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Trait-based food web model reveals the underlying mechanisms of biodiversity-ecosystem functioning relationships

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Abstract

1. The concept of biodiversity-ecosystem functioning (BEF) has been studied over the last three decades using experiments, theoretical models, and more recently observational data. While theoretical models revealed that species richness is the best metric summarizing ecosystem functioning, it is clear that ecosystem function is explained by other variables besides species richness. Additionally, theoretical models rarely focus on more than one ecosystem function, limiting ecosystem functioning to biomass or production. There is a lack of theoretical background to verify how other components of biodiversity and species interactions support ecosystem functioning.
2. Here, using simulations from a food web model based on a community assembly process and a trait-based approach, we test how species biodiversity, food web structure and predator-prey interactions determine several ecosystem functions (biomass, metabolism, production, and productivity).
3. Our results demonstrate that the relationship between species richness and ecosystem functioning depends on the type of ecosystem function considered and the importance of diversity and food web structure differs across functions. Particularly, we show that dominance plays a major role in determining the level of biomass, and is at least as important as the number of species. We find that dominance occurs in the food web when species do not experience strong predation.
4. By manipulating the structure of the food web, we show that species using a wider trait space (generalist communities) result in more connected food webs, and generally reach the same level of functioning with less species. The model shows the importance of generalist versus specialist communities on biodiversity-ecosystem functioning relationships, and as such, empirical studies should focus on quantifying the importance of diet/habitat use on ecosystem functioning.
5. Our study provides a better understanding of BEF underlying mechanisms, and generates research hypotheses that can be considered and tested in observational studies. We recommend that studies investigating links between biodiversity and ecosystem functions should include metrics of dominance, species composition, trophic structure and possibly environmental trait space. We also advise that more effort should be made into calculating several ecosystem functions and properties with data from natural multi-trophic systems.

Key words: biodiversity, dominance, ecosystem functioning, food web structure, trait space, predator-prey interactions, BEF relationship

1. Introduction

Ecosystem functioning is the ability of an ecosystem to perform and maintain a suite of key properties and processes regulating the stock and/or flux of energy and organic matter (Jax, 2005; Paterson, Defew, & Jabour, 2012). Given its direct effects and impacts on ecosystem health, resilience, and provisioning of ecosystem services, there is a strong public and scientific interest to better understand, quantify, model and manage ecosystem functions globally. Traditionally, research has predominately focused on establishing whether more diverse ecosystems lead to higher ecosystem functioning, with species richness as a main predictor. While the relationship between biodiversity and ecosystem functioning (abbreviated BEF) has been thoroughly investigated in theoretical, experimental, and field-based studies and especially in grasslands (Hooper et al., 2005), a considerable degree of variation in ecosystem functioning remains unexplained (Schneider, Brose, Rall, & Guill, 2016; Tilman, Lehman, & Thomson, 1997). This highlights that other predictors besides species richness (the most commonly used metric of biodiversity in BEF research) need to be considered to better understand and predict the changes in ecosystem functioning. In particular, the complexity of species interactions and how food web structure affects the functioning of ecosystems is largely overlooked, because a majority of BEF studies concern single trophic levels without accounting for interaction within and between adjacent trophic levels (including predators and prey). Furthermore, several measures of ecosystem functions have been described in the literature (Strong et al., 2015), and research is now focused on quantifying ecosystem multifunctionality (i.e. provision of multiple ecosystem functions by one system) (Manning et al., 2018). However, differences and potential trade-offs between multiple ecosystem functions are rarely studied, nor quantified (Hölting, Beckmann, Volk, & Cord, 2019). Consequently, there is a need to better understand the underlying mechanisms that link diversity and food web structure to deliver multiple ecosystem functions.

Theoretical models can provide such a mechanistic understanding and be used as hypothesis generating tools to interpret patterns derived from empirical studies. Because models have complete information – within their idealized description – they can accurately probe multiple ecosystem functions along with their drivers. Accordingly, theoretical models used to investigate BEF relationships emerged, including competition models or simple food webs (M. Loreau, 1998; M. Loreau & Hector, 2001; Schwartz et al., 2000; Tilman et al., 1997). Analyses of such models have identified two primary mechanisms responsible for the positive effect of biodiversity on ecosystem functioning, namely the ‘complementarity’ and the ‘selection’ effects. In the former case, complementarity among species in terms of their niches (e.g., with respect to diet and habitat) enhances ecosystem functioning due to a more efficient and complete use of the available resources. In the latter case, a few dominant and highly competitive species that are particularly adapted to a given environment may increase

in abundance and be responsible for most of the ecosystem functioning (M. Loreau & Hector, 2001; Michel Loreau, 2000; Tilman et al., 1997). Most models are based around competitive interactions within one trophic level, therefore focusing only on horizontal diversity. However, vertical diversity, considering the entire food chain composed of predator-prey interactions across multiple trophic levels (Wang & Brose, 2018), has been less studied. Fortunately, a great wealth of knowledge on food web theory has developed and can be utilized to account for such aspects within BEF research (Stouffer, 2010; R. M. Thompson et al., 2012).

The central element in any food web model is the interaction matrix that describes pair-wise predator-prey interactions, 'who eats who'. To characterize such feeding interactions, the interaction matrix is most often predefined (based on available diet information), or prescribed by statistical rules rather than emerging from the model, as in phenomenological models (Stouffer, 2010; Williams & Martinez, 2000). On the contrary, population-level models often build communities based on size-based evolutionary assembly rules (large eat small) (Loeuille & Loreau, 2005; Stouffer, 2010). Those types of models have been used to study BEF relationships (Allhoff & Drossel, 2016; Ingram, Harmon, & Shurin, 2009; Schneider et al., 2016), yet they often rely on a pre-defined number of species or evolutionary algorithms to generate diversity. However, real food webs emerge and change as a result of several natural processes, including the sequential colonization and establishment of invading species, extinction of resident species, caused by competitive exclusion and/or excessive predation from such invaders (Post & Pimm, 1983). To replicate this process, a limited number of models construct their interaction matrices through the so-called community assembly (Law & Morton, 1996).

