

# Animal movement and plant space-use drive plant diversity-productivity relationships

Georg Albert<sup>1</sup>, Benoit Gauzens<sup>2</sup>, Remo Ryser<sup>3</sup>, Elisa Thébault<sup>4</sup>, Shaopeng Wang<sup>5</sup>, and Ulrich Brose<sup>6</sup>

<sup>1</sup>University of Göttingen

<sup>2</sup>iDiv

<sup>3</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig

<sup>4</sup>Bioemco - UMR 7618 (CNRS, UPMC, ENS, IRD, AgroParisTech)

<sup>5</sup>Peking University

<sup>6</sup>German Centre for Integrative Biodiversity Research Halle-Jena-Lepizig

February 1, 2023

## 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 movement of animals 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. Movement of herbivores causes apparent competition among plants, resulting in negative relationships. However, movement 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 plant resource access and animal movement can greatly alter the strength and sign of such relationships. In particular, the scaling of animal movement effects opens new perspectives for linking landscape processes without effects on biodiversity to productivity patterns.

## 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 (Tilman *et al.* 2014; Duffy *et al.* 2017). Even though the importance of biodiversity for providing ecosystem functions is supported by increasing empirical 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 how plants use abiotic resources is the main driving force behind positive plant diversity-productivity relationships (Barry *et al.* 2019). However, the productivity of plants not only depends on how they access and compete for resources, but is also strongly influenced by interactions with herbivores and animals of higher trophic levels (Schneider *et al.* 2016; Barnes *et al.* 2020; Albert *et al.* 2022). In addition, research on BEF relationships 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 draws attention to community assembly processes that affect biodiversity maintenance in BEF experiments based on the meta-community (Bannar-Martin *et al.* 2018; Furey *et al.* 2022), highlighting the importance of also considering processes at larger spatial scales. This includes interactions of plants with animals at higher trophic levels that integrate local 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 the different scales they are associated with explain BEF patterns, such as the plant diversity-productivity relationship, and their variance at the community scale?

Traditionally, BEF research focuses on the relationship between plant diversity and productivity emerging at the community level (Cardinale *et al.* 2007). Only recently, investigating the implications of local interactions between plant individuals and their immediate neighbours (hereafter: neighbourhood scale; Fig.1; Sapijanskas *et al.* 2013; Fichtner *et al.* 2018) has started. At this scale, individual plants access different parts of the total available resources (e.g., the resource pools in the soil) 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 plant individuals (Fig. 1A) makes them complementary in their access to resources as it reduces the strength of their competitive interactions and thereby renders competitive exclusion less likely (Chesson 2000b). While this spatial segregation of plants’ resource-use facilitates coexistence, it potentially imposes constraints on 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 results in lower plant diversity, this can have negative feedback on plant community productivity, calling for a more 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 a local spatial resource overlap, animal movement couples even distant plants, for instance when herbivores move to switch resources. This movement of herbivores yields apparent competition between plants (Fig. 1C, spatially-non nested), which can impose strong negative effects on the 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 (Tucker *et al.* 2014; Hirt *et al.* 2021) will 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 (Fig. 1C). As a result, apparent competition emerges among less mobile herbivores due to a shared, more mobile predator. This spatial structure of natural food webs opposes the widespread classic concepts that assume well-mixed and therefore spatially non-nested food webs. Instead, the spatially nested food webs will display much higher levels of complexity. 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 (Schneider *et al.* 2016; Albert *et al.* 2022), spatially nested food web structures should also increase the productivity of the plant community. Considering the strong impact animals can have on plant community composition and functioning, the consequences of 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 that act 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 (Gonzalez *et al.* 2020; Furey *et al.* 2022). 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 to shape diversity-productivity relationships in plant communities. We hypothesize that, (1) positive diversity-productivity relationships can only emerge when plants are able to 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 have negative effects on 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 leading to an increase in 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 (Schneider *et al.* 2016; Albert *et al.* 2022), but implemented in a spatially-explicit context. Specifically, 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 8x8 grid with periodic boundary conditions. This allows us to include local resource interactions between neighbouring plants by manipulating their focus on using resources from their local resource pools in relation to their neighbouring resource pools. Thus, we can create a gradient of spatial overlap in resource access ('spatial resource overlap') that ranges from no overlap to an even access to all resource pools in the neighbourhood (Fig. 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 due to having different stoichiometries, allowing for a complementarity in resource-use.

We additionally consider three scenarios of animal space-use (Fig. 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, the realized spatial topologies of spatially nested and non-nested food webs can differ greatly (Fig. 1C).

