

The hidden role of multi-trophic interactions in driving diversity-productivity relationships

Georg Albert¹, Benoit Gauzens¹, Michel Loreau², Shaopeng Wang³, and Ulrich Brose⁴

¹iDiv

²Centre National de la Recherche Scientifique

³Peking University

⁴German Centre for Integrative Biodiversity Research Halle-Jena-Lepizig

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Abstract

Resource-use complementarity of producer species is often invoked to explain their generally positive diversity-productivity relationships. Additionally, multi-trophic interactions that link processes across trophic levels have received increasing attention as a possible key driver. Given that both are integral to natural ecosystems, their interactive effect should be evident but has remained hidden. We address this issue by analyzing diversity-productivity relationships in a simulation experiment of primary producer communities nested within complex food-webs, manipulating resource-use complementarity and multi-trophic animal richness. We show that both mechanisms' joint contribution to positive diversity-productivity relationships generally exceeds their individual effects, as both interactively create diverse communities of complementary producer species. Specifically, multi-trophic interactions in animal-rich ecosystems increase complementarity the most when resource-use complementarity is low. The interdependence of top-down and bottom-up forces in creating biodiversity-productivity relationships highlights the importance to adopt a more multi-trophic perspective on biodiversity-ecosystem functioning relationships.

Introduction

Most research on biodiversity-ecosystem functioning (BEF) relationships has focused on effects of varying horizontal diversity (i.e., diversity within a single trophic level), most commonly of plants in controlled experimental communities (e.g., Isbell et al. 2015). However, natural communities are characterized by complex interaction networks that integrate diversity and its effects across trophic levels (Duffy et al. 2007; Brose et al. 2019), with their BEF relationships varying substantially in strength (Barnes et al. 2014; Duffy et al. 2017; van der Plas 2019). Recent research has aimed at resolving this separation between within-trophic level and multi-trophic approaches to BEF relationships (Loreau 2010; Brose & Hillebrand 2016). For example, the vertical diversity hypothesis links ecosystem functions of primary producers, and hence their diversity effects, to variance in vertical diversity (i.e., diversity across trophic levels), specifically the maximum trophic levels and body-masses of multi-trophic ecosystems (Wang & Brose 2018). It also points to other related aspects such as food-web structure (Thompson et al. 2012; Montoya et al. 2015; Brose et al. 2017) or animal diversity (Naeem et al. 1994; Schneider et al. 2016; Zhao et al. 2019) that influence ecosystem functions at the producer trophic level. Despite ample evidence for such top-down effects on producer BEF relationships, the underlying mechanisms have remained elusive.

The many biological mechanisms involved in creating positive diversity effects in producer communities can be broadly categorized into two classes (Loreau & Hector 2001; Loreau 2010). First, complementarity mechanisms occur when functionally different species use dissimilar niches, hence have a low interspecific competition. This low competition fosters coexistence, which simultaneously increases the ecosystem func-

tioning of the whole community. Second, selection mechanisms favor species with competitive advantages. If such advantages are associated with particular functional traits such as a higher growth rate, selection can affect ecosystem functioning. Complementarity and selection are both enhanced by a larger species-pool that may provide more complementary species and strong competitors alike (i.e., sampling effect). However, they have opposite implications for realized diversity, which is maintained by complementarity but reduced by selection mechanisms. Even though the functional identity of the dominating species can be important depending on the ecosystem function in question (Loreau 2004; Hooper et al. 2005), most evidence points towards complementarity mechanisms as the dominant driver of BEF relationships (Hooper et al. 2005; Cardinale et al. 2007; Barry et al. 2018).

