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Animal and plant space-use drive plant diversity–productivity relationships

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Abstract

Plant community productivity generally increases with biodiversity, but the strength of this relationship exhibits strong empirical variation. In meta-food-web simulations, we addressed if the spatial overlap in plants' resource access and animal space-use can explain such variability. We found that spatial overlap of plant resource access is a prerequisite for positive diversity–productivity relationships, but causes exploitative competition that can lead to competitive exclusion. Space-use of herbivores causes apparent competition among plants, resulting in negative relationships. However, space-use of larger top predators integrates sub-food webs composed of smaller species, offsetting the negative effects of exploitative and apparent competition and leading to strongly positive diversity–productivity relationships. Overall, our results show that spatial overlap of plants' resource access and animal space-use can greatly alter the strength and sign of such relationships. In particular, the scaling of animal space-use effects opens new perspectives for linking landscape processes without effects on biodiversity to productivity patterns.

KEYWORDS

biodiversity–ecosystem functioning, coexistence, complementarity, complex food webs, foraging range, home range, multi-trophic interactions, primary production

INTRODUCTION

To quantify the impact of biodiversity loss on human well-being, ecological research has measured biodiversity–ecosystem functioning (BEF) relationships in experiments and in the field (Duffy et al., 2017; Tilman et al., 2014). Although the importance of biodiversity for

providing ecosystem functions is supported by increasing evidence, the quantitative relationships vary remarkably across communities and sites (Cardinale et al., 2007; Duffy et al., 2017; van der Plas, 2019), calling for a systematic understanding of the underlying mechanisms.

Many studies argue that complementarity in plants' resource-use is the main driver behind positive plant

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diversity–productivity relationships (Barry et al., 2019). However, they not only depend on how plants access and compete for resources, but are also influenced by interactions with herbivores and animals of higher trophic levels (Albert et al., 2022; Barnes et al., 2020; Ives et al., 2004; Schmitz, 2003; Schneider et al., 2016). For example, multi-trophic diversity (Duffy, 2002) or the functional composition of animal communities (Schmitz, 2009) can alter plant diversity–productivity relationships and introduce considerable variation (Duffy et al., 2007). Additionally, BEF research did not systematically address the consequences of spatial structures such as spatial heterogeneity in plant distribution and resource availability, as well as spatial integration by local and large-scale movement of animals. While resource-based interactions between plants are spatial processes constrained to a plant's immediate neighbourhood (Chesson, 2000a), recent evidence highlights meta-community assembly processes that affect biodiversity maintenance in BEF experiments (Bannar-Martin et al., 2018; Furey et al., 2022), emphasizing the importance of also considering processes at larger spatial scales. This includes interactions of plants with animals at higher trophic levels that integrate effects over larger spatial distances (McCann et al., 2005; Ryser et al., 2021). Thus, this raises the question of how the interactions between animal- and resource-based mechanisms and their different scales explain BEF patterns, such as plant diversity–productivity relationships, and their variance at the community scale.

Traditionally, BEF research focuses on plant diversity–productivity relationship at the community level (Cardinale et al., 2007). Only recently, investigating the implications of local interactions between plant individuals and their immediate neighbours ('neighbourhood scale'; Figure 1; Sapijanskas et al., 2013; Fichtner et al., 2018) has started. At this scale, plants access different parts of the total available resources (e.g. below-ground resource pools) depending on their resource acquisition strategies (e.g. functional traits) and the proportion of space they can access (e.g. spatial spread of their roots). The latter adds a spatial component to plants' resource-use. Reducing the spatial resource overlap between neighbouring plants (Figure 1a) makes them complementary in their access to resources as it reduces the strength of their competitive interactions, rendering competitive exclusion less likely (Chesson, 2000b). While this spatial segregation of plants' resource-use facilitates coexistence, it potentially constrains their resource acquisition and productivity. For example, if two plants have mostly complementary resource requirements, they may benefit from having a spatial resource overlap. These arguments suggest that an increased spatial resource overlap could increase productivity at the community scale at the cost of a higher likelihood of local competitive exclusion. As competitive exclusion reduces plant diversity, this can negatively feedback on plant community productivity, calling for a systematic understanding

of resource-mediated interactions between plants at the neighbourhood scale and their importance for plant diversity–productivity relationship.

While plants can interact through local spatial resource overlap, animal space-use couples even distant plants, for instance when herbivores move to switch resources. This yields apparent competition between plants (Figure 1c, spatially non-nested), which can strongly reduce productivity and survival of the two resource plants (Holt, 1977). At higher trophic levels, populations of larger species such as top predators with large home ranges (Hirt et al., 2021; Tucker et al., 2014) integrate energy fluxes across sub-food webs assembled from populations of plants, herbivores and smaller consumers. This creates a spatially nested food web structure with local food webs nested in the home range of top predators (Figure 1c). Hence, apparent competition emerges among less mobile herbivores due to a shared, more mobile predator. This spatial structure of natural food webs opposes the classic concepts that assume well-mixed and therefore spatially non-nested food webs. Instead, spatially nested food webs are much more complex. Additionally, a spatial coupling of energy fluxes from sub-food webs by top predators can have stabilizing effects (McCann et al., 2005). As food web stability also increases the realized diversity of plants and eventually the productivity of plant communities (Albert et al., 2022; Schneider et al., 2016), spatially nested food web structures should have similar effects. Considering the strong impact animals can have on plant community composition and functioning, representing food webs either as spatially nested or non-nested could be substantial as they significantly differ in how they couple individuals and populations.

