (Maréchaux and Chave 2017)
Dryland	MaxBiomass Maximum size/size at maturity (maxSize) [gC]	Size; maximum biomass relates to the amount of water that can be accessed
	LeafAllocation Allocation to leaf (pLeaf) [gC/gC]	Resource; allocation of biomass to leaves, i.e. photosynthetically active tissue
	StorageAllocation Allocation to storage (pStorage) [gC/gC]	Resource; allocation of biomass to water storage organs increases tolerance to resource scarcity and survival rates

all models is driven by well understood coexistence mechanisms and functional traits. Fifth, these models have been extensively validated, often using independently collected empirical data from their target systems (Reineking et al. 2006, May et al. 2009, Turnbull et al. 2013, Weiss et al. 2014, Maréchaux and Chave 2017, Clark et al. 2018, Rüger et al. 2020). To the best of our knowledge, these six models are representative of the very limited number of models that meet these criteria. We briefly describe each model below.

We classify the traits in each model as 1) size related traits, 2) resource related traits, or 3) mixed (for traits related to both size and resource acquisition). See Table 1 for full classification of size and resource traits for each model. We then use a machine learning algorithm (random forests) to quantify the degree to which size and resource traits explain species’ function (monoculture biomass) and dominance (mixture biomass) in each model. Random forests provide unbiased estimates of variable importance when the magnitudes of the variables in question are very different and when relationships between variables are likely non-linear, making it ideal for generalizing across systems (Strobl et al. 2008).

Model descriptions

Terms in bold are described further in Table 1.

Grass1 (Clark et al. 2018) explores a tradeoff between species' abilities to take up and retain resources versus to preempt other species from accessing resources. The model is designed to portray dynamics in a Minnesota tallgrass prairie and was parameterized from observations of three plant traits measured in experimental monocultures: monoculture biomass (MonoBiomass), a size-related attribute at the population level; nitrogen use efficiency (NUE1), i.e. 1/tissue nitrogen concentration per unit monoculture biomass (pNi); and nitrogen R*, i.e. the impact on biologically available soil nitrogen levels in monoculture (Table 1). The three traits are interconnected in a 2D tradeoff plane, i.e. knowledge of any two traits is sufficient for predicting the competitive hierarchy and the strength of competitive interactions. We therefore only explicitly simulate values for two of the three traits (MonoBiomass and NUE1) in subsequent analyses and draw the third trait value implicitly off the tradeoff surface, to avoid problems of collinearity in subsequent analyses. Note: MonoBiomass is at the same time a 'size trait' and our measure of 'function'. However, this circularity does not apply to the analysis of 'dominance', i.e. mixture biomass or the comparison between the two.

Grass2 (Turnbull et al. 2013) is also designed to mimic dynamics in grassland plant communities and focuses on a classic tradeoff between species nitrogen uptake rate per unit of plant mass (is also designed to mimic dynamics in grassland plant communities and focuses on a classic trade-off between species nitrogen uptake rate per unit of plant mass (theta$_i$), which corresponds to relative growth rate (*r*), and the volume of soil accessible to the species (RootingVolume), which corresponds to the carrying capacity (*K*) and is a size related attribute at the population level. We defined nitrogen uptake efficiency (NUE$_2$) as 1/theta$_i$. The model explicitly considers the effects of seasonal cycles. Fast-growing species can persist because they can rapidly exploit resources early in the growing season, before slower growing species become dominant. Again, since parameter values in the model were drawn from a 1-dimensional tradeoff (i.e. assuming a linear negative relationship), we added some noise to rootingVolume (N(mean = 0, SD = mean(rootingVolume)/5). Note: RootingVolume is at the same time a 'size trait' and closely tied to monoculture biomass, our measure of 'function'. However, this circularity does not apply to the analysis of 'dominance', i.e. mixture biomass or the comparison between the two$_i$), which corresponds to relative growth rate (*r*), and the volume of soil accessible to the species (RootingVolume), which corresponds to the carrying capacity (*K*) and is a size related attribute at the population level.

Grass3 (May et al. 2009, Weiss et al. 2014) is an individual-based and spatially explicit model. It explores tradeoffs between asymmetric competition for light and susceptibility to grazing within central European managed grasslands. It uses five species-specific functional traits, leaf mass ratio (LMR), maximum biomass (MaxMass), maximum resource utilization (Gmax), specific leaf area (SLA), and the mean length of spacers between ramets (meanSpacerLength), to parameterise resource and space use and vulnerability to grazing. To summarize the partially related traits, we performed a PCA and retained the first three components (Supporting information). The first axis reflects the tolerance to grazing (GrazingTolerance; Table 1) which distinguishes species with traits that indicate low grazing tolerance, and hence, resource conservation (low LMR, high SLA) and species with traits that maximize resource conservation through high grazing tolerance (high LMR, low SLA). The second axis (Size/Growth) distinguishes large and fast-growing species (high Gmax, high MaxMass) that are vulnerable to grazing from short and slow growing species (low Gmax, low MaxMass) that are tolerant to grazing. The third axis (Spacing) describes the space-use strategy and distinguishes species that tend to have short spacers between their clonal ramets (low meanSpacerLength) from those with longer spacers between ramets (high meanSpacerLength). Here, all simulations include a moderate level of grazing.