Complementarity between co-occurring producer species is most commonly associated with resource-use complementarity (synonymous with resource partitioning; Barry et al. 2018), expressing fundamental differences in resource-access of coexisting species. These differences can arise from varying aspects of resource-use such as differences in the chemical forms of resources used (McKane et al. 2002; Von Felten et al. 2009; Ashton et al. 2010), phenological asynchrony (Henry et al. 2001; Sapijanskas et al. 2014), or spatial separation, both above- (e.g., crown packing in Sapijanskas et al. 2014) and belowground (e.g., rooting depth in Mueller et al. 2013). Additional resource-based mechanisms such as facilitation (Wright et al. 2017) and niche plasticity (Von Felten et al. 2009; Mueller et al. 2013) can modify resource niches to decrease competition and increase complementarity among producers further.

In the presence of animal consumers, however, competition is not only resource-based (exploitative competition) but can be mediated by multi-trophic interactions (apparent competition; Holt 1977; Loreau 2010). When herbivorous feeding is complementary (i.e. herbivores have different resource-species), apparent competition between producer species is low, which fosters coexistence as it creates complementarity at the producer trophic level (Thébault & Loreau 2003; Brose 2008; Poisot et al. 2013; Wang & Brose 2018). As a result, simple herbivore communities alone are sufficient to create positive diversity effects on standing biomass and resource uptake (i.e., primary production) of producers, even without resource-use complementarity (Thébault & Loreau 2003). Increasing the vertical diversity in complex trophic networks can further enhance coexistence, indicating that complementarity scales with the diversity of the multi-trophic animal community (Wang & Brose 2018). Additionally, herbivorous feeding can amplify differences in the competitive abilities of some producer species and thereby introduce selection mechanisms that can affect ecosystem functioning both positively or negatively (Thébault & Loreau 2003). For example, large producers that have low mass-specific metabolic rates are more suited to cope with herbivory, thus are more competitive and maintain higher biomasses (Schneider et al. 2016). Investigating complementarity mechanisms without considering selection is therefore impossible when trying to understand what drives BEF relationships in multi-trophic ecosystems.

It is evident that resource-use complementarity and multi-trophic interactions can both shape BEF relationships at the producer trophic level. Complementarity from either source will favor a positive relationship between biodiversity and ecosystem functioning, while selection may interact in more complex ways, potentially having opposing effects. It is therefore important to investigate how these mechanisms most likely combine in realistic complex food-webs. Our study addresses this issue by integrating multi-trophic interactions and resource-use complementarity into a complex allometric food-web model to examine how they create and shape the positive effects of producer species richness on primary production (hereafter: net diversity effects). First, we investigate how resource-use complementarity amongst producers creates positive net diversity effects across levels of producer richness. The subsequent inclusion of multi-trophic interactions allows us to investigate how such effects are modified through changes to the producer community's functional composition, potentially driving both selection and complementarity mechanisms. By varying the species richness of the multi-trophic animal community, we investigate how diversity across trophic levels influences the mechanistic interaction with resource-use complementarity and thus determines net diversity effects.

Methods

Simulating allometric trophic networks

Species traits and specifically body-mass determine ecological processes in natural ecosystems (Brown et al. 2004), including trophic interactions (Brose et al. 2019) and their strengths (Rall et al. 2012). Based on such allometric relationships, an allometric-trophic-network model can simulate the complex dynamics of ecosystems in a controlled environment (Schneider et al. 2016). It defines trophic interactions between different species based on their body-mass ratios and utilizes a set of differential equations that describes density changes over time for two limiting resources, and varying numbers of producers and animal consumers (see Supplementary 1 for a detailed model description). For animals, densities increase with feeding on other animals or producers. The strength of those trophic relationships is determined by feeding rates that comprise capture coefficients, handling times, interference competition, functional responses, and the number of prey species. Producers increase their densities due to growth that is limited by resource availabilities. Densities of animals and producers decrease as they are consumed and due to metabolic demands. Resource densities decrease due to growth of producer species and increase based on refresh rates that assume a constant resource turnover. In comparison to its original formulation (Schneider et al. 2016), we improved the model by updating capture coefficients to depend on the feeding preferences of the interacting species (i.e., carnivorous, omnivorous, herbivorous, autotrophic; Hirt et al. 2017). Further, we used a functional response that shifts from type II to type III as predator-prey body-mass ratios increase (Kalinkat et al. 2013). Throughout the model, we updated scaling coefficients based on empirical results (Ehnes et al. 2011; Lang et al. 2017).