Including other traits conditioning trophic interactions, beyond simply size, is needed to better represent and model the natural processes by which communities and food webs are assembled and structured (Albouy et al., 2019; Brose et al., 2019; Eklöf et al., 2013). In a recent modeling study, Zhang et al. (2014) designed a food web model capable of creating communities through an assembly process, where co-existence of species is obtained by including a habitat trait, which is a theoretical representation of the species environmental niche in combination with their body size. By modelling a community assembly process, this model does not pre-define diversity and species interactions. It is therefore an ideal tool to investigate the emergent biodiversity, food web structure and their relationship with ecosystem functioning. Here, we applied this theoretical food web model for simulating a great range of hypothetical food webs to identify the key mechanisms explaining variations in multiple ecosystem functions (biomass, metabolism, production, and productivity) and BEF relationships across a richness gradient. To achieve this overall aim, we formulated and pursued the following research questions: (i) Do different ecosystem functions display distinct or similar BEF relationships? (ii) What are important predictors of ecosystem functioning besides species richness? (iii) How do differences in food web

structure affect BEF relationships? In line with previous empirical and theoretical findings, our *a priori* expectations are to find positive saturating BEF relationships across all ecosystem functions (Fung, Farnsworth, Reid, & Rossberg, 2015; Schneider et al., 2016). However, we anticipate differences in the shapes of those relationships, since each metric of ecosystem function represents a different process in the food web. Furthermore, we anticipate species richness to be a strong predictor across all ecosystem functions (Naeem & Li, 1997; Schneider et al., 2016; Tilman et al., 1997), but expect other components of diversity and food web structure to explain the remaining variability in the level of each ecosystem function considered, such as dominance, evenness, mean trophic level, connectance and completeness of the trait space.

2. Material and Methods

2.1. Description of the model and community assemblies

We employed a previously developed trait-based food web model capable of simulating community assembly where species are defined by their body size m and their habitat trait x (Zhang et al., 2014). To create a food web, regional pools of 200 species were generated with randomly assigned values of the two traits (m, x) (Fig. 1). Trait values are randomly assigned to each species, following a logarithmically uniform distribution for the size trait $m \in [1;10^{11}]$ where the size trait is discretized to 200 logarithmically even sized mass groups and a uniform distribution for the habitat trait $x \in [-25;25]$ where the habitat trait is discretized using $dx = 0.2$ (Zhang et al., 2014). To achieve a representative number of food webs, we repeated the community assembly process for a hundred randomly generated species pools. For each species pool, a community assembly process was performed where species are randomly selected from the pool and sequentially added to the assembled community at each invasion event. For every single species invasion event, we simulated community dynamics until species abundances reach equilibrium. At this point, three outcomes can emerge: (i) an unsuccessful invasion; (ii) a successful invasion where all the other species remain; (iii) or a successful invasion with a loss of resident species (mediated through competitive exclusion or predation). As a result, adding one species at each invasion does not necessarily lead to an immediate increase in the total number of species in the created community. The community assembly process described above was then repeated until a stable food web structure emerges where any further introductions of species lead to no further increase in the number of species of the assembled community (the maximum richness in assembled communities is 46). Each assembled food web is considered as an independent realization where, after reaching equilibrium, species stabilize their biomass and establish feeding links with the other species, therefore producing fully-resolved networks. In

total, we obtained 50,673 unique food webs across the hundred community assemblies. Since these food webs were unevenly distributed along the richness gradient, we randomly selected 50 food webs at each richness level, to ensure a constant number of food webs along the richness gradient (Appendix S1).

As previously mentioned, feeding interactions are determined by the preferred predator:prey body mass ratio and by the proximity in habitat positions of the potential prey species. A predator-prey interaction is defined between all pairs of species in the food web based on the two traits (m, x). A species i will be more likely to predate on species j if species j is within the size range preference of species i , calculated with the size-selection kernel $\varphi(m_i/m_j)$, where large species feed on smaller species with a log-normal preference (Hartvig, Andersen, & Beyer, 2011; Zhang et al., 2014):

$$\varphi(m_i/m_j) = \exp\left(-\left(\ln\frac{m_i}{\beta m_j}\right)^2 / (2\sigma_m^2)\right), \quad (1)$$

where m_i and m_j are the body sizes of species i and j respectively, β is the preferred predator-prey mass ratio and σ_m is the width of the selection function (Table 1). In addition, species i will be more likely to predate on species j if their habitat niche overlaps, calculated with the spatial kernel $\psi(x_i - x_j)$, (Hartvig, 2011; Zhang et al., 2014):

$$\psi(x_i - x_j) = \frac{1}{\sqrt{2\pi(\sigma_x^2(m_i) + \sigma_x^2(m_j))}} \times \exp\left(\frac{-(x_i - x_j)^2}{2(\sigma_x^2(m_i) + \sigma_x^2(m_j))}\right), \quad (2)$$

where x_i and x_j represent the positions of species i and j along the habitat axis, and $\sigma_x(m_i)$ and $\sigma_x(m_j)$ are the distribution widths along the habitat axis for species i and species j . $\sigma_x(m_i)$ is also called the home range of species i which increases with size m_i :

$$\sigma_x(m_i) = \sigma_0 + \alpha \log_{10}(m_i/m_0), \quad (3)$$

where α is the home range coefficient set to 0.5. The habitat trait acts to generate diversity within a trophic level. Without the habitat trait, species of similar body size would disappear through competitive exclusion. This mechanism contrasts other size-based food web models that use interference competition to generate diversity within size groups (Allhoff & Drossel, 2016; Loeuille & Loreau, 2005; Schneider et al., 2016). Our model combines the direct effects of competition and predator-prey relationships, as suggested by Chesson & Kuang, 2008, to generate emergent food web structures. The interaction strength between species i preying on species j is determined by the habitat and size axes as follows:

$$\theta_{j \rightarrow i} = \varphi(m_i/m_j)\psi(x_i - x_j). \quad (4)$$

Then, the total amount of food F_i for species i is the sum of feeding on other species, as specified by the interaction $\theta_{j \rightarrow i}$, and feeding on a continuous resource supply along the habitat axis, $R(x)$:

$$F_i = \sum_j B_j \theta_{j \rightarrow i} + \int R(x) \theta_{R \rightarrow i} dx, \quad (5)$$

where $\theta_{R \rightarrow i}$ is the interaction with the resource. Biomass dynamics of species i are described by the energetic gains (resource uptake, predation on species j) and losses (metabolism, predation by species j):

$$\frac{dB_i}{dt} = B_i \varepsilon m_i^{q-1} F_i - B_i \left(c m_i^{n-1} + \sum_j m_j^{q-1} B_j \theta_{i \rightarrow j} \right), \quad (6)$$

where m_i^{q-1} is the clearance rate of species i , $c m_i^{n-1}$ is metabolic costs, and ε is the efficiency of converting food to new offspring (parameters are detailed in Table 1). The resource follows a logistic growth, is continuously distributed along the habitat trait, and is preyed upon by consumers in the food web:

$$\frac{dR}{dt} = r \left(1 - \frac{R}{K} \right) R - \sum_i m_i^{q-1} B_i \theta_{R \rightarrow i} R, \quad (7)$$

where r is the intrinsic growth rate and K the carrying capacity of the system.

The model represents well observed macro-ecological patterns of diversity, size-scaling of total biomass and number of species with body size, number of trophic levels and food web structure metrics (model validation described in Appendix S2). The parameters in the model are fairly well constrained, and we discuss the sensitivity of the model outcome to changes in their values (see Appendix S3).