Forest1 (Rüger et al. 2020) is designed to simulate the dynamics of a diverse tropical rainforest at Barro Colorado Island, Panama, based on species 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, regardless of their horizontal position (perfect plasticity approximation; Purves et al. 2008). Tree species fall along two orthogonal demographic tradeoffs determined by a PCA on growth and survival rates in four canopy layers, and recruitment rates per m^2 of basal area (Rüger et al. 2020). The first one is a growth–survival tradeoff distinguishing species with fast growth and low survival from species with slow growth and high survival (GrowthSurvival; Rüger et al. 2018). A slow lifestyle (slow growth, high survival) is related to traits indicative of resource conservation, such as high wood density, LMA, LDMC and low leaf nutrient contents (Rüger et al. 2018). The second is the so-called stature–recruitment tradeoff distinguishing species with fast growth and high survival – and hence tall adult stature – and low per-basal-area recruitment from species with slow growth and low survival – and hence small adult stature – and high per-basal-area recruitment (MaxHeight; Rüger et al. 2018).

Forest2, or TROLL (Maréchaux and Chave 2017), is an individual-based and spatially explicit model of tropical forest dynamics. It uses seven species-specific functional traits (leafN, leafP, LMA, WD, three allometric traits that combine to determine adult stature MaxHeight) to parameterise tree physiological function and demographic processes, according to relationships from the literature. Individual trees compete for light within a three-dimensional grid (1 m^3 voxels), in which tree death and gap formation create horizontal and vertical heterogeneity in light availability. Seed dispersal is spatially explicit and includes both local sources and external seed inflow. To summarize the partially related traits, we performed a PCA and retained the first three components (Supporting information). The first axis reflects the leaf economics spectrum (LES; Wright et al. 2004; Table 1), which distinguishes species with traits maximizing resource acquisition (low LMA, high leafN, leafP) and species with traits maximizing resource conservation (high LMA, low leafN, leafP). The second axis (MaxHeight) distinguishes species with short versus tall adult stature. The third axis (WoodDensity) is related to the wood economics spectrum, with species with low and high WD maximizing resource acquisition and conservation, respectively (Chave et al. 2009).

Dryland (Reineking et al. 2006) is an individual-based, stochastic model based on allocation tradeoffs and environmental heterogeneity. The model is parameterised for succulent communities in the Richtersveld, South Africa. Plants compete for water, and biomass allocation to leaves (LeafAllocation), water storage (StorageAllocation), and roots (1 – (LeafAllocation + StorageAllocation)) 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 under drought. Thus, all allocation parameters describe plant strategies for resource acquisition and conservation. Species also differ in maximum biomass (MaxBiomass) and invest all productivity in seeds once MaxMass is reached.

The virtual biodiversity experiment

To determine species biomass in monoculture (function) and mixture (dominance), we conducted a virtual biodiversity experiment. For each model, we sampled a set of 64 species from a functionally diverse assemblage of its species pool. Depending on the model, this was achieved through either sampling species from the underlying tradeoff surface (Grass1, Grass2, Dryland) or by randomly sampling from 64 species clusters determined by k-means clustering ($k = 64$) on the species pool across the trait space (Grass3, Forest1, Forest2). In order to preserve trait tradeoffs, the 64 clusters grouped species with similar trait profiles. We then randomly sampled one species from each cluster to ensure that the final assemblage spans the full range of functional strategies. This 64 species pool is of similar magnitude to the largest biodiversity experiments from which evidence suggests that most 60 species mixtures decline to between 30 and 40 species (Marquard et al. 2009, Weisser et al. 2017). We simulated monocultures of all species and 64 mixtures of 32 randomly sampled species each. This design intends to overcome two major limitations of comparing in situ biodiversity experiments. First, experiments in different systems replicate species richness differently. We use the same number of species and replication for each system. Second, there is often no variation in communities at the highest species level which are simply assemblages of all the species in the experiment constraining variance at the highest diversity level. Different mixed communities were simulated to account for potential variation in performance of the species caused by the species composition of the community. To account for the additional stochasticity in Dryland, we averaged biomass across the last 11 years of the simulation.