While we use our model to investigate plant diversity-productivity relationships at the community level, our proposed framework can be used to assess, e.g., interactions between plant individuals or effects of spatial heterogeneity in a multi-trophic context. It is therefore flexible to generate further insights of the spatial processes in complex food webs that drive ecosystems and their functioning.

## Defining food web topologies

In total, we analyse 20 different 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 species (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 20 meta-food webs consists of 60 animal species with randomized body masses, 16 plant species with dynamic body masses (i.e. they change as plant individuals grow), and two limiting resources. To implement the plant diversity treatment, we compare the complete 16-species plant mixtures (i.e. 4 individuals per species, with random spatial distributions) with their 16 monocultures (i.e. all 64 individuals of the same species). Together with the plant (Fig. 1A) and animal space-use treatments (Fig. 1B), we therefore investigate a total of 5,100 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 supplementary material (Supplementary 1-2).

## Describing food web dynamics

To investigate how our treatments affect plant productivity and diversity, we simulated 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 the 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 and its parameters can be found in the supplementary material (Supplementary 3-4, Tab. S1). Food web dynamics were 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  $P$  of a community as the resource uptake of all individuals of all plant species. To account for cyclic dynamics at the end of simulations, we define plant productivity as the average of productivity values obtained for the last 1,000 timesteps of our simulations. To capture plant diversity, we measure the realized plant species richness (i.e. number of surviving plant species) and plant density (i.e. number of surviving plants) at the end of the simulation. Additionally, we calculate Shannon diversity  $H_{\text{exp}}$  to compare to species richness and thereby quantify plant dominance patterns (Jost 2006) as  $H_{\text{exp}} = \exp(-\sum_i p_i \ln(p_i))$ , with  $p_i = \frac{P_i}{P}$  where  $P_i$  is the productivity of plant species  $i$ .

## Results

### Plant diversity-productivity relationships

To investigate the potential drivers behind plant diversity-productivity relationships, we compare the effects of food-web and resource-use scenarios (see Fig. 1) on productivity at both ends of the plant diversity gradient. In monocultures without animals, we find that a spatial overlap in plant resource access ('spatial resource overlap') has no effect on productivity (Fig. 2, plant species richness of one; Fig. S1A; green points). Instead, differences occur across the different food-web scenarios. Specifically, monocultures without animals are the most productive, closely followed by those embedded in spatially non-nested food webs (dark blue points). In spatially nested food webs, plant productivity of monocultures is the lowest on average but shows the largest variation with a weakly positive response to an increased spatial resource overlap (light

blue points). We rarely found unviable monocultures. The few examples we recorded were spread across all resource-use scenarios and more common in spatially nested (93/1600) than in spatially non-nested food webs (30/1600), and never occurred in communities without animals. When focusing on monoculture productivity, an interaction with neighbouring plants through a spatial resource overlap therefore emerges as having little effect, rendering differences in food web architecture as the main driver.

Our analyses reveal some striking effects of having a spatial resource overlap on the diversity-productivity relationships in plant communities without animals (Fig. 2, green lines). Without a spatial resource overlap we find neutral relationships between productivity and species richness (Fig. 2A). However, as soon as plants are able to access resources of the neighbouring patches (i.e. with spatial resource overlap), we find positive effects of plant diversity on productivity that are similar across resource-use scenarios (Fig. 2B-E; Fig. S1B). Taken together, these results suggest that a positive response of productivity to species richness in plant communities without animals requires a spatial resource overlap, but already small amounts of spatial resource overlap (i.e. Fig. 2B) suffice to saturate these relationships.

In spatially non-nested food webs, plant communities show a strong decrease in productivity with increasing richness in most resource-use scenarios (Fig. 2A-D; Fig. S1B; dark blue lines). Diversity-productivity relationships are most negative when spatial resource overlap is smallest (Fig. 2B). Across the gradient of resource-use scenarios, plant monoculture productivity is constant (Fig. S1A), while it increases considerably at higher plant species richness (Fig. 2B-E; Fig. S1B). This culminates in neutral diversity-productivity relationships when spatial resource overlap is maximized (Fig. 2E). Thus, in communities with spatially non-nested food webs, a strong spatial resource overlap with neighbouring plants has a positive effect on plant diversity-productivity relationships.

In contrast, plant communities in spatially nested food webs display positive diversity-productivity relationships in the majority of cases (Fig. 2B-E, light blue line). We only find negative effects of plant diversity on productivity when there is no spatial resource overlap (Fig. 2A). However, productivity at both ends of the diversity gradient displays large amounts of variation. As soon as plants have access to 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 (Fig. 2B-E). Together with having the lowest average productivity in plant monocultures compared to all other food web scenarios (Fig. S1A), this makes plant communities in spatially nested food webs exhibit the most positive diversity-productivity relationships (Fig. 2B-E).