Processes at different spatial scales, ranging from competition for abiotic resources between neighbouring plants to apparent competition and large-scale integration of food webs by top predators, simultaneously affect functions within an ecosystem. Recent studies emphasized the importance of integrating such processes acting at different spatial scales in meta-communities (Furey et al., 2022) and meta-ecosystems (Gounand et al., 2018), especially when considering their implications for BEF relationships (Furey et al., 2022; Gonzalez et al., 2020). Despite their importance for community dynamics and functioning, the interactions among these processes have yet to be explored. As a result, our mechanistic understanding of how spatial interactions between plants via their resources or through higher trophic levels affect community-level functions is severely limited.

To address this issue, we introduce a spatially explicit model of plant individuals that can access local resource pools of their direct neighbours. By integrating this plant-resource model with a spatially explicit food web model, we investigate how resource competition and multi-trophic interactions interact across spatial scales

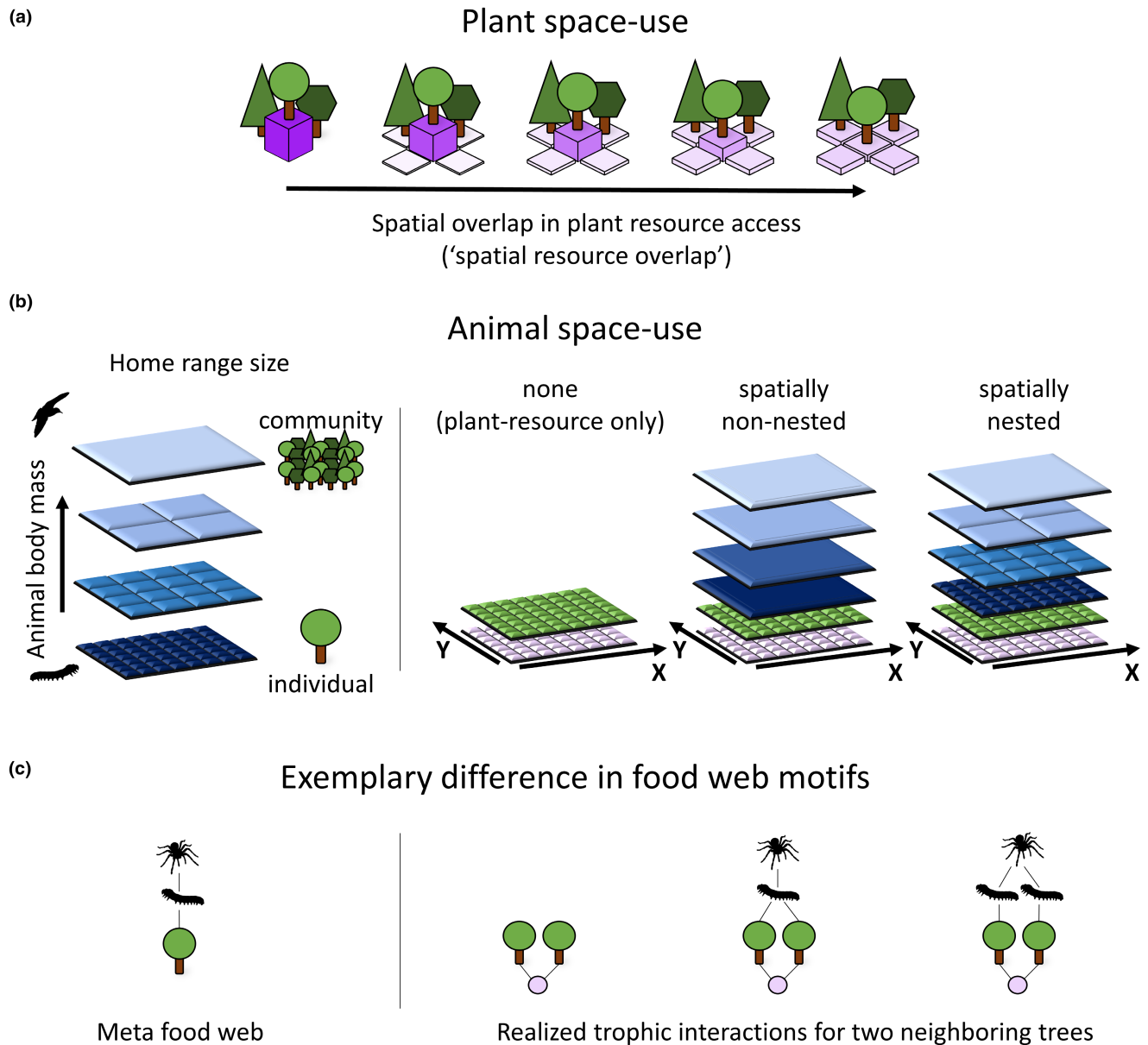


FIGURE 1 Overview of the considered spatial processes of plant and animal interactions within a plant community. (a) Differences in plant space-use are captured by a gradient of spatial overlap in plant resource access ('spatial resource overlap'), ranging from no overlap, where each plant is limited to its own patch, accessing only its local resource-pool and making exploitative competition impossible, to an even overlap with plants in neighbouring patches, maximizing exploitative competition. At intermediate steps, plants increase the spatial resources overlap as they increase their effort in taking up resources from neighbouring patches continuously from left to right. (b) We assume a home range size scaling with an animal's body mass (left). To investigate its effect, we look at three scenarios of animal space-use (right), one of which serves as a null model for animal effects by excluding them entirely ('none'). Scenarios with animals are either spatially non-nested, where animal populations are assumed to be well-mixed, or spatially nested, where animal home range sizes scale with their body mass. (c) When projecting them in space, each of the three scenarios can lead to different realized trophic interactions (right) despite a common meta-food web (left), illustrated using a simple trophic chain. Note that spatially nested food webs can also have similar interactions as spatially non-nested food webs depending on which species interact.

to shape diversity–productivity relationships in plant communities. The setup of our complex simulation experiment is based on the a-priori expectation that (1) positive diversity–productivity relationships can only emerge when plants interact through a spatial resource overlap. Further, a spatially nested food web structure will introduce processes at different spatial scales. We

therefore expect that (2) herbivore-induced apparent competition will reduce plant productivity, whereas (3) spatial integration of sub-food webs by top predators should balance local dynamics and increase apparent competition between herbivore populations, minimizing competitive exclusion of plants and increasing their diversity and productivity.

METHODS