The experimental communities were initialized with equal abundances of seeds or seedlings for each species (depending on each model's default settings). Evidence suggests that biodiversity–ecosystem functioning relationships change through time (Cardinale et al. 2007, Reich et al. 2012, Meyer et al. 2016, Zheng et al. 2024, Koricheva et al. 2025). This change in the strength of the biodiversity–ecosystem functioning relationship is often most pronounced during the establishment phase of the experiment (Reich et al. 2012). To avoid these effects, we ran each model until stable abundance distributions were achieved. A benefit of our approach is that virtual biodiversity experiments can run much longer than in situ experiments, especially in forests where most in situ biodiversity experiments are less than 20 years old (https://treedivnet.ugent.be). The equilibrium time scale differs among models because they represent different systems. Grasslands, for example, reach a stable abundance distribution more quickly than forests. While these time scales differ among models, they all represent the same relative stage of community development. The communities received a constant external seed or seedling inflow from the initial species pool. For the grassland and dryland models, this implementation generated an equal seed rain (seed biomass) per year across all species, in forest models it generated an equal number of saplings per year across all species. The external seed rain or number of saplings corresponded to average internal seed/sapling production across all equilibrium monocultures, divided by the number of species. In addition to this external seed or seedling inflow, all species reproduced within the models based on their performance in a given time-step. We then used the data from the model at equilibrium to calculate the function–dominance correlation.

Importance of traits for function and dominance

We also report here the slope of the biodiversity–ecosystem functioning relationships from these models as reported in Crawford et al. 2021. These values are the 'across-treatment' slopes of 2500 model runs of the relationship between Shannon diversity and biomass with seed rain (see Crawford et al. 2021 for more detailed methods) and range from strongly positive (17.8 for Grass1) to weakly negative (−0.4 for Forest2).

To quantify the contribution of size and resource traits (predictor variables) to species biomass in monoculture (function) and mixture (dominance, response variables), we used a random forest machine-learning algorithm (R package 'party'; Hothorn et al. 2006, Strobl et al. 2008). For each model, we performed two random forest analyses: one for the 64 monocultures and one for the 64 32-species mixtures. Thus, the monoculture analysis includes 64 data points, while the mixture analysis includes 32 (species) × 64 (different communities) = 2048 data points. We fit conditional inference trees to avoid biased results caused by including variables with very different magnitudes of change. These conditional inference trees were fit by permuting groups of variables using the R function *cforest_unbiased*(mtry = 2, ntree = 501). The importance of traits for biomass was measured by the conditional permutation importance. Traits that have a conditional permutation importance of 0 or less have insignificant impact on biomass. Thus, we removed the negative values and scaled the remaining ones with respect to the variation explained (VE) by the random forest models (r^2), where r is the correlation between simulated biomass and random forest predictions.

Finally, we calculated the degree to which size traits explained both monoculture and mixture biomass. This allowed us to test the prediction that a strong function–dominance correlation would be associated with systems in which size traits are good predictors of both monoculture and mixture biomass. To quantify the consistency of importance of size traits, we multiplied its explained variance in monoculture (VE_{mono}) and mixture (VE_{mix}) and took the square root to linearize the results:

$$\text{Consistency of importance} = \sqrt{VE_{mono} \times VE_{mix}} \qquad (1)$$

Results

As expected, size traits explained a substantial proportion of species' monoculture biomass in five out of the six models, ranging from 57% in Dryland to 88% in Forest1, with larger species attaining higher monoculture biomass (Fig. 2–3). In Grass3, Size/Growth (a combination of size and resource traits) explained only 17% of monoculture biomass. However, when analyzing the individual traits rather than the trait dimensions, maximum resource utilization (Gmax) was the most important trait in Grass3 and explained 65% of the variance (Supporting information).

In mixture, size traits continued to be the best predictors of species' biomass in three models (Grass1, Forest1, Grass2), but resource traits gained in importance compared to monoculture biomass (Fig. 2). In Grass3 and Forest2, traits related to resource acquisition (LES, GrazingTolerance) explained substantial proportions of mixture biomass. In Grass2, species with more acquisitive traits reached higher biomass (Fig. 3). In contrast, in Forest1, species with more conservative traits reached slightly higher biomass. In Dryland, mixture biomass was unrelated to traits.

