Received: 16 September 2021 | Revised: 13 October 2021 | Accepted: 2 November 2021

DOI: 10.1111/ele.13935

ECOLOGY LETTERS WILEY

LETTER

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

Georg Albert[1,2] | **Benoit Gauzens**[1,2] | **Michel Loreau**[3] | **Shaopeng Wang**[4] | **Ulrich Brose**[1,2]

[1]EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[2]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

[3]Theoretical and Experimental Ecology Station, CNRS, Moulis, France

[4]Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China

Correspondence
Georg Albert, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstr. 4, 04103 Leipzig, Germany.
Email: georg.albert@idiv.de

Funding information
National Natural Science Foundation of China, Grant/Award Number: 31988102; TULIP Laboratory of Excellence, Grant/Award Number: ANR-10-LABX-41; Deutsche Forschungsgemeinschaft, Grant/Award Number: DFG–FZT 118, GRK 2324/1 - 2018 (P9), 319936945 and 202548816

Editor: Ian Donohue

Abstract

Resource-use complementarity of producer species is often invoked to explain the 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 analysing diversity–productivity relationships in a simulation experiment of producer communities nested within complex food-webs, manipulating resource-use complementarity and multi-trophic animal richness. We show that these two mechanisms interactively create diverse communities of complementary producer species. This shapes diversity–productivity relationships such that their joint contribution generally exceeds their individual effects. Specifically, multi-trophic interactions in animal-rich ecosystems facilitate producer coexistence by preventing competitive exclusion despite overlaps in resource-use, which increases the realised complementarity. The interdependence of food-webs and producer complementarity in creating biodiversity–productivity relationships highlights the importance to adopt a multi-trophic perspective on biodiversity–ecosystem functioning relationships.

KEYWORDS
biodiversity-ecosystem functioning, complex food-webs, primary production, resource-use complementarity, selection, trophic interaction, vertical diversity

INTRODUCTION

Most research on biodiversity–ecosystem functioning (BEF) relationships has focused on effects of varying diversity within a single trophic level, most commonly of plants in controlled experimental communities (e.g. Isbell et al., 2015). However, natural communities are characterised by complex interaction networks that integrate diversity and its effects across trophic levels (Brose et al., 2019; Duffy et al., 2007), 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 (Brose & Hillebrand, 2016; Loreau, 2010). 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). This points to related aspects such as food-web structure (Brose et al., 2017; Montoya et al., 2015; Thompson et al., 2012) 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 biological mechanisms involved in creating positive diversity effects in producer communities can be broadly categorised into two classes (Loreau, 2010; Loreau & Hector, 2001). 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 functioning of the whole community. Second, selection mechanisms favour species with competitive advantages. If such advantages associate with particular functional traits (e.g. higher growth rates), selection can affect ecosystem functioning. Complementarity and selection are 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 realised 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 considered (Hooper et al., 2005; Loreau, 2004), most experimental evidence suggests complementarity mechanisms as the dominant driver of BEF relationships (Barry et al., 2019; Cardinale et al., 2007; Hooper et al., 2005).

Complementarity between co-occurring producer species is commonly associated with resource-use complementarity (also 'resource partitioning'; Barry et al., 2019), expressing fundamental differences in resource access of coexisting species. These differences can arise from varying aspects of resource-use such as differences in used resources' chemical forms (Ashton et al., 2010; von Felten et al., 2009; McKane et al., 2002), phenological asynchrony (Henry et al., 2001; Sapijanskas et al., 2014) or spatial separation, both above- (e.g. crown packing; Sapijanskas et al., 2014) and belowground (e.g. rooting depth; 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 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 (Brose, 2008; Poisot et al., 2013; Thébault & Loreau, 2003; Wang & Brose, 2018). Consequently, herbivore communities alone may be sufficient to create positive diversity effects on primary production, even without resource-use complementarity among producer species (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 competitive differences between producer species and thereby introduce selection mechanisms that can affect ecosystem functioning both positively or negatively (Thébault & Loreau, 2003). Complementarity and selection mechanisms are therefore interrelated through complex ecological interactions, calling for the simultaneous consideration of how they drive BEF relationships.

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 favour a positive relationship between biodiversity and ecosystem functioning, while selection may interact in more complex ways, potentially having opposing effects. While prior studies have shown positive effects of multi-trophic communities on primary production and its diversity effects (Naeem et al., 1994; Schneider et al., 2016; Thébault & Loreau, 2003; Wang & Brose, 2018), our study aims at revealing how trophically mediated complementarity and selection mechanisms in realistic complex food-webs interact with resource-use complementarity. We integrate multi-trophic interactions and resource-use complementarity into a complex allometric food-web model to examine how they interact in shaping positive effects of producer species richness on primary production (hereafter: net diversity effects). We show 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 producer species composition, which drives both selection and complementarity mechanisms. By varying animal species richness of the multi-trophic communities, we address how diversity across trophic levels interacts with resource-use complementarity and thus determines net diversity effects. Within this framework, we hypothesise the following. First, selection effects are driven by the dominance of producer species with competitive advantages, which however can be weakened by density-dependent top-down control in multi-trophic communities. Hence, we expect that the contribution of selection effects to positive net diversity effects decreases with animal species richness in multi-trophic communities (H1). Second, increasing animal species richness fosters coexistence of producer species, which should increase their realised resource-use complementary and thus net diversity effects (H2). Third, the ability of multi-trophic interactions to improve realised resource-use and thus enhance net diversity effects should be limited by the level of resource-use complementarity (H3).