To investigate the effects of plant and animal space-use on plant diversity–productivity relationships, we integrate both in a simulated plant biodiversity experiment. We utilize a well-established model of food web dynamics (Albert et al., 2022; Schneider et al., 2016), but implemented in a spatially explicit context. Specifically, while animal dynamics are still described at population levels, instead of describing the dynamics of plant populations, our model explicitly includes the spatial position of 64 evenly spaced plant individuals and associated local resource pools (hereafter: patch), arranged on an 8×8 grid with periodic boundary conditions. This allows us to include local resource interactions between neighbouring plants. By increasing the effort a plant puts in taking resources from its neighbouring resource pools in comparison to its own, it increases the spatial overlap in resource access ('spatial resource overlap'). This allows us to create a gradient that ranges from no overlap to an even access to all resource pools in the neighbourhood (Figure 1a). Further, our model uses two limiting plant resources. We assume that the access to both resources has the same spatial constraints within a spatial resource overlap scenario. However, we define resource requirements to differ between plant species to reflect different stoichiometries, allowing for a complementarity in resource-use.

We additionally consider three scenarios of animal space-use (Figure 1b). First, we exclude animals to create a null model without their effects. Second, in accordance with classic food-web models, we assume well-mixed animal populations that can access all of their resource species unconstrained (spatially non-nested food webs). Third, by constraining the home range of animals based on their body mass, we create spatially nested food webs in which larger species integrate multiple sub-food webs, creating a nested food web structure (McCann et al., 2005). Despite a common meta-food web (i.e. food web capturing all potential feeding interactions between species; Dunne, 2006), the realized spatial topologies of spatially nested and non-nested food webs can differ greatly (Figure 1c).

While we use our model to investigate plant diversity–productivity relationships at the community level, our proposed framework is flexible to assess, for example, interactions between plant individuals or effects of spatial heterogeneity in a multi-trophic context, enabling the generation of further insights of spatial processes in complex food webs that drive ecosystems.

Defining food web topologies

In total, we analyse 20 meta-food webs that were created to mimic topologies of aboveground terrestrial ecosystems, where most BEF experiments are conducted. In such ecosystems, carnivorous interactions commonly

follow allometric relationships, where larger predators consume smaller prey (Brose et al., 2019). However, in aboveground terrestrial ecosystems, herbivorous interactions are largely independent of body masses (Valdovinos et al., 2022). Hence, we defined herbivorous interactions to follow real-world network properties (i.e. connectance, nestedness, modularity; following Thébault & Fontaine, 2010) and combined them with allometrically scaled carnivorous interactions (following Schneider et al., 2016). Each of the 20 meta-food webs consists of 60 animal species with randomized body masses, 16 plant species with dynamic body masses (i.e. changing as plants grow), and two limiting resources.

To implement the plant diversity treatment, we compare each of the 20 complete 16-species plant mixtures (i.e. 64 plant individuals corresponding to 4 individuals per species, each mixture with a randomized spatial configuration) with their 16 monocultures (i.e. all 64 plant individuals of the same species). Together with the plant (Figure 1a) and animal space-use treatments (Figure 1b), we therefore investigate a total of 5100 different trophic networks in a fully factorial design.

By defining local resource pools for each plant individual and allowing plants to potentially support their own local food webs, our spatial representation of the plant community most closely resembles forest ecosystems. However, changing these assumptions by adapting the sizes of animal home ranges and local resource pools allows for representing other ecosystems as well. A detailed description of how we define meta-food webs and represent them in space can be found in the Supporting Information S1 and S2.