As reported in Crawford et al. 2021, the models differed in their function–dominance correlation, i.e. the average correlation between species biomass in monoculture (function) and their biomass in the 64 32-species mixtures (dominance; Crawford et al. 2021). The function–dominance correlation ranged from strongly positive ($r^2 = 0.87$ for Grass 1) to near-zero ($r^2 = 0.03$ for Dryland; Crawford et al. 2021). In models where size traits explained a large proportion of both monoculture and mixture biomass (Eq. 1), the function–dominance correlation was high and the slope of the BEF

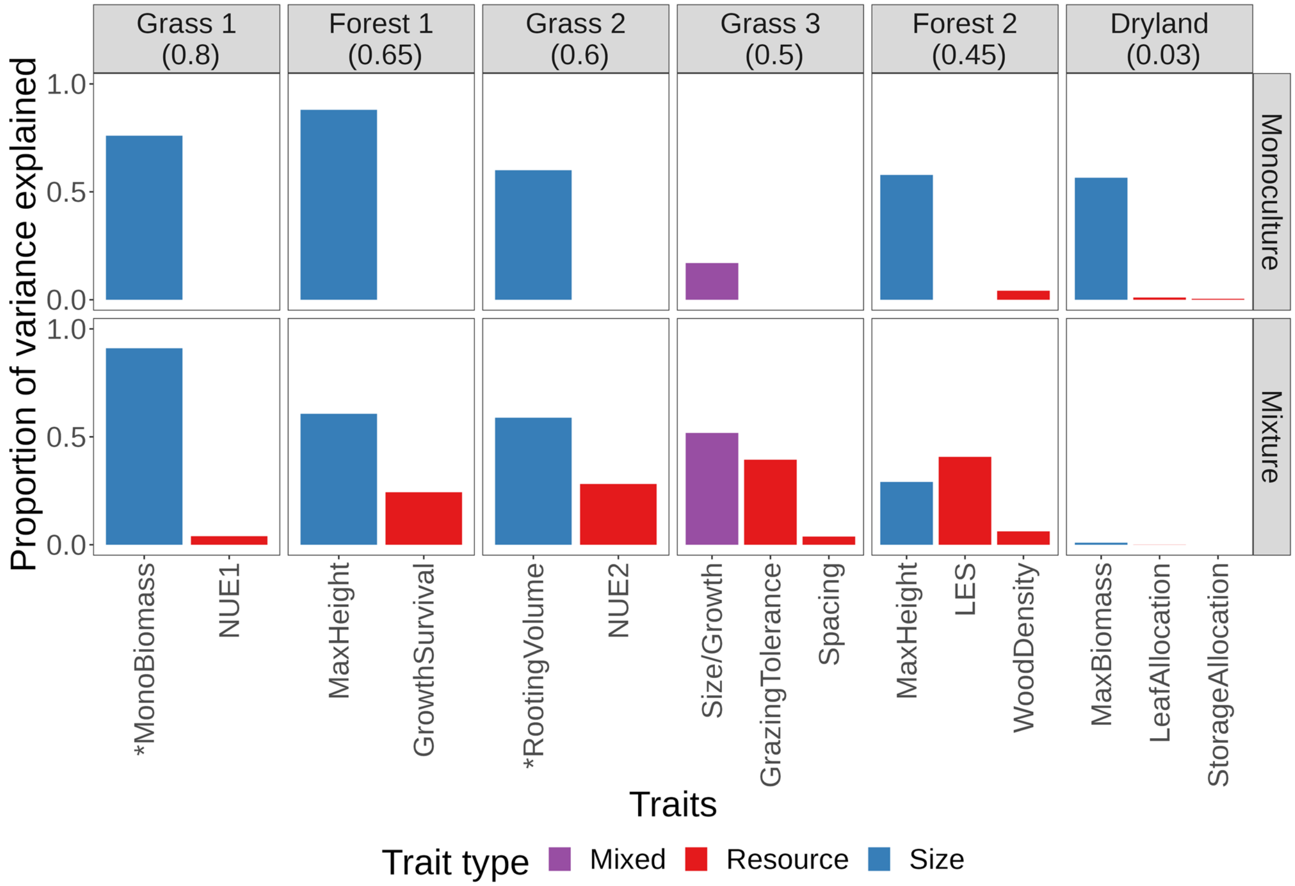

Figure 2. Importance of traits for species' biomass in monoculture and mixture for each model, arranged in a descending order of the models' function–dominance correlation (given in parenthesis under each model name). Traits are classified according to whether they are related to size or resource acquisition. Negative importance values are set to zero. Variables with an asterisk (*) are tautological.