## Plant community composition

Our prior results show that differences in the plant diversity-productivity relationships are mainly driven by varying productivity at the highest plant diversity levels (Fig. 2). To better understand these differences between food-web and resource-use scenarios, we investigated how plant community composition differs between scenarios at the highest plant diversity level of 16 species. 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 considered (Fig. 3). In communities without animals, the values are at their absolute maximum (Fig. 3, green line). In spatially non-nested food webs, the plant communities show a tendency towards lower values of realized richness and density, and Shannon diversity is clearly lower, indicating an increased heterogeneity in the plant community (Fig. 3, light blue line). For spatially nested food webs, plant communities display a slightly reduced plant species richness and density and have the lowest Shannon diversity (Fig. 3, dark blue line). Thus, spatially nested food webs support the least diverse plant communities when there is no spatial resource overlap between neighbouring plants.

The compositional response of plant communities without animals to increasing the spatial resource overlap between neighbouring plants stands out as it displays a delayed but harsh drop for all three compositional variables (Fig. 3, green lines). This leads to plant communities that lose almost half of their plant individuals when spatial resource overlap is highest (Fig. 3B), and includes the extinction of slightly more than three

species on average (Fig. 3A). Since Shannon diversity decreases more than species richness (Fig. 3A&C), an increased spatial resource overlap increases the heterogeneity in the plant communities 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 very similar patterns compared to communities without animals (Fig.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 and only about two species lost when the spatial resource overlap was highest (Fig.3A&B, dark blue lines). Shannon diversity was generally lower than in communities without animals, reaching the lowest values at maximum spatial resource overlap compared to all other scenarios (Fig. 3C, dark blue line). 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 show the weakest response to changes in spatial resource overlap. Especially realized plant species richness, which displays an average loss of only one species, was independent from spatial resource overlap (Fig.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 (Fig.3B, light blue line). Shannon diversity again decreases with increasing spatial resource overlap but ends up stabilizing over the last two steps of the spatial resource overlap gradient (Fig.3C, light blue line). Overall, these findings suggest that spatial resource overlap between neighbouring plants 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 movement 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 movement 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. The reduced plant competition together with the spatial integration of sub-food webs through the movement of top predators lead to the most positive effects of plant diversity on productivity, suggesting animal movement 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 forces them to engage in exploitative competition. In diverse plant communities, however, plants will differ in their resource requirements and thus in their competitive ability. Different resource requirements are usually accompanied by low competition (Tilman *et al.* 1997) and suggest a stoichiometric complementarity between neighbouring plants (González *et al.* 2017) that is likely to have positive impacts on plant productivity. We find this mirrored in our results, where, in the absence of animals, even a weak spatial resource overlap is enough to maximize productivity in diverse plant communities of species with different resource requirements. Accessing small amounts of otherwise inaccessible resources can therefore already suffice to lift resource limitations, leading to positive diversity-productivity relationships due to a stoichiometric complementarity.

Differences in competitive abilities across pairs of plant species are rarely associated with such performance enhancements. Instead, they should lead to local extinctions of the weaker competitor (Tilman 1982), which we find mirrored in a loss of plants when the spatial resource overlap increases. Surprisingly, this does not come at the cost of a reduced productivity. Instead, plants with a competitive advantage, either due to a

higher efficiency in resource acquisition (i.e. exploitative competition) or favourable multi-trophic interactions (i.e. apparent competition), can maximize their resource uptake and thereby increase their biomass (Wang & Brose 2018). This has the positive side effect of reducing energy requirements for metabolic processes relative to their mass (Enquist *et al.* 1998), contributing to a more energy efficient plant community. Our findings suggest that this is enough to counterbalance the loss of plants as well as the associated diversity loss.

When plants have a spatial resource overlap, diversified resource requirements create complementarity whereas selection (*sensu* Loreau 2000) due to competitive differences shift the community to be more energy efficient (Wang & Brose 2018), leading to an optimized resource uptake in both cases. Consistent with our hypothesis (H1), this increases productivity and leads to positive diversity-productivity relationships. The consistency of those relationships paired with the shifts in plant community composition additionally 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

When embedded in complex food webs, the response of plant productivity to varying plant biodiversity is rooted in food-web topology. As the number of plant species increases, there is an increasing number of apparent competition motifs in which two plant species are coupled by a shared herbivorous consumer population. In this motif, the plant species with a higher resource acquisition efficiency achieves a higher biomass density, leading to higher herbivore densities, which in turn has 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 as plant species richness increases, plant productivity decreases, which is, consistent with our hypothesis (H2), reflected in negative diversity-productivity relationships. However, when compared to scenarios without animals, the added apparent competition does not foster competitive exclusion. Instead, it seems to buffer some of the negative effects of an increased exploitative competition (i.e. increased spatial resource overlap) as more plant individuals and species are able to coexist when embedded in a food web (see also Brose 2008; Albert *et al.* 2022).