Describing food web dynamics

To investigate how our treatments affect plant productivity and diversity, we simulate food web dynamics using differential equations that describe changes in animal, plant and resource densities in response to feeding interactions and metabolic processes. Specifically, animals increase their biomass densities as they feed on other animals or plants. Feeding rates are based on non-linear functional responses that comprise capture coefficients, handling times and interference competition. Plant individuals increase their biomass based on biomass-dependent growth rates, which are limited by resource availability. We assume a constant resource turnover. Densities of resources, plants and animals decrease as they are consumed. In addition, plants and animals have metabolic demands that scale allometrically. A detailed description of the model can be found in the Supporting Information (S3 and S4, Tables S1–S3). Food web dynamics are calculated using Julia (version 1.6.1, Bezanson et al., 2017) and the DifferentialEquations package (Rackauckas & Nie, 2017), utilizing a solving algorithm based on the fourth-order Runge–Kutta

method. The code used in this study is available at <https://github.com/GeorgAlbert/SpatialFoodWebBEF>.

Measuring productivity and diversity

We measure plant productivity and diversity at the scale of plant communities. We define plant productivity Y of a community as the resource uptake of all individuals of all plant species (Supporting Information S4). To account for cyclic dynamics at the end of simulations, we define plant productivity as the average of productivity values obtained for the last 1000 timesteps of our simulations. We measure diversity as the number of surviving plant species (realized richness) and individuals (realized density) at the end of simulations. Additionally, we calculate Shannon diversity H_{exp} to compare to species richness and thereby quantify plant dominance patterns (Jost, 2006) as $H_{\text{exp}} = \exp\left(-\sum_i p_i \ln(p_i)\right)$, with $p_i = \frac{Y_i}{Y}$, where Y_i is the productivity of plant species i .

RESULTS

Plant diversity–productivity relationships

To investigate potential drivers behind plant diversity–productivity relationships, we compare the effects of food-web and resource-use scenarios (see Figure 1) on

productivity at both ends of the plant diversity gradient. In monocultures without animals, a spatial overlap in plant resource access (‘spatial resource overlap’) does not affect productivity (Figure 2, plant species richness of one; Figure S1a; green points). Instead, differences occur across food-web scenarios. Specifically, monocultures without animals are most productive, closely followed by those embedded in spatially non-nested food webs (dark blue points). In spatially nested food webs, monoculture plant productivity is lowest on average, but shows the largest variation with a weakly positive response to an increased spatial resource overlap (light blue points). The few cases of unviable monocultures are spread across all resource-use scenarios, more common in spatially nested (93/1600) than in spatially non-nested food webs (30/1600), and never occur in communities without animals. Plant interactions through spatial resource overlaps, therefore emerge as having little effect on monoculture productivity, rendering differences in food web architecture as the main driver.

In the absence of animals, plant diversity–productivity relationships clearly respond to having a spatial resource overlap (Figure 2, green lines). Without it, relationships between productivity and species richness are neutral (Figure 2a). However, when plants access resources of neighbouring patches (i.e. with spatial resource overlap), we find positive diversity–productivity relationships that are similar across resource-use scenarios (Figure 2b–e; Figure S1b). Taken together, these results suggest that positive effects of plant species richness on productivity