2.2. Metrics of ecosystem functions, diversity, and structure

In order to investigate the effects of diversity and food web structure across multiple ecosystem functions we estimated four measures of properties and processes in the food web, considered as ecosystem functions (Table 2):

- the total biomass of the species in the food web
- the metabolic losses of all species
- the new production of the food web as the amount of resource which enters the food web
- the productivity of the food web, defined as the speed at which the energy goes through the food web (Gascuel, Morissette, Palomares, & Christensen, 2008; Schramski, Dell, Grady, Sibly, & Brown, 2015).

All quantities were scaled by the carrying capacity of the resource. We calculated the ecosystem functions at equilibrium, when all the amount of resource flowing into the food web is equal to all the amount of energetic losses.

To explain ecosystem functions, we calculated the following drivers (equations in Table 2):

- species richness (the total number of species in each food web)
- metrics characterizing dominance: the maximum proportion of biomass in each food web represented by the dominant species D_1 , Simpson's evenness index D_2 and absolute biomass of the dominant species in each food web D_3
- metrics characterizing the topology and vertical diversity of the assembled food webs: the connectance, the mean trophic level, the maximum trophic level and the number of top-predators
- completeness of the trait space: proportion of trait space filled by species, using the size of the trait space T_{size} .

To calculate this last metric, we used a grid representing the trait space containing all combinations of the habitat trait (ranging from -25 to 25) and the size trait (ranging from 1 to 10^{11} defined in log-scale). A grid cell in the trait space was considered 'filled' if the sum of the interaction coefficients of all species in a grid cell exceeds 0.001 (several thresholds were tested in Appendix S4).

2.3. Links between biodiversity, food web structure, and ecosystem functioning

For each of the four ecosystem functions, we investigated and compared their relationship with species richness and their coefficient of variation. After standardizing the number of food webs along the richness gradient (section 2.1 and Appendix S1), we obtained and used 2000 food webs from 1 to 40 species for all analyses. To quantify the shapes of the BEF relationships we fitted linear and non-linear (Michaelis-Menten, power and sigmoidal) mathematical functions and selected the best fit based on the explained variance and the Akaike Information criteria (Appendix S5). We explored the relationship between ecosystem functions by their correlations, potentially revealing trade-offs between them (Appendix S6). To investigate the single and combined effects of predictors on ecosystem functioning, we performed variance partitioning analyses on each ecosystem function using the R package 'vegan' and the function *varpart* (Oksanen et al., 2017). We grouped explanatory variables into four categories: (i) horizontal diversity, represented by species richness; (ii) vertical diversity, including connectance, mean trophic level, maximum trophic level and the number of top-predators;

(iii) the proportion of filled trait space; (iv) dominance. To take into account non-linear relationships, we included squared terms when relevant by applying the following transformation to predictor X : $(X - \bar{X})^2$ (Appendix S7). We further investigated the importance of dominance for biomass, and explored which food web configurations favor dominance in the model.

2.4. Manipulation of food web structure

To investigate the role of food web structure on diversity and ecosystem functioning, we manipulated the predator-prey interactions by modifying the home range coefficient α from the initial value of $\alpha = 0.5$ (equation 3) to a value of $\alpha = 2$ (Fig. 1). This manipulation indirectly increases the connectance of the food web, because each species is able to access a larger number of prey and establish a higher number of feeding links. We repeated a similar methodology and ran 100 community assemblies based on random species pools for the high home range coefficient and obtained 54,755 food webs with a maximum of 26 species. We performed similar richness standardization (section 2.1 and Appendix S1) to get the same number of food webs per richness level. We were able to obtain 1100 food webs ranging from 1 to 22 species for the second set of community assemblies. We investigated the differences in food web structure between the food webs from the two sets of community assemblies.

3. Results

3.1. Different BEF relationships across ecosystem functions

We found generally positive and saturating BEF relationships but with marked differences in the shape of the relationships among the four ecosystem functions considered, with respect to their initial rate of increase and level of saturation (Fig. 2; Appendix S5). For instance, the relationship between richness, biomass and metabolism saturated at considerably lower species richness (~20 species), compared to production and productivity (that saturated at ~35 species). Interestingly, only a moderate degree of variability in ecosystem functions could be explained by richness alone, especially for biomass and metabolism where the maximum of the explained variation of the best fitted sigmoidal functions amounted to 40% and 14%, respectively (Appendix S5). The pronounced variability in the level of each function around its mean trend is primarily evident at low levels of richness, as illustrated by a strong decreasing trend in the coefficient of variation with increasing richness (Fig. 2e, f, g, h), especially for biomass (approximately from 0.8 to 0.05). This change in variation along the richness gradient can be related to the trait space, which is only partly occupied at low

richness but mostly filled at high richness (from 0 to 80-90%, see Appendix S4). This in turn is reducing the variation and range of biomass, production, metabolism and productivity, (Fig. 2e to h).

The analysis of differences between ecosystem functions using correlation and multidimensional statistics highlights that synergies and trade-offs seem to occur since food webs are not maximizing all ecosystem functions simultaneously (Appendix S6). Biomass has a strong correlation with metabolism and production. Metabolism is strongly related to biomass, but not to production and productivity.

3.2. Drivers of ecosystem functions

While the variability of the four ecosystem functions is well captured by the variance partitioning analysis (explained variance >75%), the importance of each category of drivers (e.g. species richness, dominance, trait space and vertical diversity), as well as the joint effects of drivers, vary between functions. Species richness alone explains a low variance in ecosystem functions (0% for biomass, 3% for metabolism, 3% for production and 2% for productivity; Fig. 3 and Appendix S7). However, species richness is rarely acting as a single driver. For instance, a combined effect of species richness, completeness of the trait space, dominance and vertical diversity explain a large variation of production and productivity (72% and 57%, respectively, Fig. 3c and d). On the contrary, we notice the importance of dominance, which alone explains 49% and 37% of biomass and metabolism variance, respectively (Fig.3a and b). Similarly, vertical diversity explains 20% of the variance in metabolism (Fig.3b).

3.3. Variance in biomass explained by dominance

In addition to the pronounced differences in the variability of ecosystem functions at low and high levels of richness, we observed a marked difference in food web structure and resource use between low and high diversity food webs (Fig. 4a, b, and c). In high-diversity food webs, the trait space is fully occupied and species with low trophic levels are predated upon (Fig. 4b). In contrast, the trait space in low-diversity food webs is generally not fully occupied, in which case a particular situation might emerge where low trophic level species are not strongly predated upon (Fig. 4d). Under such conditions, the species is relieved from predation and competition, and will become dominant and accumulate high biomass (Fig. 4e). More particularly, dominance arises from species isolation in the trait space (Appendix S8). Consequently, species poorly exposed to predation but predating strongly on resource and/or other species contribute greatly to the total biomass of the assembled community.