MATERIALS AND METHODS

Simulating producer and animal population dynamics by allometric trophic networks

We built model communities with varying numbers of producers (1–16) and animals (0–70). In each community, we randomly assigned body-masses to species and used allometric scaling relationships to predict their biological properties, including population dynamical rates (e.g. metabolism, Brown et al., 2004) and feeding kernels constraining the body-mass ranges of each consumer's prey species. The centre and width of these ranges depend on consumer body-masses and include some random variation to generate a gradient from diet specialists to generalists in the food-web. Based on such allometric relationships, an allometric-trophic-network model can simulate the dynamics of complex food-webs (Schneider et al., 2016). Differential equations describe biomass density changes over time for two limiting abiotic resources, and varying numbers of producers and animal consumers (see Supplementary 1 for a detailed model description). Animal densities increase with feeding on other animals or producers as described by non-linear functional responses that comprise capture coefficients, handling times and interference competition. Producers increase their densities due to growth that is limited by resource availability. Densities of animals and producers decrease as they are consumed and due to metabolic demands. Resource densities decrease due to producers' growth and increase based on refresh rates assuming a constant resource turnover. Compared to its original formulation (Schneider et al., 2016), we improved the model by updating capture coefficients to depend on feeding preferences of the interacting species (i.e. carnivorous, omnivorous, herbivorous, autotrophic; Hirt et al., 2017). Additionally, we updated scaling coefficients based on empirical results (Ehnes et al., 2011; Lang et al., 2017; see Table S1). Finally, we introduced an interaction-specific functional response based on empirical evidence suggesting a shift from type II to type III as predator–prey body-mass ratios increase (Kalinkat et al., 2013).

Experimental setup

To quantify diversity effects of the producer community, we compared primary production at different levels of producer species richness. Specifically, we measured primary production as the resource uptake rate in equilibrium at the end of the simulations (Supplementary 1), which we used as yield Y to calculate net diversity effects 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 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. Furthermore, we included resource-use complementarity by manipulating the resource-use dissimilarity (RUD) of producer species over 16 steps with an additional random scenario (see detailed description below). We simulated all producer communities in a full factorial design with all levels of animal and producer richness, and all scenarios of RUD, totalling 81,600 simulations. 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 https://github.com/GeorgAlbert/Multi-trophic.interactions.

Introducing resource-use complementarity

We introduced producers' resource-use complementarity to our models based on two 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 maximised if all species use resources from distinct resource compartments.

To simulate resource-use complementarity, we therefore introduced differences between producer species by limiting their resource-use to certain compartments of each resource (Figure 1). Species that access the same compartments compete for resources within those compartments. To investigate resource-use scenarios where all species utilise resources from different compartments (i.e. no competition), the number of resource compartments C for each of the two resources was defined as the maximum producer richness considered in our design (i.e. 16). We assumed that all compartments were quantitatively the same. By gradually increasing the resource-use dissimilarity (RUD) between the 16

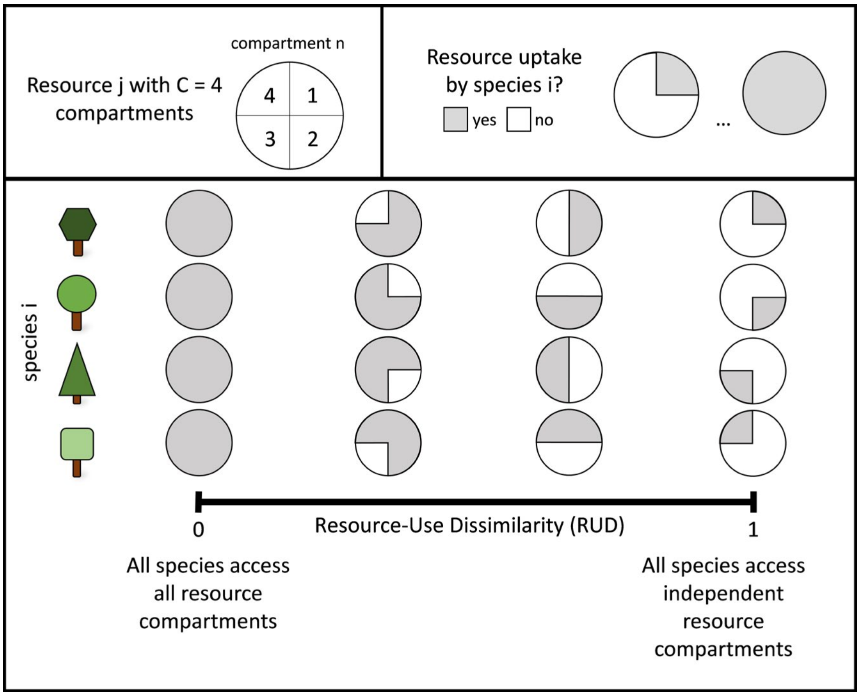

FIGURE 1 Conceptual figure of a gradient of resource-use dissimilarity (RUD) as a measure of resource-use complementarity, exemplified for a primary producer community with four tree species in the species-pool. We assume that each resource has as many compartments C as there are species in the species-pool. Each species has access to at least one and, in this example, 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 RUD ranging from no dissimilarity (RUD = 0) to complete dissimilarity between all species (RUD = 1)

producer species within a species-pool, we created a gradient from no complementarity (i.e. all species access all compartments, RUD = 0) to maximum complementarity (i.e. each species has its own resource compartment, RUD = 1; Figure 1). We ensured that (1) all producer species had access to the same number of compartments at a given level of the RUD gradient and that (2) accessed resource compartments were the same for both resources considered. To test the robustness of our results, we added random resource-use scenarios where access to resource compartments was randomly assigned to each producer species.