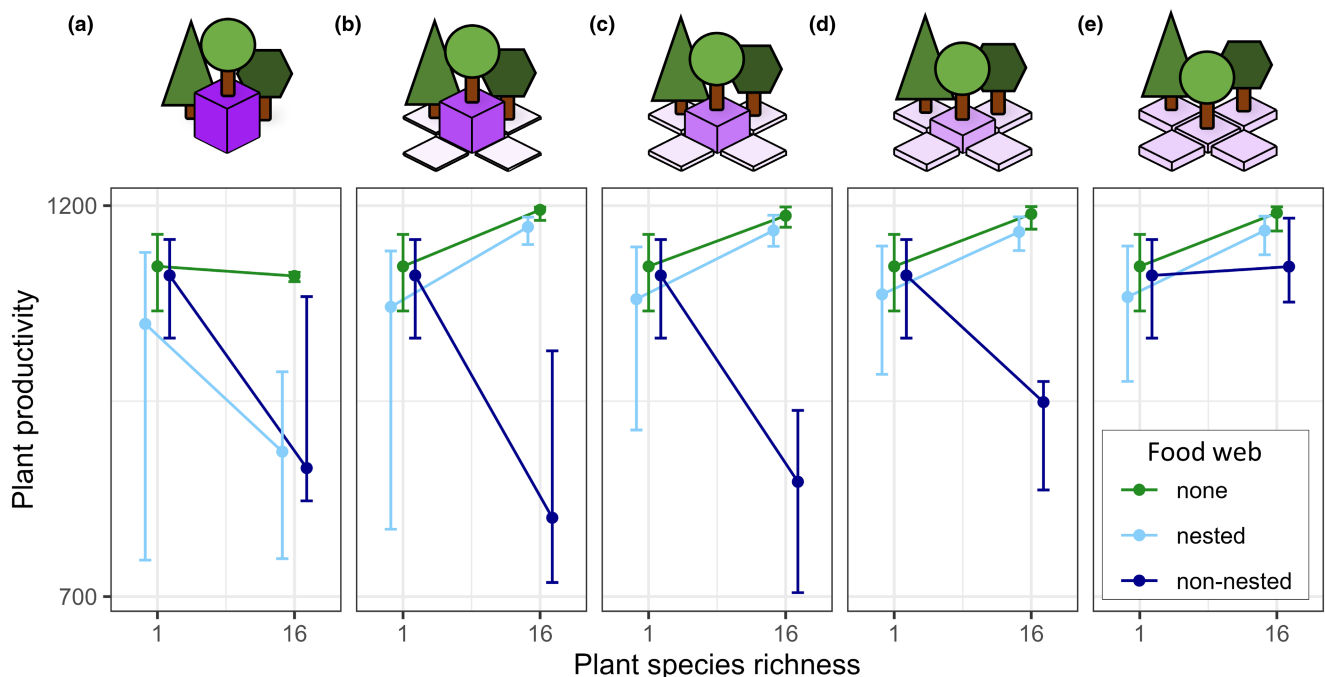


FIGURE 2 Plant diversity–productivity relationships for the three food web scenarios considered, that is, without food webs (‘none’, green), with spatially nested food webs (‘nested’, light blue) and with spatially non-nested food webs (‘non-nested’, dark blue). Plant productivity is measured for the entire community. (a–e) Effects of increasing the spatial overlap in plant resource access (‘spatial resource overlap’). Points show 50th percentile (i.e. median); error bars show 25th and 75th percentile. Unviable monocultures are not included.

in communities without animals require a spatial resource overlap, but small overlaps (Figure 2b) already suffice to saturate these relationships.

In spatially non-nested food webs, plant communities show strong decreases in productivity with increasing richness in most resource-use scenarios (Figure 2a–d; Figure S1b; dark blue lines). Diversity–productivity relationships are most negative when spatial resource overlaps are smallest (Figure 2b). Across the gradient of resource-use scenarios, plant monoculture productivity is constant (Figure S1a), while increasing considerably at higher species richness (Figure 2b–e; Figure S1b). This culminates in neutral diversity–productivity relationships at maximized spatial resource overlap (Figure 2e). Thus, increasing the spatial resource overlap positively affects plant diversity–productivity relationships in spatially non-nested food webs.

In contrast, plant communities in spatially nested food webs display similarly positive diversity–productivity relationships in the majority of cases (Figure 2b–e, light blue line). Only when there is no spatial resource overlap, relationships are negative and display large amounts of variation (Figure 2a). As soon as plants access resources of neighbouring patches (i.e. with spatial resource overlap), productivity increases with diversity, reaching values with little variation that are similar to those in plant communities without animals (Figure 2b–e). As plant monocultures also display the lowest average productivity compared to all other food web scenarios (Figure S1a), spatially nested food webs exhibit the most positive plant diversity–productivity relationships (Figure 2b–e).

Herbivory and total biomass (i.e. plants and animals combined) tend to increase with plant diversity and are higher in nested than in non-nested scenarios (Figures S2 and S3). While herbivory is higher and total biomass lower without a spatial resource overlap, the strength of the overlap has little effect on either food-web scenario. Herbivory and total biomass can therefore only partially explain differences in plant diversity–productivity relationships (Figure 2), rendering shifts in metabolic demands due to an altered plant community composition as an important driver (cf. equation 7 in Supporting Information S4).

Plant community composition

Our results show differences in plant diversity–productivity relationships being mainly driven by varying productivity at high plant diversity (Figure 2). To better understand these differences, we investigate how plant community composition differs between food-web and resource-use scenarios. Without a spatial resource overlap (i.e. spatial resource overlap at 0), realized species richness, realized plant density and Shannon diversity display the highest values within each food web scenario (Figure 3). Without animals, values are at their absolute maximum (Figure 3, green line). In spatially non-nested food webs, plant communities tend to display lower values of realized richness and density, while Shannon diversity is clearly lower, indicating more heterogeneous