3.4. Food web structure influences BEF relationships

By modifying the home range coefficient for all species in the community, the maximum level of function reached in the two types of communities is similar, but the species richness at which this maximum level is reached is different (Fig. 5a-d). More specifically, the level of biomass, metabolism, production, and productivity saturates at a considerably lower level of richness when the home range is broader. In addition, the proportion of the resource used in the food web is slightly higher in communities with a broader home range (Fig. 5f), which can explain a slightly higher production and productivity. We observed that the maximum number of species in the food web is lower when the home range is broader (~20 species compared to ~40 species at a low home range). These differences are likely due to the degree of trait space occupied and proportion of the resource used by the species, where in the broad home range scenario, a higher proportion of the resource is used and the trait space is filled with a lower number of species (Fig. 5e, f).

Because of the increase in the home range coefficient, species have access to more prey (they can establish more predator-prey relationships) and may reach a higher trophic level. This results in food webs exhibiting a higher connectance and mean trophic level (Appendix S9). Ultimately, this explains the wider use of the trait space at lower richness (Fig. 5e), where fewer species are more efficient at covering the trait space, since they have a better access to prey on the habitat axis.

4. Discussion

Theoretical models provide powerful tools to simulate and understand complex system dynamics such as food webs. Consequently, food web theory is increasingly incorporated and used in BEF research (Barnes et al., 2018; Hines et al., 2015; Poisot, Mouquet, & Gravel, 2013; Wang & Brose, 2018). Yet, such models are rarely used to investigate the role of food web structure and biodiversity on several ecosystem functions. In this study, we used a trait-based food web model, capable of simulating a community assembly process, to investigate and compare the role of food web structure and various aspects of biodiversity on multiple ecosystem functions. Among the functions considered, all demonstrated a positive saturating relationship with species richness. This is well in agreement with previous modelling studies (Loreau 1998, Hooper et al. 2005, Schneider et al. 2016), indicating that no matter the type of model used, saturating BEF relationships are emergent to the system modelled. Whilst the model represents well-known relationships across functions, it is also a useful tool to generate research hypotheses and improve our *a priori* expectations on how diversity and food web structure influence several ecosystem functions in real ecosystems. Here, we focus on three hypotheses emerging from

the model and answering our three research questions: (i) BEF relationships vary across ecosystem functions, (ii) Dominance, food web structure and the trait space are important drivers of functions besides species richness, (iii) Food web structure can control diversity in the food web and modify BEF relationships.

Distinct positive saturating BEF relationships

We tested the relationships between diversity and multiple ecosystem functions and our results showed marked differences in the shape of BEF relationships among the functions considered, particularly with regards to their degree of saturation. For instance, biomass and metabolism saturated at a lower level of richness with less species (from 10 to 20), compared to production and productivity (from 30 to 40 species). This difference can be explained by the features they depend on: production is related to the resource growth rate and biomass is controlled by the trait space that species occupy and predation. Theoretical models are rarely used to quantify different functions and study their differences in relation to biodiversity. Ecosystem functioning is often limited to biomass or production (Barnes et al., 2018; Fung et al., 2015; Thebault & Loreau, 2003). Recently, relationships between species richness, functional diversity (similar to our trait space), and various ecosystem functions such as metabolic loss, consumer biomass, intraguild predation were established with size-based models (Allhoff & Drossel, 2016; Schneider et al., 2016), but the differences between ecosystem functions are neglected or the shapes of the relationships unquantified. Compared to the model from Schneider, Brose, Rall, & Guill, 2016, our model seems to show stronger saturation of the richness-metabolism relationship, while the richness-biomass relationship seems to be similar (but their richness gradient goes up to 100 species). Our findings highlight that different BEF relationships can be expected for different ecosystem functions.

Field-based studies often consider single ecosystem functions, therefore limiting a multifaceted concept to one metric (van der Plas, 2019). More importantly, neglecting multiple metrics of ecosystem functioning might mask trade-offs between ecosystem functions (Gamfeldt, Hillebrand, & Jonsson, 2008; Hölting et al., 2019). The existence of such trade-offs has pronounced implications for natural resource management since maximizing one ecosystem function might not maximize all other ecosystem functions simultaneously. Fortunately, methods to quantify several ecosystem functions exist and can be used in large-scale and food web field-based BEF studies. Metabolism can be readily estimated from the body size of species, while production and productivity can be estimated in different ways based on other species traits, such as growth parameters and trophic level (Gascuel et al., 2008; Greenstreet et al., 2012; Maureaud et al., 2017). However, such estimations depends greatly on the quality of the trait data (Bellwood, Streit, Brandl, & Tebbett, 2019). Still,

many metrics of ecosystem functioning are available in the literature and can somewhat be extended to observations (Brandl et al., 2019; Saint-Béat et al., 2015), and therefore used in monitoring and management.

The BEF relationships produced by the trait-based model are also characterized by a decreased variation in ecosystem functioning along the richness gradient, slightly variable across ecosystem functions. This effect is referred to as an increase in ‘reliability’ or ‘predictability’ (McGrady-Steed, Harris, & Morin, 1997; Naeem & Li, 1997; Schneider et al., 2016), because the trait space is filled by species and, as a result, less flexibility in functioning is allowed in the system (Schwartz et al., 2000). The increase in predictability is created by the trait space – which can be defined as the range of possibilities along the trait axes species can use to predate – and will enhance the ‘insurance’ effect (Yachi & Loreau, 1999). The ‘insurance’ effect refers to the fact that the level of an ecosystem function will be insured to be high and less variable under environmental fluctuations with a high number of species in the system.

Predictors of ecosystem functioning besides species richness

To address our second research question, we investigated the importance of multiple drivers on ecosystem functions. We showed that functions are explained differently by the single or joint contribution of drivers considered. Biomass is strongly related to dominance (explaining a larger variance of biomass than species richness). Metabolism is related to dominance, but also to vertical diversity. This is not surprising because metabolism is scaled with the species size (e.g. equation 6), leading to higher metabolism for shorter food chains. Production and productivity are explained by a combination of the occupancy of the trait space – which may be considered similar to functional diversity indices (Villéger, Mason, & Mouillot, 2008) – the number of species, dominance and vertical diversity. This means that a higher occupancy of the trait space might lead to longer food chains and to higher species richness, highlighting an interplay between horizontal and vertical diversity (Brose et al., 2019; Duffy et al., 2007) and potentially revealing trophic complementarity (Poisot et al., 2013). Whether higher production is driven by horizontal, vertical diversity or dominance is important because those effects are not related to the same mechanisms (resource complementarity, predation, selection, respectively). Very likely, the shared explained variance by all categories reflects the importance of several of these mechanisms, which are not due to species richness alone. Hence, considering only species richness may lead to misinterpretation of which mechanism explains the variation in food web ecosystem functioning. We encourage empirical studies to investigate several drivers to explain ecosystem functioning, as each of them might reflect the underlying mechanisms driving ecosystem functioning.