In all RUD scenarios, except RUD = 1, producer species overlap in their access to resources. Thus, species in monocultures are released from competition and have improved access to resources. At maximum producer richness, species within a community where RUD < 1 compete for resources with at least two other producer species with overlapping compartments. 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 the competitive outcome, we quantified how resource-use and thus productivity Y was distributed among coexisting producer species i by calculating the realised resource-use dissimilarity as Shannon diversity $H_{\mathrm{exp}} = \exp(-\Sigma_i\ \mathrm{pi}\ \ln(p_i))$, with $p_i = Y_i/\Sigma_i\ Y_i$. H_{exp} reflects aspects of producer species richness (i.e. how many species coexist) and abundance (i.e. how much resources each species uses) alike. It is maximised at the number of coexisting species. Lower values indicate an uneven distribution of resource-use (Jost, 2006). In comparison to RUD, H_{exp} is based on realised instead of fundamental resource niches.

Partitioning of net diversity effects

By calculating net diversity effects ΔY as defined above, we could apply an additive partitioning approach (Loreau & Hector, 2001) separating complementarity effects (CE) from selection effects (SE) as

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

with N being the species richness of the mixture, ΔRY_i being the deviation of the observed 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 calculate complementarity and selection effects for a given mixture, knowing the productivity of all its monocultures was necessary. Thus, we could not calculate them for mixtures containing producer species with unviable monocultures that lead to global extinctions when simulated. We therefore had to omit around 5% of all simulated communities when analysing complementarity or selection effects.

RESULTS

In absence of animals, producer communities show positive diversity–productivity relationships across all levels of resource-use dissimilarity (RUD; Figure 2a, 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 logarithmic scale of producer richness (Figure 2a, coloured lines). Only in the special case where all producers exploit the same resource compartments (i.e. RUD = 0, Figure 2a), the relationship is neutral.

At maximum producer species richness, all producer communities access all resource compartments. This effectively maximises yields regardless of RUD (Figure 2a, b). Oppositely, access to resources in monocultures directly depends on RUD: without RUD, all monocultures access all resource compartments, whereas, at maximum RUD, each monoculture can only utilise one-sixteenth of the resources (i.e. one resource compartment). Consequently, monoculture yields (Figure 2a, yields at $\log_2$ producer richness of zero) and thus expected yields Y_E (Figure 2b, red dots) decrease linearly with increasing RUD. Consequently, net diversity effects at maximum producer richness increase linearly with RUD, starting at zero net diversity effects when RUD = 0 (Figure 2c). In comparison, the realised resources-use dissimilarity H_{exp} increases almost exponentially along the RUD gradient (Figure 4b, Figure S1). Net diversity effects almost exclusively partition into complementarity effects, with selection effects only playing a minor role (Figures S2–S4). This changes when using random RUD scenarios, where differences in the number of accessible resource compartments lead to positive selection effects. However, they do not exceed complementarity effects. Increasing complementarity from RUD allows more producer species to coexist (Figure 4a, Figure S5). Thus, RUD exhibits the behaviour expected from resource-use complementarity.

At intermediate levels of producer richness (i.e. 2, 4 or 8 species), producer communities fail to maximise yields at high levels of RUD (Figure 2a, b), leading to reduced net diversity effects (Figure 2c). For example at maximum RUD, where all species access species-specific resource compartments, a loss of species directly lowers the resource availability, thus primary production. As the number of species necessary to utilise all resource compartments increases with RUD, losing species has the most severe effects on net diversity effects at higher levels of RUD. The value of RUD at which net diversity effects are maximised shifts from its maximum in 16-species mixtures towards intermediate values in 2-species mixtures. Consequently, the ability of RUD to explain the strength of net diversity effects depends on the completeness of the species-pool. Regardless, as long as species differ in their access to resource compartments (i.e. RUD > 0), net diversity effects are consistently positive (Figure 2c).

Introducing multi-trophic interactions and increasing animal richness increases net diversity effects on primary production (Figure 3a, Figure S2). This is largely related to decreases in monoculture productivity of

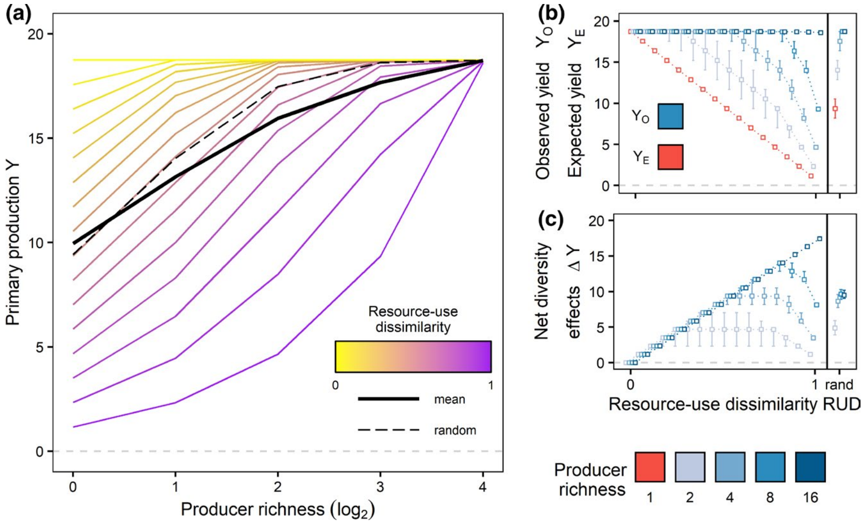

FIGURE 2 Diversity effects and resource-use dissimilarity (RUD) without multi-trophic interactions. (a) Mean diversity–productivity relationships at different levels of the RUD gradient (coloured lines), their overall average (thick black line), and the random RUD scenario (black dashed line). (b) Observed 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. rand denotes the random RUD scenario. Error bars in (b) and (c) show 25th and 75th; squares show 50th percentile (i.e. median)