Experimental setup

To quantify diversity effects of the producer community, we measured and compared primary production at different levels of producer species richness. Specifically, we measured primary production as the resource uptake at the end of the simulations (see Supplementary 1), which we used as yield Y to calculate net diversity effects ΔY as $\Delta Y = Y_O - Y_E$ (Loreau & Hector 2001). They capture the over- or underperformance of producer species mixtures in comparison to their monocultures as the difference between observed mixture yields Y_O and expected mixture yields Y_E , which are the sum of monoculture yields relative to their seeded proportion in mixture (i.e., their starting densities). To create a diversity gradient of the producer communities, we drew 30 random 16-species mixtures, all their monocultures, and five mixtures at each of three intermediate levels of species richness (2, 4, 8) that we randomly assembled from their respective 16-species species-pools.

To investigate the effects of multi-trophic interactions, we embedded the producer communities in food-webs at varying levels of animal richness (0, 10, 30, 50, 70). Systems without animals served as a null-model for the effects of multi-trophic interactions. Further, we included resource-use complementarity by manipulating the resource-use dissimilarity (RUD) of producer species over 16 steps (see below for a detailed description). We simulated all producer communities in a full factorial design for a total of 76,800 simulations, 960 for each possible combination of RUD and animal richness. We ran all simulations in Julia 1.2.0 (Bezanson et al. 2017) using the DifferentialEquations package (Rackauckas & Nie 2017). Simulations were limited to 150,000 time-steps, where they usually reached equilibrium. The code used for the simulations is available at <public.repository>.

Introducing resource-use complementarity

While multi-trophic interactions were intrinsic to our food-web model, incorporating resource-use complementarity required a modification of the producer-resource interaction. We introduced it based on two simple assumptions: First, resource-use complementarity can only occur if species differ in their access to resources, forming different resource compartments, for example, due to differences in chemical forms of resources used or their spatial distribution (e.g., access to different soil layers). Second, we assumed that resource-use complementarity is maximized if all species take up resources from distinct resource compartments.

We therefore introduced differences between producer species by limiting their resource-use to certain compartments of the resource pool to simulate resource-use complementarity (Fig. 1). Species that access the same compartments directly compete for the resources within those compartments. To investigate resource-

use scenarios where all species utilize resources from different compartments (i.e., no competition), the number of resource compartments C was defined as the maximum of producer species richness considered in our design (i.e., 16). Further, we assumed that all compartments were quantitatively the same. By increasing the dissimilarity between resource-use strategies of the 16 producer species within a species pool, we created a gradual change from no complementarity (i.e., all species access all compartments) to maximum complementarity (i.e., each species has its own resource compartment; Fig.1). For this gradient of resource-use dissimilarity (RUD), we ensured that (1) all producer species had access to the same number of compartments at a given level of RUD and that (2) accessed resource compartments were the same for both resources considered.

At maximum producer richness, species within a community where $RUD < 1$ initially always compete for resources with at least two other producer species with overlapping compartments, up to having all species competing with each other when $RUD = 0$. The competitive outcome is determined by which species can lower the resources the most ('R*-rule', Tilman 1982), whether resource competition can be weakened by trophic processes (Brose 2008), or both. To capture how the resource-use and thus productivity Y was distributed among coexisting producer species i , we calculated Shannon diversity H_{exp} as $H_{exp} = - \sum_i p_i \ln(p_i)$, with $p_i = Y_i / \sum_i Y_i$. H_{exp} reflects aspects of richness (i.e., how many species coexist) and abundance (i.e., how much resources each species uses) alike and is maximized at the number of coexisting species if all species use resources evenly (Jost 2006). Lower values indicate an uneven distribution of resource-use. In comparison to RUD, H_{exp} is based on realized instead of fundamental resource niches.