In addition to demonstrating the importance of multiple drivers for ecosystem functions, we investigated the importance of dominance for biomass. Our trait-based model showed that species evenness is as important as the number of species in determining the level of biomass. In particular, differences in evenness can largely explain the pronounced variability around the mean level of biomass at a given level of richness. Such an effect of evenness on variability can largely be explained by species dominance, which occurs primarily for lower trophic level species that are isolated within the trait space, hence experiencing limited competition and predation. The effect of dominance has already been shown in competition and resource-consumer models (Petchey, 2000; Tilman et al., 1997), but not in food webs. The biomass of dominant species could be controlled by self-regulation factors due to other reasons than direct effects of competition and predator-prey interactions, such as disease, interference competition or limitation by the size of the physical habitat. Such effects will tend to diminish the biomass of such dominant species. Previous food web modelling studies found similar variability of ecosystem functions at each richness level (Schneider et al., 2016), but it remains to be shown that the importance of dominance and the mechanism behind it are similar with models including self-regulation and interference competition (Ritterskamp, Bearup, & Blasius, 2016; Schneider et al., 2016). To summarize, our model shows that: (i) dominance is an important predictor of biomass in large food webs; (ii) dominance can lead to higher levels of biomass at low richness compared to high richness; (iii) dominance occurs because of species interactions and traits.

Dominance of species associated to a lack of predation has been shown to occur also in nature. For instance, species can be dominant when they invade an ecosystem, especially when they are not predated but able to forage efficiently in their new environment. This is the case of the invasive round goby, which has a generalist diet, high consumption rates but faces limited predation by native predators in the Baltic Sea (Nurkse, Kotta, Orav-Kotta, & Ojaveer, 2016). Such patterns of dominance are also shown by small pelagic fish species dominating in highly productive upwelling ecosystems where they thrive and represent huge abundances (Cury, 2000). Dominance of low trophic level species may also occur via predation release mediated by high exploitation or overfishing of top-predators, causing top-down trophic cascading effects. Evidence of such phenomenon has been demonstrated in several ecosystems in the North Atlantic and North Pacific (Baum & Worm, 2009). Overall, our results confirm the importance of both ‘complementarity’ and ‘selection’ mechanisms, displayed by the number of species and dominance, respectively. However, dominance effects on ecosystem functioning are overall much less investigated than the effects of the number of species in empirical studies, despite their strong prevalence in ecosystems (Hillebrand & Cadotte, Marc WBennett, 2008).

Fortunately, multiple methods and indices exist to quantify dominance of species (Magurran, 2004) and can be easily computed in empirical studies.

Food web structure effects on BEF relationships

By manipulating the food web structure in the model, we show that trophic interactions and food web structure can influence BEF relationships; in particular the way species feed and use their habitat. Our food web manipulation gave species a higher connectance by increasing the home range coefficient ($\alpha = 2$). This leads to fewer coexisting species but with similar levels of ecosystem functions and implies a steeper initial rate of increase in ecosystem functions and saturation at a lower level of species richness. Such an approach has already been considered in a plant-herbivore model showing that generalist herbivores may maintain higher levels of biomass than specialists (Thebault & Loreau, 2003), along a lower range of species richness. Similarly, our modification of home range coefficient can be interpreted as a change in species diet and/or habitat niches allowing us to compare communities characterized by either specialist species (low home range coefficient, low connectance) or generalist species (high home range coefficient, high connectance). In generalist communities, the trait space is occupied with less species, and food webs are more connected (higher connectance and number of links per species). Our results are similar to another modelling study, where species-poor generalist communities can reach the same level of ecosystem functions as species-rich specialist communities, at least under constant environments (Richmond, Breitburg, & Rose, 2005). Our approach is highly idealized in the sense that the whole community is entirely composed of generalist or specialist species. Including a degree of generalism in the community would give more realistic community assemblies and results, but requires the inclusion of a trade-off for being generalist (MacArthur, 1984), for instance in terms of costs associated with increased predation or lower performance under environmental fluctuations. Future model development aiming to quantify and incorporate such costs and trade-offs of generalism under different environmental forcing would allow for a better understanding of BEF relationships.

Since being a generalist species is related to the number of feeding links established per species and to how they are distributed in space and along latitudinal gradients (Cirtwill, Stouffer, & Romanuk, 2015; Kortsch et al., 2018), the increase in availability of fully resolved food web data might allow us to empirically study and better understand the influence of specialism versus generalism (R. Thompson & Caffrey, 2019). Species can be specialists or generalists not only in terms of their diet but also in the way they are able to cope with a certain range of environmental conditions and habitats. Indices can be easily computed to assess the degree of habitat specialization and have already been applied to bird communities (Julliard, Clavel, Devictor, Jiguet, &

Couvet, 2006). Several methods exist to determine the degree of specialization of species and communities in terms of habitat, diet, and morphology (Brandl, Robbins, & Bellwood, 2015; Devictor et al., 2010). Such metrics could be used to assess how generalist versus specialist communities influence ecosystem functioning in nature. Hence, while we highlight a theoretical and empirical gap in our knowledge regarding the way food web structure and specialism/generalism influence BEF relationships, we acknowledge that methods and data exist to start answering such questions.

5. Conclusions

Our modelling study provides support and inspiration for future theoretical and empirical work on BEF. In particular, we have demonstrated the importance of considering multiple ecosystem functions, because the relationship with diversity can differ substantially between ecosystem functions. Such differences may in turn give rise to trade-offs between ecosystem functions with particular implications for natural resource managers. We provide evidence that dominance and food web structure, resulting from species interactions and habitat use, may dramatically influence the level of functioning at a given species richness. We encourage further theoretical and empirical studies to use fully resolved food web data, metrics of dominance and habitat use, and multiple ecosystem functions to better understand the complexity of links and mechanisms between biodiversity, food web structure, and ecosystem functions.

Authors' contributions

A.M., K.H.A and M.L. designed the study. L.Z. produced the food web simulations and A.M. analyzed the results. A.M. wrote the first draft and all co-authors contributed in writing and editing the manuscript.