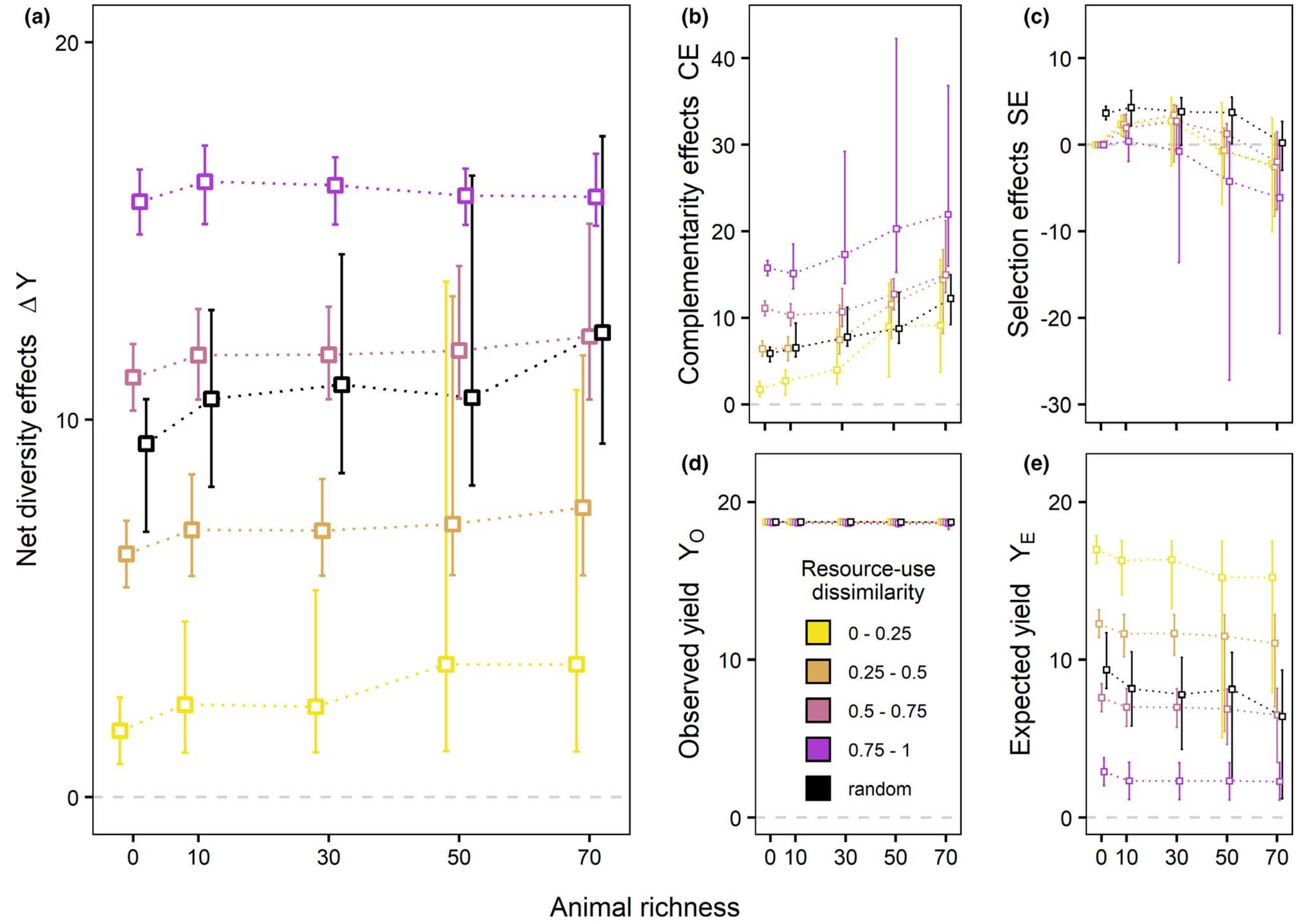

FIGURE 3 Effects of animal richness (i.e. multi-trophic animal richness of 0, 10, 30, 50 and 70) on (a) net diversity effects $\Delta Y = Y_O - Y_E = \mathrm{CE} + \mathrm{SE}$, (b) complementarity effects CE and (c) selection effects SE, as well as (d) observed yield Y_O and (e) expected yield Y_E.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

some producers due to consumption (i.e. lower expected yields; Figure 3e, Figure S6), which are compensated in mixtures by competing species with shared resource compartments. Thus, productivity in mixtures is maximised in most cases (Figure 3d, Figure S6). The strength of multi-trophic effects on monoculture productivity and net diversity effects scale negatively with RUD. The bottom-up control of RUD therefore weakens effects of increasing animal richness and reduces the variability of net diversity effects (Figure 3a, Figure S2). The consistently positive richness–biomass density relationship of the producer community (Figure S7) additionally suggests a density dependence of net diversity effects that varies slightly with RUD. In the specific case of RUD = 1, multi-trophic interactions affect net diversity effects negatively compared to no-animal scenarios. This is because primary productivity losses due to consumption cannot be compensated by other producer species. A loss of producer species expands the range of RUD for which producers can be limited to use distinct resource compartments. This makes multi-trophic interactions more likely to affect net diversity effects negatively and shifts the level of RUD at which net diversity effects maximise from high to medium values (Figure S2).