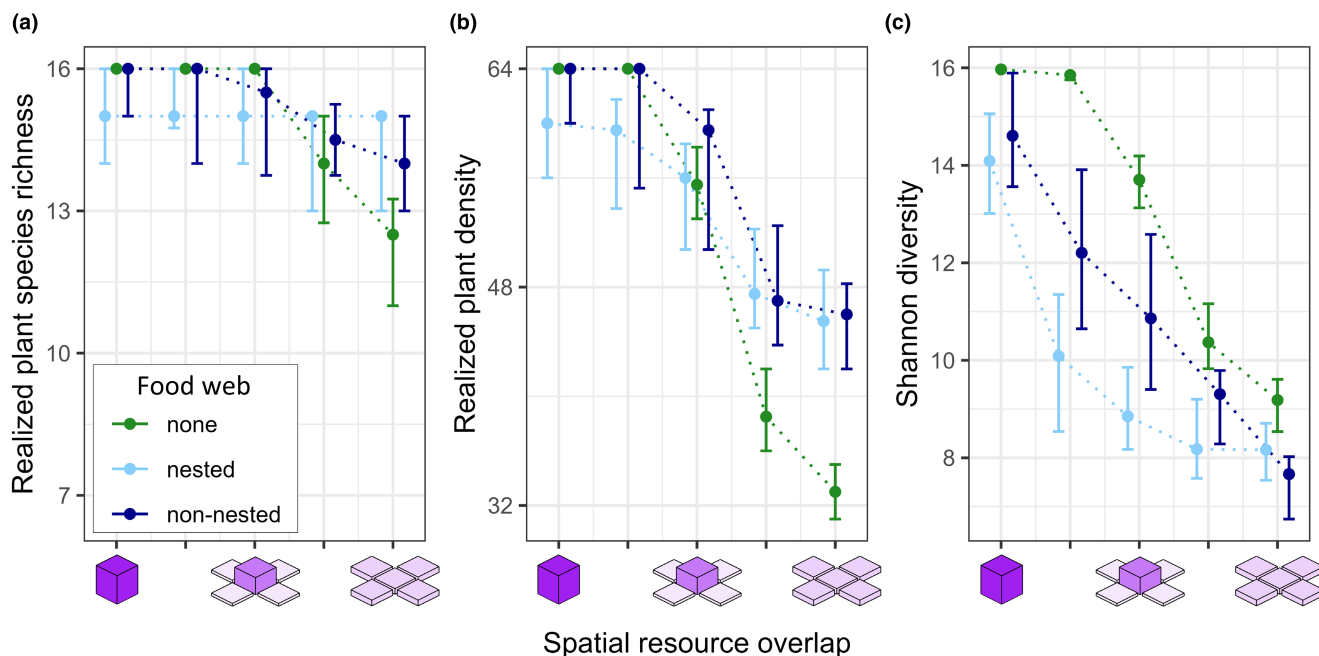


FIGURE 3 Effects of increasing the spatial overlap in plant resource access ('spatial resource overlap') on plant community composition in plant communities assembled from 16 species and in three different food web scenarios, that is, without food webs ('none', green), with spatially nested food webs ('nested', light blue) and with spatially non-nested food webs ('non-nested', dark blue). Biodiversity is expressed in (a) realized species richness, (b) realized plant density and (c) Shannon diversity. Points show 50th percentile (i.e. median); error bars show 25th and 75th percentile.

plant communities (Figure 3, light blue line). For spatially nested food webs, plant communities display a slightly reduced richness and density and have the lowest Shannon diversity (Figure 3, dark blue line). Thus, spatially nested food webs support the least diverse plant communities without a spatial resource overlap between neighbouring plants.

The compositional response of plant communities without animals to an increased spatial resource overlap displays a delayed but harsh drop for all three compositional variables (Figure 3, green lines). This leads to plant communities losing almost half of their plant individuals (Figure 3b), averaging more than three species (Figure 3a), when spatial resource overlap is highest. Since Shannon diversity decreases more than species richness (Figure 3a,c), an increased spatial resource overlap increases plant community heterogeneity without animals. Taken together, the effects of increasing the spatial resource overlap are most severe for plant communities without animals.

Plant communities in spatially non-nested food webs follow patterns similar to communities without animals (Figure 3, dark blue lines). However, the negative effects of increasing the spatial resource overlap are less pronounced for plant richness and density, culminating in about a quarter of plants, averaging about two species, lost when the spatial resource overlap is highest (Figure 3a,b). Shannon diversity is generally lower than without animals, reaching the lowest values at maximum spatial resource overlap across all scenarios (Figure 3c). When spatial resource overlap is high, spatially non-nested food webs are therefore enhancing differences between plant species more than any other scenario.

Compared to the other food-web scenarios, plant community composition in spatially nested food webs shows the weakest response to changes in spatial resource overlap. Realized plant species richness, which displays average losses of one species, is even independent from spatial resource overlap (Figure 3a, light blue line). Similar to spatially non-nested food webs, only about a quarter of plants are lost when spatial resource overlap is highest (Figure 3b). Shannon diversity again decreases with increasing spatial resource overlap but stabilizes over the last two steps (Figure 3c). Surprisingly, the clear plant-compositional differences between spatially nested and non-nested food webs only lead to minor differences in the diversity of the animal community (Figure S4). Overall, these findings suggest that spatial resource overlap matters the least in spatially nested food webs.

DISCUSSION

In our meta-food-web approach, we show that spatial processes related to plant resource exploitation and animal space-use strongly affect plant diversity–productivity relationships. Positive relationships arise only when plant

resource access overlaps spatially (‘spatial resource overlap’) at the cost of exploitative competition. Herbivore space-use introduces apparent competition between plants, which can reduce plant productivity in diverse communities, yielding negative diversity–productivity relationships. However, a realistic body mass scaling of animal home range sizes moves apparent competition motifs up the food chain. Reduced plant competition together with the spatial integration of sub-food webs in the home range of top predators leads to the most positive effects of plant diversity on productivity, suggesting animal space-use as a crucial driver of plant diversity–productivity relationships.

Plant–resource interactions

A spatial resource overlap between neighbouring plants has two important implications for plants. While it allows each plant to access a larger share of resources available in the ecosystem, it also induces exploitative competition. Diverse plant communities, however, are assembled from plants with different and therefore complementary resource requirements. This suggests a stoichiometric complementarity between neighbouring plants (González et al., 2017) that counteracts negative effects of competition (Tilman et al., 1997) arising from increased spatial resource overlaps. Meanwhile, it allows a more complete use of available resources, hence enhancing plant productivity. This is mirrored in our results, where, in the absence of animals, even a weak spatial resource overlap maximizes productivity in diverse plant communities. Accessing small amounts of otherwise inaccessible resources can therefore suffice to lift resource limitations, leading to positive diversity–productivity relationships due to a stoichiometric complementarity.