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Data Accessibility

The data aggregated after model simulations and R code used to produce figures is available on GitHub, <https://github.com/AquaAuma/BEFwithTrait-BasedFoodWebModel> and citable, DOI 10.5281/zenodo.3529498 (Maureaud, Andersen, Zhang, & Lindegren, 2019)

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Figures and Tables with captions

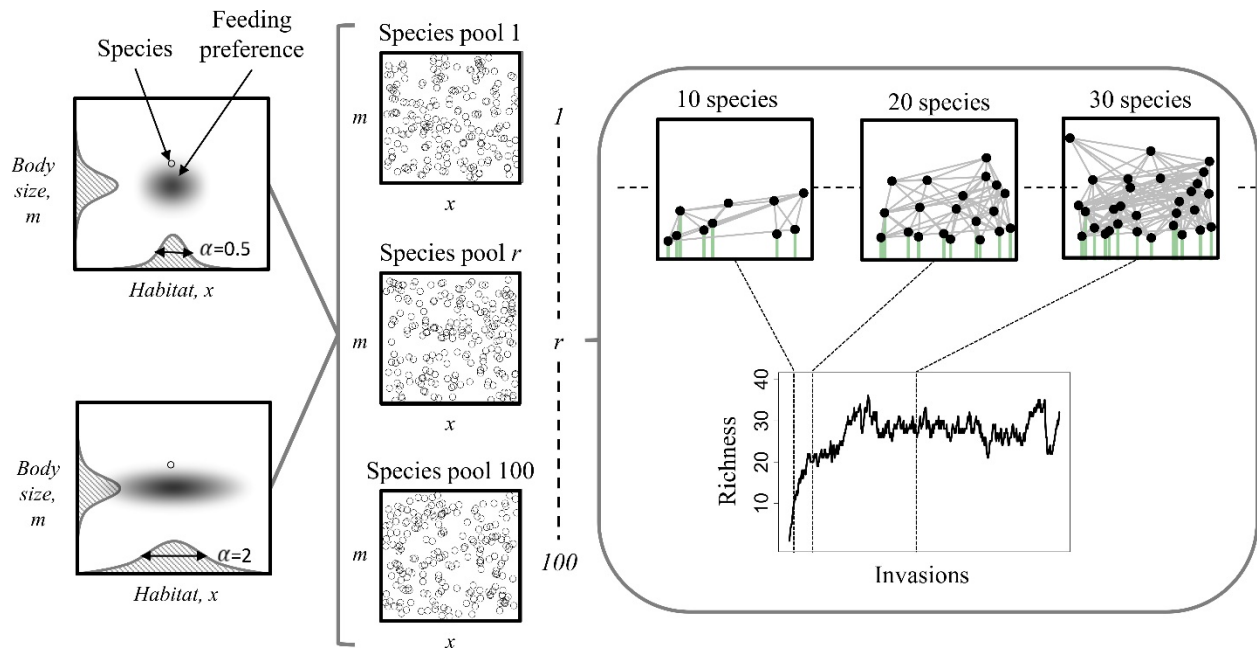


Figure 1: Description of the community assembly. A species is defined by its size m and habitat x . Density functions on each trait axis indicate the affinity of the species for all trait values. The grey shaded areas below the species indicate the feeding preference, where dark grey indicate higher preference. From each of the 100 different species pools, each containing 200 species, we run a various number of food web community assemblies, by adding one species at each invasion attempt. The maximum number of species in the community is less than 40 in this example. Three examples of food webs for 10, 20 and 30 species are shown, grey links show the predator-prey links and green links the consumer-resource links (non-animal resource). The parameter α represents the home range coefficient introduced in equation 3.

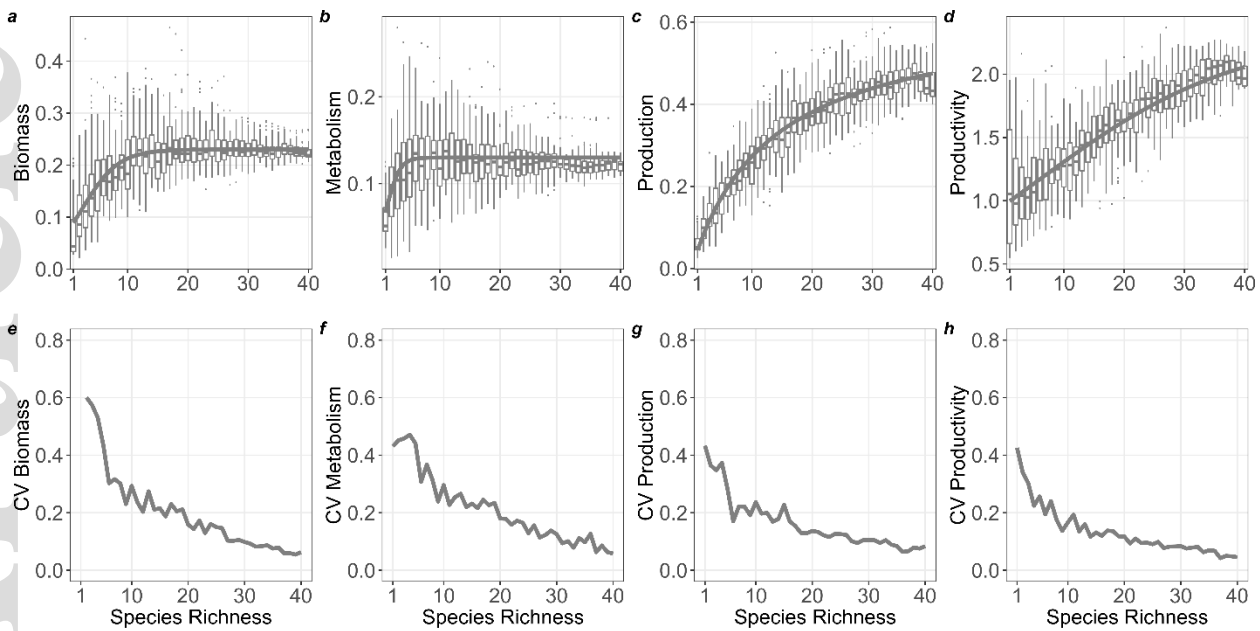


Figure 2: Relationships between species richness and ecosystem functions for simulated food webs. Top row (a to d) are boxplots each ecosystem function against the number of species (Appendix S5): (a) the proportion of biomass in the system relative to the carrying capacity K , (b) metabolism divided by the carrying capacity, (c) production divided by the carrying capacity, and (d) productivity. For each relationship, the best-fitted mathematical curve is represented (sigmoidal for (a), sigmoidal for (b), Michaelis-Menten for (c) and sigmoidal for (d)). Bottom row (e to h) shows the coefficient of variation (CV) of the simulated food webs against richness. Each figure includes 50 food webs per richness level (2000 in total).