Partitioning of net diversity effects

By calculating net diversity effects ΔY as defined above, we were able to apply an additive partitioning approach (Loreau & Hector 2001) that separates complementarity effects (CE) from selection effects (SE) as

$$Y = Y_O - Y_E = N \overline{RY_i} \overline{M_i} + N \text{cov}(RY_i, M_i) = CE + SE,$$

with N being the species richness of the mixture, ΔRY_i being the deviation of the observed relative productivity from the expected relative productivity of species i , and M_i being the absolute monoculture productivity of species i . Complementarity effects quantify the average difference in productivity of the considered producer species mixture as compared to its monocultures, whereas selection effects quantify a possible bias towards better or worse than average performing monoculture species. To successfully calculate complementarity and selection effects for a given mixture, it was necessary to know the productivity of all its monocultures. Thus, we could not calculate them for mixtures that contained producer species with unviable monocultures that lead to global extinctions when simulated.

Results

In the absence of animals, simple producer communities show positive diversity-productivity relationships across all levels of resource-use dissimilarity (RUD; Fig. 2a, overall average relationship shown by black line). The shape of the diversity-productivity relationship depends on the level of RUD and can be exponential (high RUD), sigmoidal (intermediate RUD), or saturating (low RUD) on a \log_2 -scale of horizontal diversity (Fig. 2a, colored lines). Only for the special case in which all producers exploit the same resource compartments (i.e., $RUD = 0$, Fig. 2a), the relationship is neutral

At maximum producer species richness, all resources were accessible in all RUD scenarios, effectively maximizing yields regardless of RUD (Fig. 2a&b). On the contrary, the access to resources in monocultures directly depends on RUD: without RUD, all monocultures have access to all resource compartments, whereas, under the highest RUD, each monoculture can only utilize one-sixteenth of the total resource pool (i.e., one resource compartment). Consequently, monoculture yields (Fig. 2a, \log_2 yields at producer richness of zero) and thus expected yields Y_E (Fig. 2b, red dots) decreased linearly with increasing RUD. As a result, net diversity effects at maximum producer richness increased linearly with RUD, starting at zero net diversity effects when $RUD = 0$ (Fig. 2c). Since net diversity effects almost exclusively partition into complementarity effects with selection effects only playing a minor role (Fig. S1-3), RUD exhibits the behavior expected from

resource-use complementarity. In comparison, the realized complementarity of the resources used by the producer community (i.e., H_{exp}) did not change linearly along the RUD gradient (Fig. 4b, Fig. S4).

Communities initialized with intermediate levels of producer richness (i.e., 2, 4, or 8 producer species) all failed to maximize yields at high levels of RUD (Fig. 2a&b), which led to reduced net diversity effects (Fig. 2c). For example, at maximum RUD, where species are never functionally redundant as they all access species-specific resource compartments, the loss of species directly lowers the resource availability and thus the primary production of the producer community. With decreasing horizontal diversity, net diversity effects became lower over more extensive parts of the RUD gradient. As the number of species necessary to fully utilize all resource compartments increases with RUD, losing species has the most severe effects at higher levels of RUD. Even though the resource availability might decrease, more species could coexist with increasing RUD (Fig. 4a, Fig. S5). The value of RUD at which net diversity effects were maximized shifted from its maximum in 16-species mixtures towards intermediate values in 2-species mixtures. Consequently, the power of RUD to explain the strength of net diversity effects depends on the completeness of the species pool. Regardless, as long as species differed in their access to resource compartments (i.e., $\text{RUD} > 0$), net diversity effects were consistently positive (Fig. 2c).