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 any 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 move between resource patches, larger species travel longer distances and have larger habitats (Tucker *et al.* 2014; Tamburello *et al.* 2015; Hirt *et al.* 2021). As a result, meta-food webs have a structure in which smaller species from local food webs are spatially integrated within the home ranges of larger species. Apparent competition between plants in spatially nested food webs is therefore spatially constrained depending on the home range size of the herbivore. In addition, an increased amount of apparent competition motifs between sub-populations of herbivores reduces their top-down control on plants. Hence, instead of the negative plant diversity-productivity relationships found in spatially non-nested food webs, relationships in spatially nested food webs are the 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 has additional dynamic benefits. In particular, biomass overshooting and unstable dynamics leading to local extinctions are buffered in spatially nested food webs by large top predators that stabilize biomass minima of populations in the local food webs away from critically low values (McCann *et al.* 2005). This is reflected in the relatively stable plant diversity of spatially nested food webs despite differences in the spatial resource overlap of plants. Consistent with our hypothesis (H3), 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. The clear 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 meta-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. Schuldt *et al.* 2019; Barnes *et al.* 2020; Albert *et al.* 2022). This development has shown that multi-trophic interactions can facilitate plant coexistence and thereby increase productivity. In our study, we extended this development by applying meta-ecosystem (i.e. plant-resource exploitation bridges between local habitats) and meta-food web approaches (i.e. spatially-explicit structure of the food webs). 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 (Thébault & Loreau 2003; Brose 2008; Albert *et al.* 2022), we found that under the assumption of spatially segregated plants (i.e. each plant inhabits its own local habitat) this is not necessarily the case. Spatially non-nested animal communities paired with spatially segregated plants instead result in negative relationships, which finds an explanation in the systematic increase in apparent competition motifs. In contrast, the spatially nested structure of animal communities yields strongly positive diversity-productivity relationships due to the positive effects of an apparent competition shift up the food chain (i.e. from between plants to between herbivores) and the spatial integration of sub-food webs by top predators.

By relaxing the classic assumption of well-mixed systems (e.g. Schneider *et al.* 2016; Albert *et al.* 2022), we gained accuracy in the description of the processes that drive ecosystems and their functioning. The assumption of a well-mixed system is also at the core of BEF research, as it usually compares the functioning of entire communities of varying diversity. While this helped to identify complementarity mechanisms as the main driver of positive BEF relationships, it remains difficult to identify their concrete causes (Barry *et al.* 2019), which may be related to focusing on the wrong spatial scale. Indeed, competition and the associated BEF processes (i.e. complementarity and selection; Loreau 2000) act between a few organisms and are thus spatially constrained. Our work demonstrates that a multi-trophic investigation of spatially-explicit plant-resource interactions additionally requires a spatially-explicit consideration of the entire food web. Moreover, our simulations show that the sign and strength of diversity-productivity relationships depends on the joint effects of animal movement and spatial resource overlap of plants. This renders the spatial organisation of multi-trophic communities, which can vary across landscapes, an important but often neglected aspect that can help to explain the variation observed in empirical BEF relationships (Cardinale *et al.* 2007). Overall, our findings on diversity-productivity relationships clearly demonstrate the importance of spatial community structure and animal movement in driving BEF relationships in meta-food webs.

## Future directions

The development of accounting for spatial processes in BEF relationships can be progressed in multiple ways. We have advanced this field in one dimension by synthesizing spatially-explicit processes related to animal foraging movement 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.* 2017), (2) neighbouring habitats coupled by lateral nutrient flows in meta-ecosystems (Loreau *et al.* 2003; Gounand *et al.* 2018), (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) offer 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, the positive effects of diversity on productivity in plant communities are a widely recognized pattern that is consistent across ecosystems (Cardinale *et al.* 2007). To date, the most prominent among the proposed mechanisms driving these patterns and their variability is complementarity in the resource-use of plants (Barry *et al.* 2019), which has more recently been supplemented by multi-trophic complementarity (Poisot *et al.* 2013; Albert *et al.* 2022). 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 due to selection. 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 managing biodiversity while explicitly accounting for the spatial processes that underpin the ecosystem functions that are 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.