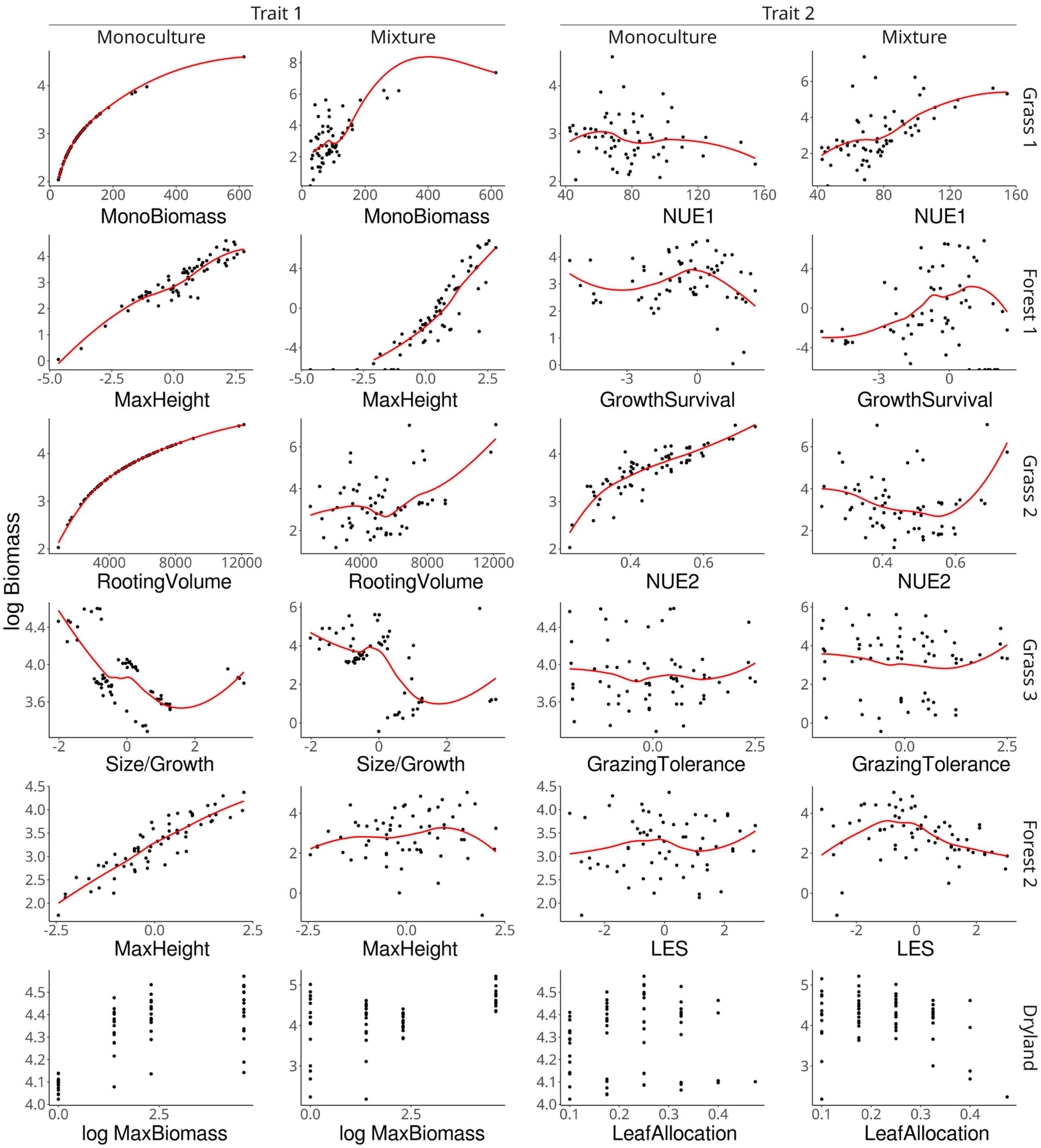

Figure 3. The relationships between biomass (y-axis) and the two most important traits (ranked with the random forest analysis; trait values shown for each trait in the x-axis of each facet), in monoculture and mixture. The red line represents a loess fit line to better show the trend in the data, and not the model fit. We do not include the loess line for Dryland which has categorical traits.

relationship across species richness levels was strongly positive, e.g. Grass1, Grass2, and Forest1 (Fig. 4). Conversely, in models where size traits had a low consistency of importance in monoculture and mixture (Eq. 1), the function–dominance correlation was intermediate (Forest2) or low (Dryland) and the slope of the BEF relationship was close to zero (Dryland) or negative (Forest2).

Discussion

We performed an experiment using six models of plant community dynamics with the goal of understanding which traits underlie the function–dominance correlation, and hence biodiversity–ecosystem functioning relationships. We found that size traits, but not resource traits, predicted species'