Introducing multi-trophic interactions and increasing animal richness increased net diversity effects on primary productivity (Fig. 3a, Fig. S1). For multi-trophic interactions to increase horizontal diversity effects, reductions in primary production due to animals feeding on producer species had to be larger in monocultures than in mixtures. A decrease in productivity of some producer species, which was apparent in monocultures and thus expected yields (Fig. 3e, Fig. S6), could be compensated in mixtures by competing producer species that shared resource compartments. Independent from animal richness, this maximized productivity in mixtures in most cases (Fig. 3d, Fig. S6) while also allowing more producer species to coexist (Fig. 4a, Fig. S5). Because the degree to which multi-trophic interactions could reduce monoculture productivity and thus expected yields does depend on how many resource compartments were accessible, increasing RUD reduced the potential of animals to alter horizontal diversity effects. This bottom-up control led to weaker effects of increasing animal richness and reduced variability of net diversity effects when increasing RUD (Fig. 3a, Fig. S1). When resource-use was not overlapping (i.e., $\text{RUD} = 1$), all producer species had access to independent resource compartments. Without animals, this led to maximum net diversity effects (Fig. 2c). In scenarios with animals, primary productivity losses due to consumption could not be compensated by other producer species. As a result, we found weak negative effects of multi-trophic interactions compared to no-animal scenarios in that specific case (Fig. S1). A loss of producer richness expanded the range of RUD in which producers could be limited to use distinct resource compartments, which makes multi-trophic interactions more likely to affect net diversity effects negatively.

With increasing animal richness, we found that complementarity effects increased from low levels in scenarios without animals to values that could be several times higher. The positive impact of animal richness on complementarity effects was exceptionally high in scenarios with low RUD (Fig. 3b, Fig. S2). A reduced producer richness can weaken these positive effects. Similar to scenarios without animals, the loss of producer species shifts the level of RUD at which net diversity effects maximize from high to medium values (Fig. S1). Further, the introduction of animals created both positive and negative selection effects. Neutral selection effects occurred in producer communities without animals. With increasing animal richness, we found that selection effects first increased (positive selection effects at low animal richness) and then decreased (negative selection effects at high animal richness). When RUD was high, selection effects were mostly neutral or negative (Fig. 3c, Fig. S3).

Complementarity and selection effects describe a gradual switch between two ways by which animals increase diversity effects: First, the positive selection effects found predominantly at lower animal richness indicate that more productive species in monoculture, i.e., species that experienced a lower feeding pressure, were on average also more productive in mixtures (Fig. 3c, Fig. S3). Second, negative selection effects found at high animal richness indicate that less productive monoculture species benefit more when growing in mixtures (Fig. 3c, Fig. S3). Because complementarity effects increase more than selection effects decrease, we found

an overall increase of net diversity effects with increasing animal richness (Fig. 3a, Fig. S1). Without animals, selection and complementarity effects were entirely determined by RUD. Only when adding multi-trophic interactions, selection and complementarity effects directly responded to producer coexistence rather than RUD (Fig. S7-8). This effect was less apparent for net diversity effects (Fig. S9). Thus, increasing animal richness caused higher realized producer species richness (Fig. 4a, Fig. S5) and consequently higher realized complementarity in resource-use (i.e., H_{exp} ; Fig. 4b, Fig. S4). In multi-trophic communities, producer species of low body-mass were less likely to survive as their productivity was reduced more due to herbivorous feeding. In simple producer communities, producer species survival and productivity were mostly independent of body-mass (Fig. S10, Fig. S11). Hence, the patterns in selection effects with increasing animal richness (Fig. 3c, Fig. S3) can be partially attributed to systematic shifts in the producer communities' body-mass structure. Interestingly, we found that the survival of animal species was roughly constant at 80% across gradients of animal and producer richness (Fig. S12).