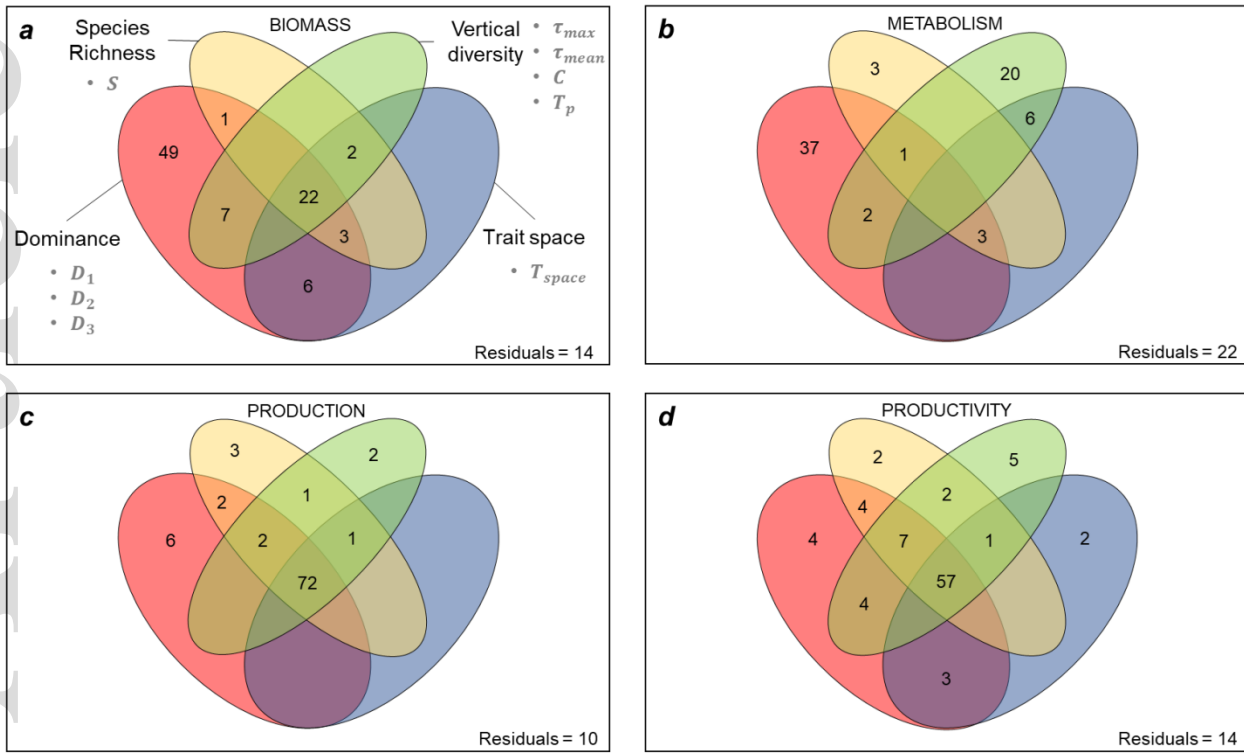


Figure 3: Variance partitioning analyses showing the relative contribution of horizontal diversity (or species richness, in yellow), vertical diversity/food web structure (in green), trait space (in blue) and dominance (in red) in explaining each ecosystem function: (a) biomass, (b) metabolism, (c) production and (d) productivity. Each number on the colored section indicates the explained variance (%) by each combination of drivers (full description in Appendix S7). Residuals show the unexplained variance. Only values higher than 1% are included.

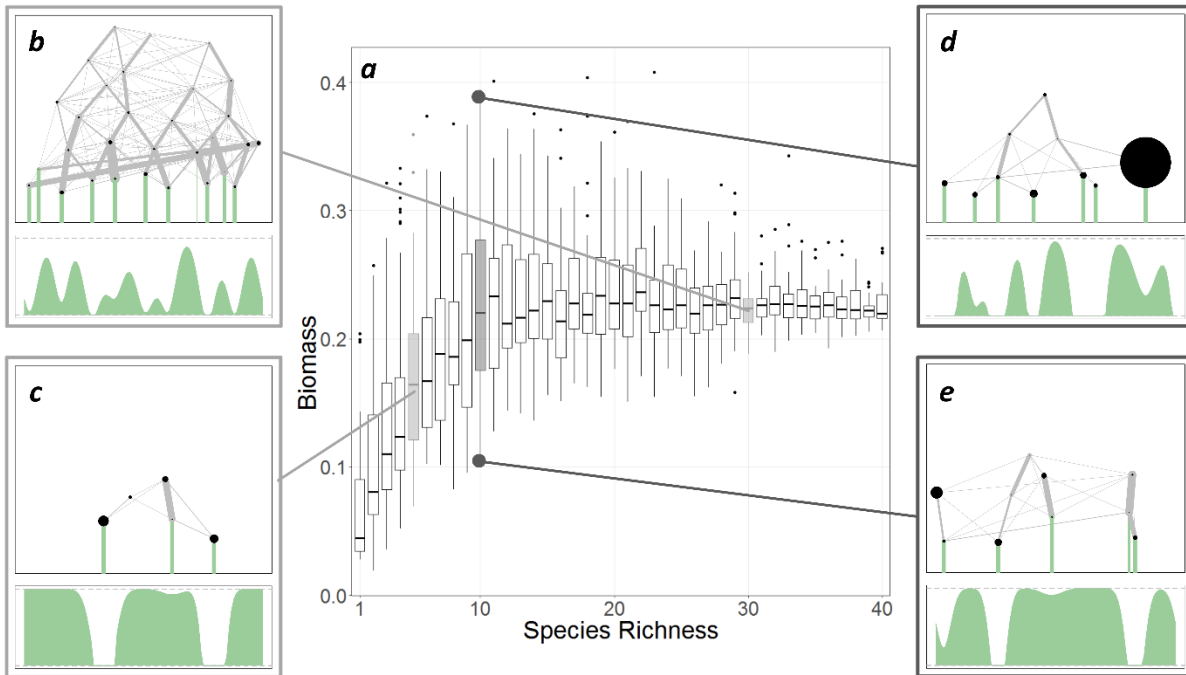


Figure 4: Biomass is explained by richness and dominance: (a) relationship between biomass and species richness for the 2000 food webs; examples of simulated food webs (b) 30 species and mean biomass, (c) 5 species and mean biomass, (d) 10 species, high biomass and high dominance, (e) 10 species, low biomass and low dominance. In each box, the top graph represents the species size m against the habitat trait x , species are circles and lines are predator-prey links in grey, and links to the resource in green. The bottom graph represents the resource levels along the habitat trait.