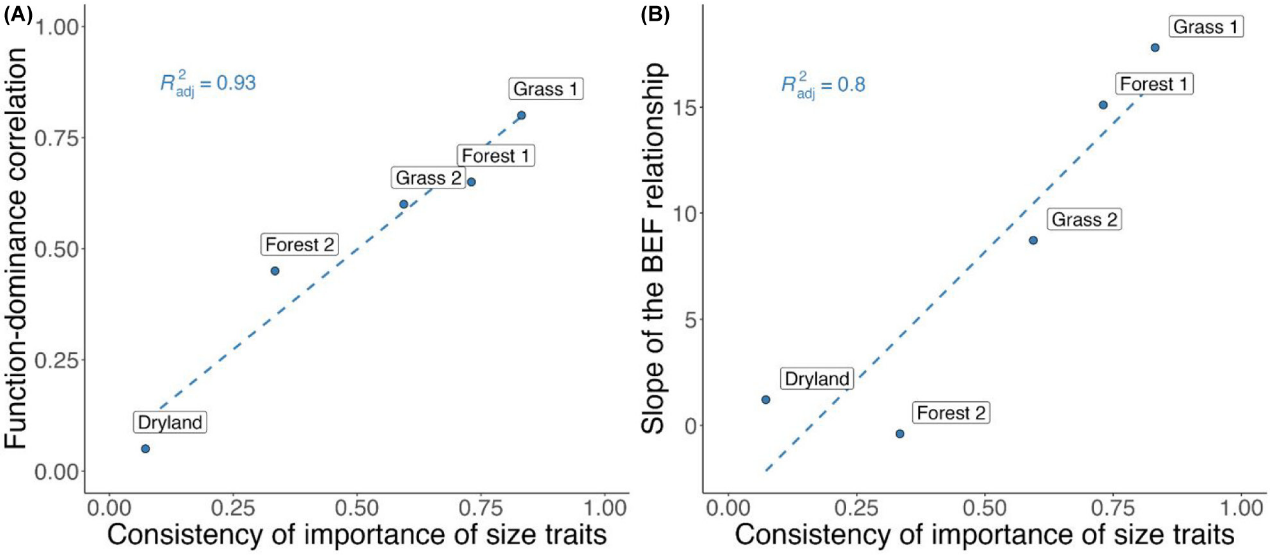

Figure 4. (A) Relationship between the consistency of importance of size traits (measured as the square root of the monoculture variance explained multiplied by the mixture variance explained) and the strength of the function–dominance correlation (Crawford et al. 2021). (B) The relationship between the consistency of importance of size traits and the slope of the across treatment biodiversity–ecosystem function relationship (Crawford et al. 2021). Grass3 did not have a specific size trait and was excluded from the regressions.

monoculture biomass (function) in five out of the six models. The degree to which size and resource traits were good predictors of species' mixture biomass varied among models. In models where size traits were consistently important predictors of biomass variance in both monoculture and mixture, the function–dominance correlation was strongly positive and there was a strong positive BEF relationship. Conversely, in models where size traits were not consistently important predictors of biomass variance in both monoculture and mixture, the function–dominance correlation was weak. This trait-based analysis of models that span different types of systems and coexistence mechanisms reveals general insights into the trait underpinnings of variation of biodiversity–ecosystem functioning relationships across different ecological communities.

As expected, in five out of the six models (all except for Grass3 which did not have an explicitly size related trait), size traits were the most important predictors for biomass in monoculture (function). The largest individuals can access the largest volume of space and resources because they extend their organs higher up (leaves) and deeper down (roots) than smaller species, and consequently attain the highest biomass (Violle et al. 2009, Garnier and Navas 2012). For Grass1 and Grass2 this strong link is to be expected because the size trait is a direct measure of average monoculture biomass. However, in Grass3, the size trait (MaxMass) is unrelated to monoculture biomass (Supporting information). In this model, this is because negative density dependence causes larger species to self-limit more than smaller species (May et al. 2009). Thus, the same area supports more individuals of smaller species than of larger species, and hence, similar biomass. In this model, a resource trait (Gmax) more strongly determined monoculture biomass, but this effect was diluted when we combined traits into independent trait dimensions.

Size traits were also the most important predictors of species biomass in mixture in two of the three grassland models (Grass1, Grass2), but resource traits were more important than they were for monoculture biomass. In Grass1, monoculture biomass is an important component of the mechanistic derivation of mixture biomass, and for highly competitive species mixture biomass is purely a function of their monoculture biomass (Clark et al. 2018). Additionally, more conservative species (low NUE) reached higher biomass in monoculture than more acquisitive species, but this effect was negligible (Fig. 2) and was also the opposite of the trend observed for the same trait in mixtures (Fig. 3). In contrast, in Grass2, more acquisitive species were more successful in mixture than more conservative species, because phenological differences, i.e. temporal niche partitioning, help shield these species from competitive effects (Fargione and Tilman 2005).