Discussion

Most biodiversity-ecosystem-functioning studies address the effect of diversity within a trophic level, such as plants, on functions such as primary productivity (e.g., Isbell et al. 2015). We have introduced an integrated model of producer species richness and resource-use complementarity that yields positive diversity-productivity relationships consistent with patterns found in experimental (Isbell et al. 2015) and natural communities (Duffy et al. 2017; van der Plas 2019). When introducing resource-use complementarity by creating dissimilarities in how producer species access resource-pool compartments, monocultures generally become less productive than species mixtures as they utilize a smaller proportion of the total resource pool (Tilman et al. 1997; Loreau 2001). By increasing this resource-use dissimilarity across primary producers, we could enhance such net diversity effects through bottom-up mechanisms. However, trophic interactions can affect diversity-productivity relationships in producer communities in similar ways. We find that adding animal communities embedded in food-webs of multi-trophic interactions strengthened the net diversity effect on primary production. This similarly results from a reduction in monoculture productivity. Such top-down reductions due to herbivory can be compensated in more species-rich producer communities (e.g., Jactel et al. 2021), where trophic interactions shape the composition and interactions among producer species (e.g., Naeem et al. 1994; Thébault & Loreau 2003; Brose 2008; Zhao et al. 2019). By addressing the interplay of resource-use complementarity and multi-trophic interactions, our study synthesizes bottom-up and top-down drivers of BEF relationships. While both create complementarity to create positive net diversity effects, our model suggests that diversity across trophic levels can additionally change selection mechanisms and thereby producer community composition. Specifically, a dominance of highly productive monoculture species (positive selection effects) at low animal richness shifts to a community that also includes the less productive monoculture species (negative selection effects) as animal richness increases. An increased complementarity among producer species at high animal richness therefore allows more species to coexist. In consequence, complementarity effects increase with animal richness and overcompensate the negative selection effects. To which degree multi-trophic mechanisms can increase net diversity effects is determined by resource-use dissimilarity. At high levels of resource-use dissimilarity, multi-trophic interactions show only weak effects, whereas lower levels of resource-use dissimilarity allow top-down mechanisms to enhance net diversity effects more. Hence, our results suggest that multi-trophic interactions and resource-use complementarity among producers shape diversity-productivity relationships interactively. This finding implies that processes across trophic levels are strongly interwoven, which renders the integration of multi-trophic mechanisms in the analysis of diversity effects in complex communities highly important.

In simple communities without animals, we tested for the consequences of resource-use dissimilarities between producer species. It promotes coexistence, creates complementarity and consequently positive net diversity effects, thereby confirming findings of earlier theoretical studies (Vandermeer 1981; Tilman 1982; Loreau 2004). Further, resource-use dissimilarity can create a range of different shapes of diversity-productivity relationships (e.g., exponential, sigmoidal, or saturating on a \log_2 -scale of producer richness), as found in experimental and natural studies (Balvanera et al. 2006; Duffy et al. 2017). Our simulated producer communities show how at low levels of resource-use dissimilarity (i.e., substantial overlap in the resource com-

partments used by different producer species), saturating diversity-productivity relationships emerge where only a few species are necessary to maximize primary production. On the contrary, at high levels of resource-use dissimilarity (i.e., producer species mostly exploit different compartments of the total resource pool), the majority of producer species is necessary to maximize productivity. This highlights how an increasing resource-use dissimilarity not only increases complementarity between species but also reduces their functional redundancy in resource-use (Loreau 2004). When producer species are lost, communities with a low functional redundancy are more prone to become less productive and thus show weaker net diversity effects. Resource-use dissimilarity that enhances complementarity and thus drives net diversity effects in producer communities can therefore also be responsible for weakening such effects as species are lost.

In ecosystems with animal species, our results confirm that multi-trophic interactions can create positive net diversity effects even without any resource-use dissimilarity amongst producers (Thébault & Loreau 2003). As long as producer species are not limited to access distinct resource compartments, multi-trophic interactions consistently enhance net diversity effects. Whether herbivores are predominantly specialists or generalists determines if such effects are strong or negligible, respectively (Thébault & Loreau 2003; Jactel et al. 2021). In our simulations, generalism is constraint by predator-prey body-mass ratios known from aquatic and belowground ecosystems (Schneider et al. 2016). Regardless, they are sufficient to reproduce the decreasing influence of herbivores on primary production as producer diversity increases that is common to forests, grasslands, and agroecosystems alike (Barnes et al. 2020; Wan et al. 2020; Jactel et al. 2021). We find that animals largely influence net diversity effects by reducing primary production in monocultures (Barry et al. 2018). In mixtures, reductions in productivity can be compensated by producers that access the same resource compartments (i.e., functional redundancy in resource-use; Naeem 1998). The potential of compensatory effects therefore scales with resource-use dissimilarity and producer species richness. When animals are present, a lack of compensation inevitably leads to a reduced primary production in mixture. Even though this may weaken the positive impact of multi-trophic interactions on net diversity effects, our results suggest that it is rarely the case.