Differences in competitive abilities across plant species pairs are rarely associated with such performance enhancements. Instead, they should lead to local extinctions of weaker competitors (Tilman, 1982), which we observe as a loss of plants when the spatial resource overlap increases. Surprisingly, this does not reduce productivity. Instead, plants with competitive advantages, either due to higher efficiencies in resource acquisition (exploitative competition) or favourable multi-trophic interactions (apparent competition), can maximize their resource uptake, thereby increasing their biomass (Wang & Brose, 2018). As a positive side effect, this reduces energy requirements for metabolic processes relative to their mass (Enquist et al., 1998), making single plants contribute disproportionately to a more energy-efficient plant community. Our findings suggest that this is enough to counterbalance the loss of plants and the associated diversity.

When plants have a spatial resource overlap, diversified resource requirements create complementarity whereas selection (i.e. in the context of BEF research,

sensu Loreau, 2000) due to competitive differences shifts the community to be more energy efficient (Wang & Brose, 2018), leading to an optimized resource uptake in both cases. As expected (E1), this increases productivity and leads to positive diversity–productivity relationships. The consistency of those relationships paired with the shifts in plant community composition implies that the contribution of complementarity and selection processes to maximizing productivity varies depending on the strength of the competitive interaction between plants.

Plant–animal interactions

In complex food webs, the response of plant productivity to varying plant biodiversity is rooted in food-web topology. As plant species richness increases, more apparent competition motifs in which two plant species are coupled by a shared herbivorous consumer population emerge. In this motif, plant species with higher resource acquisition efficiencies achieves higher biomass densities, leading to higher herbivore densities, which in turn have negative top-down effects on other plant species with lower resource acquisition efficiencies (Holt, 1977). Accordingly, our simulations of spatially non-nested food webs have shown that increasing plant species richness reduces plant productivity, which is, as expected (E2), reflected in negative diversity–productivity relationships. However, compared to scenarios without animals, the added apparent competition does not foster competitive exclusion. Instead, it seems to buffer some negative effects of increased exploitative competition (i.e. increased spatial resource overlap) as more plant individuals and species can coexist when embedded in food webs (see also Albert et al., 2022; Brose, 2008).

While the high levels of maintained plant individuals and species are similar between spatially nested and non-nested food webs, the effects of apparent competition on productivity are not. Specifically, our simulations of spatial non-nested food webs assume a well-mixed system without differences in local biomass densities of animal species. Ignoring such differences results in herbivore populations that can feed simultaneously on different plants regardless of their location. In nature, however, animal communities have a complex spatial organization (e.g. Gonçalves-Souza et al., 2015). While almost all animal species integrate several resource patches (corresponding to our nested organization of space-use), larger species travel longer distances and have larger home ranges than smaller species (Hirt et al., 2021; Tamburello et al., 2015; Tucker et al., 2014). Hence, meta-food webs have a realized structure in which larger species spatially integrate smaller species from local food webs in their home ranges. Additionally, apparent competition between plants in spatially nested food webs is spatially

constrained depending on the home range size of the herbivore. An increased amount of apparent competition motifs between sub-populations of herbivores further reduces their top-down control on plants, which is mediated by the plant composition. Hence, instead of the negative plant diversity–productivity relationships found in spatially non-nested food webs, relationships in spatially nested food webs are most positive, peaking at levels similar to plant communities without animals.

Apart from the positive effects of an altered spatial topology (i.e. effects of apparent competition) on diversity–productivity relationships in spatially nested food webs, the spatial integration of sub-food webs can have additional dynamic benefits. Specifically, biomass overshooting and unstable dynamics leading to local extinctions can be buffered in spatially nested food webs by large top predators, stabilizing biomass minima of populations in local food webs away from critically low values (McCann et al., 2005). This is reflected in a similarly high plant and animal diversity in spatially nested food webs across the spatial resource overlap scenarios. Consistent with our expectation (E3), we thus conclude that a spatial integration of sub-food webs associated with spatially nested food webs has positive effects on plant diversity–productivity relationships. Dynamic and topological differences between spatially nested and non-nested food webs, which may be negligible for biodiversity maintenance, can therefore have strong implications for plant productivity, leading to vastly different plant diversity–productivity relationships.

BEF: From multi-trophic to spatially resolved food webs

BEF research has evolved from focusing on single functional groups (e.g. plant communities) to the complex multi-trophic structure of natural communities (e.g. Albert et al., 2022; Barnes et al., 2020; Schuldt et al., 2019). This progression revealed that multi-trophic interactions play a crucial role in promoting plant coexistence and thereby increasing productivity. Systematic variation in food-web structures highlighted the importance of the specialist-generalist gradient (Thébault & Loreau, 2003), the diversity of animals (Albert et al., 2022; Schneider et al., 2016) and the vertical diversity (i.e. the maximum trophic level; Wang & Brose, 2018). In our study, we expanded this advancement by employing meta-ecosystem approaches (i.e. plant-resource exploitation bridges across local habitats) and spatially realizing meta-food webs, thereby accounting for the spatially explicit structure of natural animal communities.