The increase in net diversity effects with increasing animal richness (Figure 3a, Figure S2) resembles increases of complementarity effects (Figure 3b, Figure S3). They coincide with increases of realised producer species richness (Figure 4a, Figure S5) and consequently realised complementarity in resource-use (i.e. H_{exp}; Figure 4b, Figure S1). The positive effect of animal richness on complementarity effects gets weaker as RUD increases (Figure 3b, Figure S3, Table S2). Additionally, introducing animals creates both positive and negative selection effects. At low animal richness, we find positive selection effects that decrease as animal richness increases. At high RUD, selection effects were mostly neutral or negative. The positive selection effects in the random RUD scenario only decrease at high animal richness (Figure 3c, Figure S4). Herbivorous feeding reduces productivity and survivability of low body-mass producer species. In simple producer communities, producer species survival and productivity are mostly independent of body-mass (Figures S8–S9). Hence, the

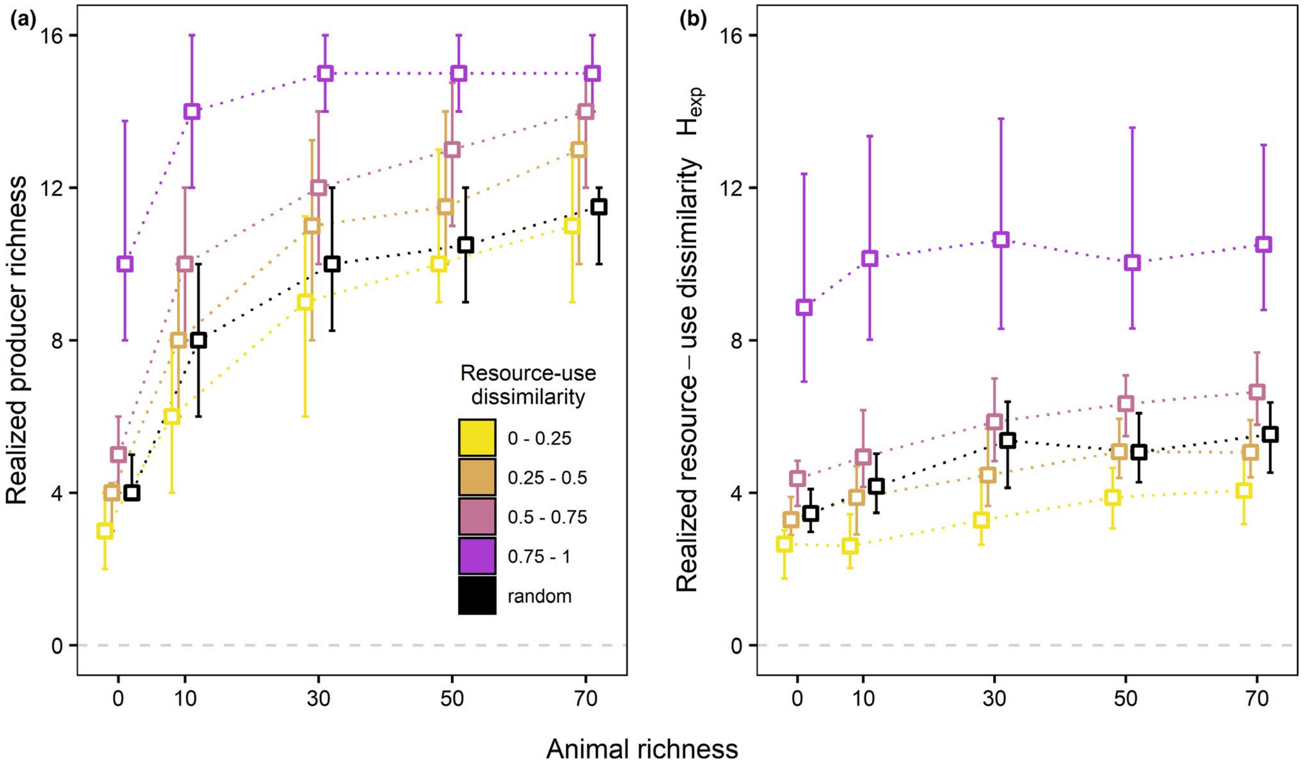

FIGURE 4 Effects of animal richness (i.e. multi-trophic animal richness of 0, 10, 30, 50 and 70) on (a) realised species richness and (b) realised resource-use dissimilarity H_{exp} of the producer community. Summarised at primary producer richness of 16 for different ranges of the resource-use dissimilarity (RUD) gradient (0–0.25, 0.25–0.5, 0.5–0.75 and 0.75–1) and the random RUD scenario. Error bars show 25th and 75th; squares show 50th percentile (i.e. median)

patterns of selection effects with increasing animal richness (Figure 3c, Figure S4) can be partially attributed to systematic shifts in the producer communities' body-mass structure. Without animals, RUD determines selection and complementarity effects entirely. Only when adding multi-trophic interactions, selection and complementarity effects respond to producer coexistence rather than RUD (Figures S10–S11). This was less apparent for net diversity effects (Figure S12). Interestingly, we found that the survival of animal species was roughly constant at 80% across gradients of animal and producer richness (Figure S13).