Our findings show that enhanced net diversity effects in multi-trophic ecosystems can largely be attributed to complementarity mechanisms (Thébault & Loreau 2003; Barry et al. 2018), which reduce interspecific competition among producer species. Apart from competing for resources, animals can shift the competitive interaction to being additionally mediated by consumers and their trophic interactions (Holt 1977; Loreau 2010). For example, multi-trophic interactions reduce competition between producer species by limiting productivity and thereby inhibiting the dominance of single species (Brose 2008). As a result, producer species can coexist even if their resource-niches overlap entirely (Brose 2008; Loreau 2010). Similar to an increased vertical diversity (Wang & Brose 2018), we found that an increased animal richness can enable more producer species to coexist, which is indicative for the higher complementarity among them. In addition, a complementarity in herbivorous feeding links sorts producer species into different trophic groups common to our simulated and natural food-webs alike (Gauzens et al. 2015; Schneider et al. 2016). This top-down aspect of trophic complementarity can enhance net diversity effects similar to the bottom-up complementarity of resource-use (Thébault & Loreau 2003; Poisot et al. 2013). Despite the increased complementarity, a limited resource availability caps primary productivity in multi-trophic ecosystems to not exceed primary production in ecosystems without animals.

While multi-trophic interactions determine net diversity effects in producer communities largely through complementarity mechanisms, selection effects draw a less conclusive picture. Differences in the functional expression of producer species in monoculture are a fundamental requirement for non-neutral selection effects (Loreau & Hector 2001). In our simulations, the maximum productivity of all producer species is largely determined by their access to resource compartments, which is the same for all co-occurring species. Their functional expression in monoculture (i.e., primary production without competition) is therefore equal in the absence of animal consumers. Hence, we do not find selection effects in simple producer communities. This model simplification disregards processes such as associations between competitive ability and productivity that can determine selection in producer communities (Tilman et al. 1997), but it enables us to isolate multi-trophic selection mechanisms. Specifically, we find that the productivity of large producer species is

less susceptible to herbivory. The low mass-specific metabolic rates of large species may play an important role in minimizing losses to herbivory (Brown et al. 2004; Schneider et al. 2016). The ability of large species to better cope with herbivory also increases their chances to persist in mixtures (Schneider et al. 2016; Wang & Brose 2018), which should lead to positive selection effects. However, we find negative selection effects at high animal richness and resource-use dissimilarity, which both tend to enhance complementarity. Because complementarity mechanisms reduce interspecific competition, the small producer species that are excluded when complementarity is low can persist in mixtures. Once in the mixture, a disproportionately strong effect of herbivores on strong competitors (Brose 2008) elevates the productivity of the otherwise excluded, small and less productive producer species. Even though this does not imply their dominance, it alters community composition enough to turn selection effects negative in response to an increasing complementarity. This interdependence of complementarity and selection effects in multi-trophic ecosystems becomes apparent in our findings of their inverse relationship to realized producer richness. However, not all complementarity mechanisms have to be linked to selection mechanisms that influence net diversity effects (e.g., resource-use dissimilarity as defined in this study). Identifying causes of selection can therefore serve as an important tool to disentangle drivers of diversity effects.