In the forest models, size and resource traits jointly determined mixture biomass. In both forest models (Forest1, Forest2), taller species reached more biomass than smaller species, which is consistent with evidence from forests where the largest individuals typically hold disproportional amounts of biomass (Bastin et al. 2018). In Forest1, which simulates the dynamics of a tropical forest in Panama, more conservative species, i.e. species with higher survival, slower growth, and higher shade tolerance (Rüger et al. 2018), were more dominant than more acquisitive species. This is consistent with findings from boreal, temperate and subtropical forests, where tree species that maximize resource-efficiency, e.g. through high shade-tolerance, may outcompete taller less resource-efficient species (Koike 2001, Schulze et al. 2005). However, in Forest2, which simulates the dynamics of a tropical forest in French Guiana, species with acquisitive leaf traits were more dominant than species with more conservative leaf traits (Fig. 3). In this model, species with more acquisitive leaf traits reach their reproductive size more rapidly than species with conservative leaf traits (Maréchaux and Chave 2017), giving them a competitive advantage. As a result, species that are tall, but also characterized by acquisitive leaf traits, dominate the community in mixture. This trait combination describes 'long-lived pioneers' in this system, where stature and the leaf economic and wood economic spectra are known to vary independently from each other (Table 1; Baraloto et al. 2010).

Finally, in the Dryland model, mixture biomass was unrelated to traits. This pattern is in part because dynamics of biomass in Dryland are stochastic. Further, in Dryland, the biomass of a species varies greatly as a function of which other species are present in the mixture. This is because in this model different combinations of traits lead to high biomass in mixtures than those that lead to high biomass in monocultures. In this model, small species may perform relatively better than medium-sized species because they invest less in unproductive structural biomass and thus convert water into biomass more efficiently. However, large species may benefit from their ability to capture water over a large area. Because the success of a species depends on the traits of the competitors in this model, there is a large variation in biomass for the same species across different species pools.

In sum, while larger species often become dominant in mixtures, the evidence for resource-acquisitive and -conservative species is more mixed. In some models more acquisitive species have an advantage (Grass2, Grass3, Forest2), in others more conservative species are more successful in mixture (Grass1, Forest1) depending on their community assembly mechanisms.

Limitations of our approach

Here, we leverage existing models to answer our questions and use model intercomparison to provide essential insights. In spite of the power of this approach, four main aspects limit our insights into both real-world experiments and observational systems. First, the trait pool of this model experiment is limited. Two of our models contain only two traits (Grass1, Grass2) of which one is monoculture biomass. Forest1 collapses trait variation into two principal components which represent general strategies. Similarly, even in models where we have more than two traits (Forest2, Grass3), we simplify these traits for our analysis into principal components that are related to general plant strategies to increase comparability between models. These simplifications limit our capacity to understand what is happening in real-world systems where many more traits are important for plants' functioning and can vary within high-dimensional spaces (Laughlin 2014). Second, in our models, some interactions between species are hardwired. We know that species in Grass3, for example, are maintained through prescribed negative density dependence. Third, and relatedly, some relationships between our traits and our measures of function and dominance are also hardwired. Monoculture biomass is, for example, one of only two traits in both Grass1 and Grass2. Therefore, there is a tautological relationship between these traits and our measure of function in these models (as highlighted in Figure 2). Fourth, these models represent both very different hypotheses for how plants interact and very different systems. We can likely have a more complete understanding of how traits affect the function–dominance correlation and BEF relationships if we more systematically explore how different coexistence mechanisms alter outcomes. For example, Grass1 and Grass2 represent similar hypotheses for the drivers of community dynamics. Future analyses could focus less on these relatively simple models and include models where coexistence mechanisms can vary. These more complex models could also include greater explicit representation of the mechanisms that are likely to result in complementarity effects such as explicitly modeling plant–pathogen interactions, plant mutualist interactions, and facilitation between plant species.

The function–dominance correlation and implications for BEF research

A large share of the literature on BEF relationships focuses on the additive partitioning schema where BEF relationships are partitioned into selection and complementarity effects (Loreau and Hector 2001, Barry et al. 2019, Clark et al. 2019). The selection effect represents the contribution of the covariance between species' monoculture performance (often biomass) and mixture performance to a net biodiversity effect based on relative performance. The complementarity effect represents the remainder of a 'net biodiversity effect' and is often attributed to positive interactions between species such as resource partitioning, abiotic facilitation and biotic feedbacks (reviewed by Barry et al. 2019). Both selection and complementarity effects may arise due to so-called 'sampling effects' whereby species with certain characteristics are more likely to be selected based on chance to be grown in higher diversity mixtures because more species are selected for higher diversity mixtures (Loreau and Hector 2001). These characteristics can be related to any of the mechanisms underlying complementarity and/or the species dominance underlying selection. For example, a 16 species mixture is more likely to contain a facilitative species than a monoculture because 16 species are chosen rather than one. This facilitative species can drive a positive complementarity effect. While the function–dominance correlation is likely related to the selection effect, our metric avoids issues related to low and zero monoculture biomass species and is not based on relative performance (Crawford et al. 2021). Additionally, our original analysis focused both on patterns within a species richness level and across species richness levels and the function–dominance correlation can easily reflect both resolutions. Further, many of the mechanisms highlighted as contributors to complementarity effects are incorporated in our models. For example, in our grass models, Grass1 and Grass2 rely largely on resource partitioning while Grass3 relies on negative density dependence. Importantly, any of the underlying mechanisms of complementarity effects including facilitation can result in negative density dependence. We therefore expect that where we find positive BEF relationships and positive function–dominance correlations in this original analysis (Grass1, Grass2, Forest 1), they would likely be related to both selection and complementarity effects. While these effects are likely related to both selection and complementarity effects, they may underemphasize the contribution of facilitative interactions to complementarity effects because none of our models explicitly include these interactions.