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. Cardinale et al., 2012). We have introduced an integrated model of producer species richness, resource-use complementarity and multi-trophic interactions that yields positive diversity–productivity relationships consistent with patterns found in experimental (Cardinale et al., 2012) and natural communities (Duffy et al., 2017; van der Plas, 2019). The presence of resource-use complementarity, simulated as dissimilarities in producer's resource-use, causes monocultures to be generally less productive than mixtures as they utilise a smaller proportion of the resources pool (Loreau, 2001; Tilman et al., 1997), leading to positive net diversity effects. Similarly, adding animal communities embedded in food-webs of multi-trophic interactions allows herbivores to reduce productivity in monoculture but rarely in mixtures. By addressing the interplay of resource-use complementarity and multi-trophic interactions, our study synthesises 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. 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 for our understanding of biodiversity–ecosystem functioning relationships.

The effects of multi-trophic interactions on community composition of producer species coincide with positive effects of animal species richness on producer species coexistence. This has two implications for diversity effects. First (H1), the community is dominated by highly productive monoculture species at low animal diversity (positive selection effects). As animal richness increases, less productive monoculture species can persist, leading to neutral or negative selection effects. Second (H2), the higher realised producer richness yields an increased realised complementarity among producer species. Taken together, our results demonstrate that complementarity effects increase with animal richness and overcompensate any negative selection effects, which yields positive effects of animal richness on net diversity effects. The degree to which multi-trophic mechanisms increase net diversity effects (H3) is determined by resource-use dissimilarity. At high levels of resource-use dissimilarity, multi-trophic interactions show only weak effects, whereas lower levels 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 community composition and thereby diversity–productivity relationships interactively.

In simple communities without animals, we observed that resource-use dissimilarities between producer species promote coexistence, create complementarity and consequently have positive net diversity effects, thereby confirming findings of earlier theoretical studies (Loreau, 2004; Tilman, 1982; Vandermeer, 1981). Furthermore, they create a range of different shapes of diversity–productivity relationships known from experiments and field studies (Balvanera et al., 2006; Duffy et al., 2017). For example our simulated producer communities show saturating diversity–productivity relationships at low resource-use dissimilarity (i.e. substantial overlap in resource compartments used by different producer species), where only a few species are necessary to maximise primary production. Oppositely, at high levels of resource-use dissimilarity (i.e. producer species differ substantially in their access to resource compartments), the majority of producer species is necessary to maximise 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 hence 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 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 (Jactel et al., 2021; Thébault & Loreau, 2003). In our simulations, an allometric constraint on consumer generalism is sufficient to reproduce the decreasing influence of herbivores on primary production that is commonly observed in forests, grasslands and agroecosystems when producer diversity increases (Barnes et al., 2020; Jactel et al., 2021; Wan et al., 2020). This is due to the ability of producer communities to compensate reductions of producer densities by herbivory. Specifically, the higher productivity of the consumed producer at lower density due to lower intraspecific competition, but also other producers in mixtures that access the same resource compartments (i.e. functional redundancy in resource-use; Naeem, 1998) contribute to compensate productivity losses. The potential of the latter scales negatively with the producers' resource-use dissimilarity and positively with their species richness. A compensation by producer species that are less vulnerable to herbivory or reach higher biomass densities can therefore maximise productivity in mixtures. The positive effect of multi-trophic interactions on net diversity effects is thus rooted in the interaction of herbivores with the producer community.

The food-webs we studied, however, are not limited to herbivores and producers but additionally vary in the number of consumers from higher trophic levels, specifically carnivores and omnivores. Increasing diversity at these higher trophic levels can induce trophic cascades by imposing top-down control on herbivores (O'Gorman et al., 2008). Depending on the vertical diversity and the resulting length of food-chains, trophic cascades can both favour or disfavour herbivores (Jochum et al., 2012; Oksanen et al., 1981). Additionally, increasing intra-guild predation among animals can dampen trophic cascades (Finke & Denno, 2005). We find that animals impose the strongest top-down control in monocultures (Barnes et al., 2020; Barry et al., 2019; Jactel et al., 2021; Wan et al., 2020) suggesting a strengthening of trophic cascades in favour of herbivores in these relatively simple communities. In mixtures, however, the higher diversity at the food-web base facilitates more complex patterns of interwoven food-chains and intra-guild predation at higher trophic levels. Depending on the trophic environment, herbivory can therefore have both positive and negative effects, resulting in complex patterns in the response of primary production to animal species richness. In our study, this is most evident for combinations of low resource-use dissimilarity with high animal species richness, where net diversity effects exhibited substantial variation (as indicated by the large error bars in Figure 3a). We anticipate that this is caused by variation in food-web structure (Thébault & Lorau, 2003). By integrating food-web models with complementarity and selection effects, our study paves the way for future analyses of how network structure determines ecosystem functioning.

Our findings support concepts of multi-trophic interactions enhancing net diversity effects through complementarity mechanisms (Barry et al., 2019; Thébault & Loreau, 2003), which reduce interspecific competition among producers. Animals can shift the competitive interaction amongst producers from nutrient exploitation to apparent competition mediated by herbivores (Holt, 1977; Loreau, 2010). For example multi-trophic interactions reduce competition between producer species by inhibiting the dominance of single species (Brose, 2008). Consequently, multiple 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 facilitates producer coexistence, which yields higher realised 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 (Poisot et al., 2013; Thébault & Loreau, 2003). Taken together, our results reveal that multi-trophic interactions promote coexistence among producer species, which increases their net diversity effects through higher complementarity in resource-use.