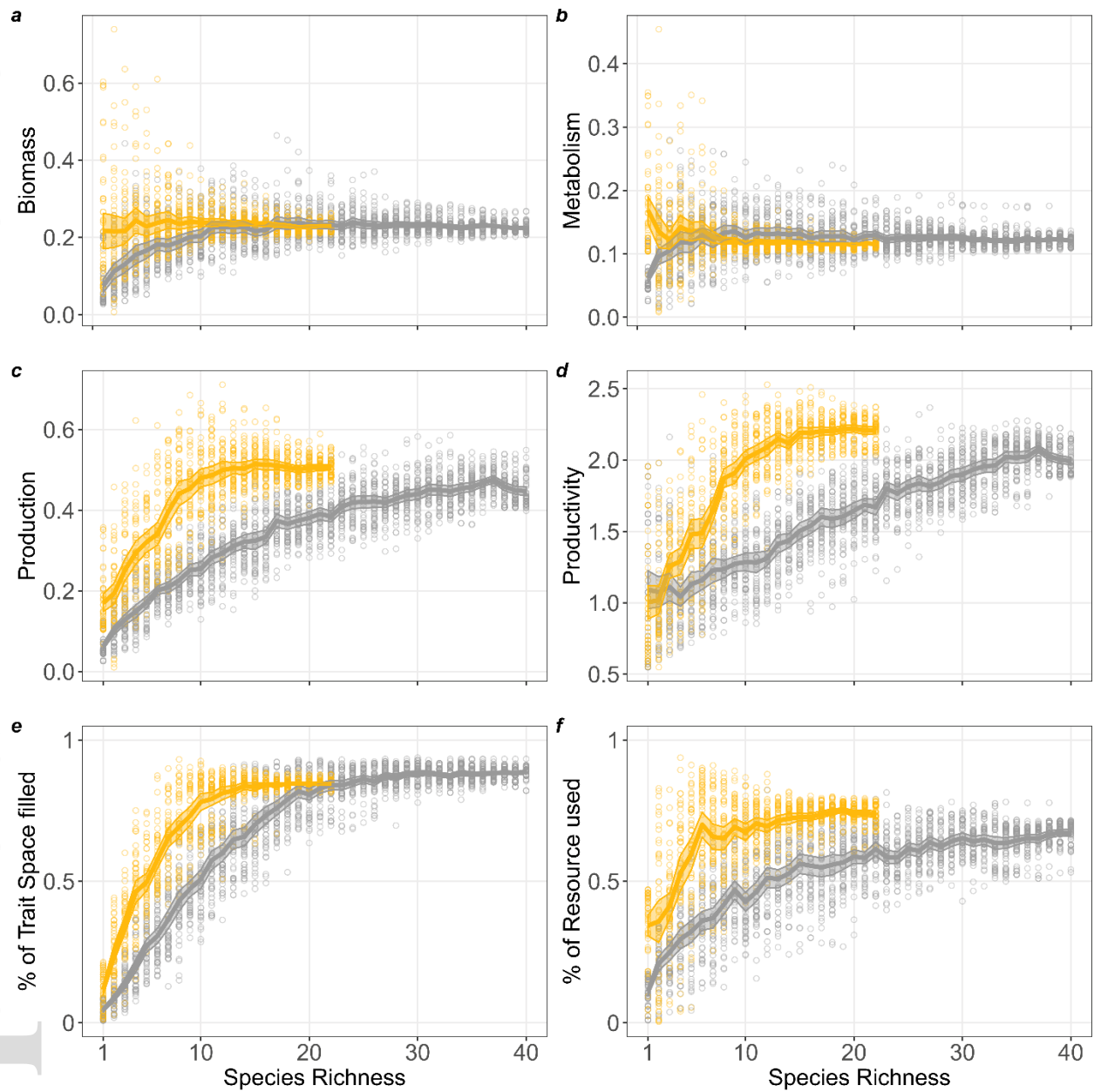


Figure 5: Comparisons of richness-function relationships for communities with a low home range (grey, $\alpha = 0.5$, 2000 food webs) and a high home range (yellow, $\alpha = 2$, 1100 food webs): for biomass (a), metabolism (b), production (c) and productivity (d), the percentage of trait space filled (e) and the proportion of total resource used (f). Lines represent means of the y-value and the shades show the standard deviations.

Table 1: Model parameters from Zhang et al., 2014.

Parameter	Description	Unit	Value	Source
α	Home range coefficient	-	0.5	(Zhang et al., 2014)
σ_m	Width of selection function	-	1	(Ursin, 1973)
σ_0	Home range of m_0 sized species	-	$\sqrt{2}/2$	(Hartvig, 2011)
β	Preferred predator:prey mass ratio	-	100	(Ursin, 1973)
ε	Conversion efficiency	-	0.2	(Rossberg, Ishii, Amemiya, & Itoh, 2008)
c	Constant for intrinsic mortality	$[w/t]$	3.3	(Zhang et al., 2014)
n	Exponent of metabolic costs	-	0.75	(West, Brown, & Enquist, 1997)
q	Exponent of volumetric search rate	-	0.75	(Andersen & Beyer, 2006)
r	Resource intrinsic growth rate	$[1/t]$	30	(Zhang et al., 2014)
K	Resource carrying capacity	$[w]$	510	(Zhang et al., 2014)

Table 2: Metrics of diversity, structure and ecosystem functioning used in the study with their respective equations, dimension, and parameters.

Property	Metric	Unit	Equation
Ecosystem functioning	Biomass	[w/w]	$B = \frac{1}{K} \sum_i B_i$
	Metabolism	[w/(wt)]	$M = \frac{1}{K} \sum_i B_i \times km_i^{n-1}$
	Production	[w/(wt)]	$P = \frac{1}{K} \sum_i B_i \times \varepsilon m_i^{q-1} \int R \theta_{R \rightarrow i} dx$
	Productivity	[1/t]	$Q = P/B$
Horizontal diversity	Species richness	-	s
Dominance	Dominance	-	$D_1 = \max \left(\frac{B_1, B_2, \dots, B_s}{\sum_{i=1}^s B_i} \right)$
	Simpson's evenness	-	$D_2 = \frac{1}{s \sum_{i=1}^s \left(\frac{B_i}{\sum_i B_i} \right)^2}$
	Biomass of dominant species	[w/w]	$D_3 = \max(B_1, \dots, B_i, \dots, B_s)$
Vertical diversity and food web structure	Trophic level	-	$\tau_i = 1 + \sum_j \tau_j \times \frac{\theta_{j \rightarrow i} B_j}{B_i}$
	Mean trophic level	-	$\tau_{\text{mean}} = \frac{1}{B} \sum_{i=1}^s \tau_i \times B_i$
	Maximum trophic level	-	$\tau_{\text{max}} = \max(\tau_1, \dots, \tau_i, \dots, \tau_s)$
	Number of feeding links	-	L
	Connectance	-	$C = \frac{L}{s^2}$
	Number of top-predators	-	T_p
Trait space	Trait space of species i	-	$T_{\text{space},i} = \iint \varphi \left(\frac{m_i}{m} \right) \psi(x_i - x) dx dm$