As expected, the systems where size traits determined species' monoculture and mixture biomass also were characterized by a strongly positive function–dominance correlation and strongly positive BEF relationship (Crawford et al. 2021). In our analysis, these included two grassland systems and a forest system (Grass1, Grass2, Forest1). Thus, in systems like these the loss of large-statured species from the community may have severe consequences for community biomass, while losses of small-statured species will likely have a smaller effect. Conversely, in systems where monoculture and/or mixture biomass was moderately or weakly driven by size traits (Grass3, Forest2, Dryland), the function–dominance correlation was lower and BEF relationships were weak. In these cases, the effect of the loss of a large-statured species will depend on its other traits. In the unlikely case that large-statured species provide the most function, but small-statured species are more dominant in mixture, the function–dominance correlation would be negative, and losing these dominant species would lead to an increase in community biomass. Importantly, the function–dominance relationship is not independent of other proposed reasons for biodiversity ecosystem functioning relationships. Our model-based analysis sheds light on the functional significance of our 'master traits', i.e. categories of traits related to plant size and resource use, for the function–dominance correlation and biodiversity–functioning relationships. However, in naturally assembled terrestrial plant systems, species loss is not random. Rather, species may increase or decrease in abundance in the regional species pool. Species with specific traits may be more or less likely to be lost or gained. Our results suggest that the loss of species that are dominant because of their size will have much larger effects on community biomass than the loss of subordinate species or species that are dominant because of their resource use efficiency (Mori et al. 2015).

Our systematic simulation experiment allowed us to explore the traits that underlie the function–dominance correlation across a wide variety of model types (theoretical, individual-based) and systems (grasslands, forests, and drylands). The model systems covered a wide range of community assembly process, function–dominance correlations, and resulting BEF relationships, thereby mirroring the context dependence observed in natural systems. This allowed us to examine generalities in the consequences of diversity for ecosystem functioning, including systems where biodiversity experiments can only represent a very small proportion of the species and possible species combinations, e.g. tropical old-growth forests. These predictions may help us to reconcile field observations of biodiversity–ecosystem functioning relationships with those from experiments with limited species pools. Further, these predictions of how functional traits underlie the function–dominance correlation can be validated with data from established biodiversity experiments with well-examined dominance patterns. Data for many of the traits used here are readily available for the species used in these experiments from e.g. the TRY database (www.try-db.org/TryWeb/Home.php). The metrics computed here such as the consistency of importance could be computed for any trait, including those outside the scope of this analysis and understanding which traits underly function in mixture versus monoculture is likely to result in predictions for the function–dominance correlation and thereby BEF relationships in those systems. Further, data from national forest inventories may also prove informative for exploring how species traits drive function and dominance in natural communities.

Considered together, our results provide important tools for conceptualizing conservation and restoration efforts. For example, adding and removing species with traits that allow them to dominate mixtures may closely mimic the effects of invasive species and help predict the consequences of species invasions on ecosystem functioning. Similarly, our results suggest that selecting seed mixtures with a suite of size traits will be ideal in restorations when the goal is to restore diverse communities with high biomass. Knowing how traits influence ecosystem functioning in a diversity-dependent context provides the mechanistic underpinnings needed to utilize findings from BEF experiments in real world applications.

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Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Resources (equal); Writing – review and editing (equal). **Jens Kattge**: Conceptualization (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Emma Ladouceur**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Jeremy W. Lichstein**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Isabelle Maréchaux**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Akira S. Mori**: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Björn Reineking**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Software (equal); Writing – review and editing (equal). **Lindsay A. Turnbull**: Conceptualization (equal); Software (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Kathryn E. Barry**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Resources (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (lead). **Nadja Rüger**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Software (equal); Supervision (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

All data and the code used to produce these analysis and figures are publicly available and can be found at Github: https://github.com/mscrawford/SimNet (Ceballos-Núñez et al.2025)

Supporting information

The Supporting information associated with this article is available with the online version.

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