Some of our results on the effects of multi-trophic interactions differ significantly from previous conclusions. While prior studies reported generally positive effects of multi-trophic interactions on plant coexistence and diversity–productivity relationships

(Albert et al., 2022; Brose, 2008; Li, Schmid, et al., 2023; Thébault & Loreau, 2003), we found that this is not necessarily true. The absence of a spatially organized community structure in both plants, characterized by their spatially segregated distribution (i.e. each plant inhabits its own local habitat), and animals, marked by their spatially non-nested distribution (i.e. all animals have the same home range), leads to negative BEF relationships. These negative relationships can be attributed to the systematic prevalence of apparent competition motifs. In contrast, the spatially nested structure observed in natural animal communities yields strongly positive diversity–productivity relationships. This can be attributed to the positive effects of apparent competition motifs, which are shifted up the food chains (i.e. from effects between plants to effects between herbivores sharing enemies), and the spatial integration of sub-food webs by top predators. Although our scenarios of spatially nested and non-nested food webs may represent two ends of a gradient, they illustrate that the spatial realization of meta-food webs and associated modifications of competition impact the complementarity among plants. Contrary to niche complementarity arising from interactions with pathogens sharing the spatial dimension of their plant hosts, multi-trophic complementarity arises from the intricate spatial structure defined by plant and animal space-use. Understanding the complex spatial structure underlying complementarity is thus key to identifying the factors driving observed variation in empirical BEF relationships (Cardinale et al., 2007).

By relaxing the classic assumption of well-mixed systems (e.g. Albert et al., 2022; Schneider et al., 2016), we gained accuracy in describing the processes that drive ecosystems and their functioning. Our work demonstrates that multi-trophic investigations of spatially explicit plant–resource interactions additionally require a spatially explicit consideration of the entire food web to reproduce the positive diversity effects observed in experiments (Cardinale et al., 2007) and the field (van der Plas, 2019). Moreover, our simulations show that the sign and strength of diversity–productivity relationships depends on joint effects of animal and plant space-use. Recent evidence additionally suggests that diverse neighbouring patches can maintain plant diversity through seed dispersal (Furey et al., 2022) and dilute the diversity of herbivores (Li, Wang, et al., 2023). The within-ecosystem spatial processes investigated in our study are thus embedded in large scale meta-ecosystem processes. However, the continuity of animal home range sizes (Tucker et al., 2014) blurs the line between spatial scales. Thus, our work provides a framework to better understanding cross-scale feedback (Gonzalez et al., 2020), including effects of anthropogenic disturbances (e.g. due to top-predator extinctions or altering species' mobility; Estes et al., 2011; Stabach et al., 2022), on BEF relationships and their underlying processes.

Future directions

Accounting for spatial processes in BEF relationships can be progressed in multiple ways. We contributed by synthesizing empirically supported structures of animal space-use with spatially explicit plant–resource exploitation. Our model is flexible to also include other aspects of community structure across spatial scales, including (1) local factors and species traits influencing exploratory movement during foraging (Hirt et al., 2021), such as effects of species' cognitive abilities (Heathcote et al., 2023), (2) neighbouring habitats coupled by lateral nutrient flows in meta-ecosystems (Gounand et al., 2018; Loreau et al., 2003), (3) meso-scale landscape structures in community assembly models (Bannar-Martin et al., 2018; Saravia et al., 2022), including plant and animal dispersal (Ryser et al., 2021) and (4) biogeographic differences between species pools (e.g. of plants; Sabatini et al., 2022). In this vein, merging our spatially explicit meta-food web approach with food web assembly models (Bauer et al., 2022; Saravia et al., 2022) offers a particularly exciting avenue of future research as it allows to understand how local spatial processes scale to the diversity and ecosystem functioning patterns observed at larger spatial scales.

CONCLUSION

Despite its variability, positive effects of diversity on productivity in plant communities are a widely recognized pattern consistent across ecosystems (Cardinale et al., 2007). To date, the most prominent among the proposed mechanisms driving these patterns and their variability is resource-use complementarity of plants (Barry et al., 2019), which has more recently been supplemented by multi-trophic complementarity (Albert et al., 2022; Poisot et al., 2013). To better understand their differences, we explicitly modelled the different spatial scales at which both mechanisms operate in a simulated biodiversity experiment. We could show that a spatial overlap in resource access between neighbouring plants is a fundamental requirement for positive plant diversity–productivity relationships, highlighting the tight association of exploitative competition with resource-use complementarity and plant compositional shifts. The realistic, spatially explicit representation of meta-food webs that integrate nested local sub-food webs stabilizes plant coexistence and yields the strongest diversity–productivity relationships we observe. Our modelling framework can serve as a foundation to further enhance our mechanistic understanding of multi-trophic processes in driving plant diversity–productivity relationships. It provides a novel approach to manage biodiversity while explicitly accounting for the spatial processes that underpin ecosystem functions at the basis of our human society.

Advancing in this direction is therefore crucial for guiding conservation efforts to maintain biodiversity and the functioning of ecosystems.

AUTHOR CONTRIBUTIONS

UB, SW and GA conceptualized the study. All authors contributed to developing the simulation framework, and GA conducted the simulations. UB and GA wrote the first draft of the manuscript and all authors contributed substantially to revision.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

No data were used in this study but the underlying code is available at <https://github.com/GeorgAlbert/SpatialFoodWebBEF> <https://doi.org/10.5281/zenodo.8144298>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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