While multi-trophic interactions determine net diversity effects in producer communities largely through complementarity mechanisms, their constraints on selection effects draw a less conclusive picture. Specifically, we find that producer species whose monocultures are the least susceptible to herbivory and thus most productive have also a competitive advantage in mixtures. This explains their dominance irrespective of animal richness, which should lead to positive selection effects. The emergence of negative selection effects, however, indicates that vulnerable producer species, with low productivity in monocultures, benefit disproportionately from growing in a mixture as soon as they can persist. This is the case when interspecific competition is weak due to strong complementarity mechanisms caused by high animal richness or high resource-use dissimilarity. This finding highlights the interdependence of complementarity and selection mechanisms. Since complementarity effects are consistently positive and stronger than selection effects, which is consistent with experimental results (Hooper et al., 2005), there is a net positive effect of animal richness on net 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 (Barry et al., 2019; Tilman et al., 2014). We find that both mechanisms increase the strength of diversity–productivity relationships by lowering primary production in monocultures and increasing producer complementarity in mixtures. 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. Additionally, high resource-use dissimilarity promotes producer coexistence by reducing competition in mixtures, which minimises the potential effect of multi-trophic interactions on realised producer coexistence and complementarity. A high resource-use dissimilarity therefore limits the ability of multi-trophic interactions to enhance net diversity effects. In both cases, bottom-up forces of resource-use dissimilarity fundamentally limit the strength of top-down mechanisms by multi-trophic interactions to foster producer coexistence and net diversity effects on productivity.

As with any modelling study, ours achieves generality of predictions at the cost of simplifying assumptions. In our simulations, producer species differ randomly in some functional aspects including their half-saturation densities of resource-uptake and their body-masses that constrain growth rates. While these parameters affect the relative biomass densities of the producers, their maximum productivity is largely determined by their access to resource compartments. It is the same for all co-occurring species within each resource-use dissimilarity scenario, which explains the lack of selection effects in simple producer communities. However, when producers differ in their access to resource compartments (random scenario), species that can access more compartments tend to be more productive and dominate mixtures. Therefore, positive selection effects emerge. In this case, having access to more resource compartments is a competitive advantage without any trade-off. Adding trait-based models of access to resource compartments would be a highly interesting extension of our approach. Additionally, the parameters of our producer model are static. Whether competition and trophic interactions alone, as in our model, are sufficient to explain 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) remains unclear. While our approach provides a general framework to analyse interactive effects of multi-trophic interactions and resource-use dissimilarity on producer diversity–productivity relationships, it is also flexible to remove model assumptions as empirical support is provided.

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. Our study has elucidated the interdependence of the various causes of complementarity with their respective selection mechanisms, which helps to unravel the drivers of diversity–productivity relationships. 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, emphasising the need to adopt a multi-trophic view on BEF relationships.

ACKNOWLEDGEMENTS

We thank the members of the EcoNetLab and the Theoretical Ecology Lab for helpful discussions, and Matthieu Barbier for constructive comments on the manuscript. GA was supported by the International Research Training Group TreeDì funded by the German Research Foundation (DFG; GRK 2324/1 - 2018 (P9), 319936945). SW was supported by the National Natural Science Foundation of China (31988102). ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41). GA, BG and UB gratefully acknowledge the support of iDiv funded by the German Research Foundation (DFG–FZT 118, 202548816). Open Access funding enabled and organized by Projekt DEAL.

AUTHORSHIP

UB, SW and GA conceptualised the study. GA conducted the simulations. UB and GA wrote the first draft of the manuscript and all authors contributed substantially to revision.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13935.

DATA AVAILABILITY STATEMENT

No empirical data were used for this study. The code to simulate the data can be found at https://github.com/GeorgAlbert/Multi-trophic.interactions (https://doi.org/10.5281/zenodo.5675080).

ORCID

Georg Albert https://orcid.org/0000-0001-5007-2043
Benoit Gauzens https://orcid.org/0000-0001-7748-0362
Michel Loreau https://orcid.org/0000-0002-0122-495X
Shaopeng Wang https://orcid.org/0000-0002-9430-8879
Ulrich Brose https://orcid.org/0000-0001-9156-583X

REFERENCES

Ashton, I.W., Miller, A.E., Bowman, W.D. & Suding, K.N. (2010) Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology*, 91, 3252–3260.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146–1156.

Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. et al. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications*, 5(1), 1–7. https://doi.org/10.1038/ncomms6351

Barnes, A.D., Scherber, C., Brose, U., Borer, E.T., Ebeling, A., Gauzens, B. et al. (2020) Biodiversity enhances the multitrophic control of arthropod herbivory. *Science Advances*, 6, 6603–6609.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y. et al. (2019) The future of complementarity: disentangling causes from consequences. *Trends in Ecology & Evolution*, 34, 167–180.

Bezanson, J., Edelman, A., Karpinski, S. & Shah, V.B. (2017) Julia: a fresh approach to numerical computing. *SIAM Review*, 59, 65–98.

Brose, U. (2008) Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society B-Biological Sciences*, 275, 2507–2514.

Brose, U., Archambault, P., Barnes, A.D., Bersier, L.-F., Boy, T., Canning-Clode, J. et al. (2019) Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, 3, 919–927.

Brose, U., Blanchard, J.L., Eklöf, A., Galiana, N., Hartvig, M.R., Hirt, M. et al. (2017) Predicting the consequences of species loss using size-structured biodiversity approaches. *Biological Reviews*, 92, 684–697.

Brose, U. & Hillebrand, H. (2016) Biodiversity and ecosystem functioning in dynamic landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1694), 20150267. https://doi.org/10.1098/rstb.2015.0267

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S. et al. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences*, 104, 18123–18128.