Despite the evidence that multi-trophic interactions (Thébault & Loreau 2003) and resource-use complementarity (Tilman et al. 1997) can create positive net diversity effects on primary production independently, how they interact has remained speculative (Tilman et al. 2014; Barry et al. 2018). We find that both mechanisms create positive net diversity effects by lowering primary production in monoculture. Hence, an already low monoculture primary production at high resource-use dissimilarity, which leads to high net diversity effects on its own, cannot be reduced much further by animals before driving the single producer species and thus the entire food-web extinct. A high resource-use dissimilarity therefore limits the ability of multi-trophic interactions to enhance net diversity effects. Similarly, it promotes the coexistence of producer species by reducing competition but simultaneously limits the ability of multi-trophic mechanisms to alter competition in favor of a more diverse producer community (Brose 2008). In both cases, bottom-up forces fundamentally limit the strength of top-down mechanisms to improve either net diversity effects or species coexistence. Plastic responses in resource-use to changes in producer diversity (Von Felten et al. 2009; Mueller et al. 2013), consumer diversity, or vertical diversity (Zhao et al. 2019) might affect such limitations but should not change our conclusion that multi-trophic interactions become especially important when the resource-use dissimilarity of producers is low.

The interactive effect of resource-use complementarity and multi-trophic interactions creates positive net diversity effects that generally exceed their independent effects. Both mechanisms jointly support diverse communities of complementary producer species. However, multi-trophic interactions determine the community composition of the producer species depending on the animal diversity of the multi-trophic ecosystem, whereas selection in simple producer communities is solely driven by resource competition. Hence, different mechanisms can similarly create complementary communities, but the associated selection mechanisms may differ. To identify drivers of positive diversity effects common to natural ecosystems, instead of focusing on identifying causes of complementarity it may therefore be more expedient to identify causes of selection and understand how they relate to complementarity mechanisms. In bridging the gap between food-web and BEF theory, our novel simulation-framework can guide such efforts as it integrates effects of diversity within and across trophic levels on functions of complex, multi-trophic ecosystems. Its results highlight the interplay between bottom-up and top-down forces in these ecosystems, emphasizing the need to adopt a multi-trophic view on BEF relationships.

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Figure captions

Figure 1: Conceptual figure of resource-use dissimilarity (RUD) as a measure of resource-use complementarity, exemplified for a primary producer community with four tree species in the species pool. We assume that the resource pool has as many compartments C as there are species in the species pool. Each species has access to at least one and up to $C = 4$ compartments. Species accessing the same compartment compete for resources within that compartment. By systematically varying the resource-access of all species, we can define a gradient of resource-use dissimilarity (RUD) ranging from no dissimilarity ($RUD = 0$) to complete dissimilarity between all species ($RUD = 1$).

Figure 2: Diversity effects and resource-use dissimilarity (RUD) without multi-trophic interactions. (a) Mean diversity-productivity relationships at different levels of RUD (colored lines) and overall average (thick black line). (b) Observed yield Y_O (different shades of blue at different levels of producer richness) and expected yield Y_E (red) as functions of RUD. (c) Net diversity effects $\Delta Y = Y_O - Y_E$ for different levels of producer richness. Error bars in (b) and (c) show 25th and 75th; squares show 50th percentile (i.e., median).

Figure 3: Effects of animal richness (i.e., multi-trophic animal richness of 0, 10, 30, 50, and 70) on (a) net diversity effects $\Delta Y = Y_O - Y_E = CE + SE$, (b) complementarity effects CE and (c) selection effects SE , as well as (d) observed yield Y_O and (e) expected yield Y_E . Summarized at primary producer richness = 16 for different ranges of resource-use dissimilarity (0 - 0.25, 0.25 - 0.5, 0.5 - 0.75, and 0.75 - 1). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

Figure 4: Effects of animal richness (i.e., multi-trophic animal richness of 0, 10, 30, 50, and 70) on (a) realized species richness of the producer community and (b) Shannon diversity H_{exp} of the producer community's resource-use as a measure of realized resource-use dissimilarity. Summarized at primary producer richness of 16 for different ranges of resource-use dissimilarity (0 - 0.25, 0.25 - 0.5, 0.5 - 0.75, and 0.75 - 1). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

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