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E. & Loreau, M. (2007) The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, 10, 522–538.

Duffy, J.E., Godwin, C.M. & Cardinale, B.J. (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature*, 549, 261–264.

Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecology Letters*, 14, 993–1000.

Finke, D.L. & Denno, R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, 8, 1299–1306.

Gauzens, B., Thébault, E., Lacroix, G. & Legendre, S. (2015) Trophic groups and modules: two levels of group detection in food webs. *Journal of the Royal Society, Interface*, 12(106), 20141176. https://doi.org/10.1098/rsif.2014.1176

Henry, M., Stevens, H. & Carson, W.P. (2001) Phenological complementarity, species diversity, and ecosystem function. *Oikos*, 92, 291–296.

Hirt, M.R., Lauermann, T., Brose, U., Noldus, L.P.J.J. & Dell, A.I. (2017) The little things that run: a general scaling of invertebrate exploratory speed with body mass. *Ecology*, 98, 2751–2757.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12, 197–229.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75, 3–35.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C. et al. (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.

Jactel, H., Moreira, X. & Castagneyrol, B. (2021) Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. *Annual Review of Entomology*, 66, 277–296.

Jochum, M., Schneider, F.D., Crowe, T.P., Brose, U. & O'Gorman, E.J. (2012) Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2962–2970.

Jost, L. (2006) Entropy and diversity. *Oikos*, 113, 363–375.

Kalinkat, G., Schneider, F.D., Digel, C., Guill, C., Rall, B.C. & Brose, U. (2013) Body masses, functional responses and predator-prey stability. *Ecology Letters*, 16, 1126–1134.

Lang, B., Ehnes, R.B., Brose, U. & Rall, B.C. (2017) Temperature and consumer type dependencies of energy flows in natural communities. *Oikos*, 126, 1717–1725.

Loreau, M. (2001) Microbial diversity, producer-decomposer interactions and ecosystem processes: a theoretical model. *Proceedings of the Royal Society B-Biological Sciences*, 268, 303–309.

Loreau, M. (2004) Does functional redundancy exist? *Oikos*, 104, 606–611.

Loreau, M. (2010) *From populations to ecosystems: theoretical foundations for a new ecological synthesis*. Princeton: Princeton University Press.

Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412(6842), 72–76. https://doi.org/10.1038/35083573

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B. et al. (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415, 68–71.

Montoya, D., Yallop, M.L. & Memmott, J. (2015) Functional group diversity increases with modularity in complex food webs. *Nature Communications*, 6(1), 1–9. https://doi.org/10.1038/ncomms8379

Mueller, K.E., Tilman, D., Fornara, D.A. & Hobbie, S.E. (2013) Root depth distribution and the diversity-productivity relationship in a long-term grassland experiment. *Ecology*, 94, 787–793.

Naeem, S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology*, 12, 39–45.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734–737.

O'Gorman, E.J., Enright, R.A. & Emmerson, M.C. (2008) Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. *Oecologia*, 158, 557–567.

Oksanen, L., Fretwell, S.D., Arruda, J. & Niemela, P. (1981) Exploitation ecosystems in gradients of primary productivity. *American Naturalist*, 118, 240–261.

Poisot, T., Mouquet, N. & Gravel, D. (2013) Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecology Letters*, 16, 853–861.

Rackauckas, C. & Nie, Q. (2017) DifferentialEquations.jl – a performant and feature-rich ecosystem for solving differential equations in Julia. *Journal of Open Research Software*, 5, 1–10.

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N. & Loreau, M. (2014) Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, 95, 2479–2492.

Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016) Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, 7, 1–8.

Thébault, E. & Loreau, M. (2003) Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences*, 100, 14949–14954.

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L. et al. (2012) Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Tilman, D. (1982) *Resource competition and community structure*. Princeton: Princeton University Press.

Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology Evolution and Systematics*, 45, 471–493.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, 94(5), 1857–1861. https://doi.org/10.1073/pnas.94.5.1857

van der Plas, F. (2019) Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews*, 94, 1220–1245.

Vandermeer, J. (1981) The interference production principle: an ecological theory for agriculture. *BioScience*, 31, 361–364.

von Felten, S., Hector, A., Buchmann, N., Niklaus, P.A., Schmid, B. & Scherer-Lorenzen, M. (2009) Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. *Ecology*, 90, 1389–1399.

Wan, N.-F., Zheng, X.-R., Fu, L.-W., Kiær, L.P., Zhang, Z., Chaplin-Kramer, R. et al. (2020) Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nature Plants*, 6, 503–510.

Wang, S. & Brose, U. (2018) Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, 21(1), 9–20. https://doi.org/10.1111/ele.12865

Wright, A.J., Wardle, D.A., Callaway, R. & Gaxiola, A. (2017) The overlooked role of facilitation in biodiversity experiments. *Trends in Ecology & Evolution*, 32, 383–390.

Zhao, Q., Van den Brink, P.J., Carpentier, C., Wang, Y.X.G., Rodríguez-Sánchez, P., Xu, C. et al. (2019) Horizontal and vertical diversity jointly shape food web stability against small and large perturbations. *Ecology Letters*, 22(7), 1152–1162. https://doi.org/10.1111/ele.13282

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Albert, G., Gauzens, B., Loreau, M., Wang, S. & Brose, U. (2022) The hidden role of multi-trophic interactions in driving diversity–productivity relationships. *Ecology Letters*, 25, 405–415. Available from: https://doi.org/10.1111/ele.13935