## Acknowledgements

We thank the members of the EcoNetLab for helpful discussions. GA was supported by the International Research Training Group TreeDi funded by the German Research Foundation (DFG; GRK 2324/1 - 2018 (P9), 319936945). ET was supported by the Agence Nationale de la Recherche (ANR-17-CE32-0002/ECOSTAB). SW was supported by the National Natural Science Foundation of China (31988102). GA, BG, RR and UB gratefully acknowledge the support of iDiv funded by the German Research Foundation (DFG-FZT 118, 202548816).

## References

- Albert, G., Gauzens, B., Loreau, M., Wang, S. & Brose, U. (2022). The hidden role of multi-trophic interactions in driving diversity-productivity relationships. *Ecol. Lett.* , 25, 405–415.
- Bannar-Martin, K.H., Kremer, C.T., Ernest, S.K.M., Leibold, M.A., Auge, H., Chase, J., *et al.* (2018). Integrating community assembly and biodiversity to better understand ecosystem function: the Community Assembly and the Functioning of Ecosystems (CAFE) approach. *Ecol. Lett.* , 21, 167–180.
- 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. *Sci. Adv.* , 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 Ecol. Evol.* , 34, 167–180.
- Bauer, B., Berti, E., Ryser, R., Gauzens, B., Hirt, M.R., Rosenbaum, B., *et al.* (2022). Biotic filtering by species' interactions constrains food-web variability across spatial and abiotic gradients. *Ecol. Lett.* , 25, 1225–1236.
- Bezanson, J., Edelman, A., Karpinski, S. & Shah, V.B. (2017). Julia: A fresh approach to numerical computing. *SIAM Rev.* , 59, 65–98.
- Brose, U. (2008). Complex food webs prevent competitive exclusion among producer species. *Proc. R. Soc. B Biol. Sci.* , 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. *Nat. Ecol. Evol.* , 3, 919–927.
- 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. *PNAS* , 104, 18123–18128.
- Chesson, P. (2000a). General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theor. Popul. Biol.* , 58, 211–237.
- Chesson, P. (2000b). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* , 31, 343–366.
- 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.
- Enquist, B.J., Brown, J.H. & West, G.B. (1998). Allometric scaling of plant energetics and population density. *Nature* , 395, 163–165.
- Fichtner, A., Hardtle, W., Bruelheide, H., Kunz, M., Li, Y. & Von Oheimb, G. (2018). Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nat. Commun.* , 9, 1–8.
- Furey, G.N., Hawthorne, P.L. & Tilman, D. (2022). Might field experiments also be inadvertent metacomunities? *Ecology* , 103, 1–12.
- Goncalves-Souza, T., Araujo, M.S., Barbosa, E.P., Lopes, S.M., Kaminski, L.A., Shimizu, G.H., *et al.* (2015). Fine-scale Beta-diversity Patterns Across Multiple Arthropod Taxa Over a Neotropical Latitudinal Gradient. *Biotropica* , 47, 588–594.
- Gonzalez, A., Germain, R.M., Srivastava, D.S., Filotas, E., Dee, L.E., Gravel, D., *et al.* (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecol. Lett.* , 23, 757–776.
- Gonzalez, A.L., Dezerald, O., Marquet, P.A., Romero, G.Q. & Srivastava, D.S. (2017). The multidimensional stoichiometric niche. *Front. Ecol. Evol.* , 5, 1–17.
- Gounand, I., Harvey, E., Little, C.J. & Altermatt, F. (2018). Meta-Ecosystems 2.0: Rooting the Theory into the Field. *Trends Ecol. Evol.* , 33, 36–46.
- Hirt, M.R., Barnes, A.D., Gentile, A., Pollock, L.J., Rosenbaum, B., Thuiller, W., *et al.* (2021). Environmental and anthropogenic constraints on animal space use drive extinction risk worldwide. *Ecol. Lett.* , 24, 2576–2585.
- Hirt, M.R., Lauermaun, 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. *Theor. Popul. Biol.* , 12, 197–229.
- Jost, L. (2006). Entropy and diversity. *Oikos* , 113, 363–375.
- Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* , 91, 3–17.
- Loreau, M., Mouquet, N. & Holt, R.D. (2003). Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol. Lett.* , 6, 673–679.
- McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett.* , 8, 513–523.
- van der Plas, F. (2019). Biodiversity and ecosystem functioning in naturally assembled communities. *Biol. Rev.* , 94, 1220–1245.

- Poisot, T., Mouquet, N. & Gravel, D. (2013). Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecol. Lett.* , 16, 853–861.
- Rackauckas, C. & Nie, Q. (2017). DifferentialEquations.jl – A Performant and Feature-Rich Ecosystem for Solving Differential Equations in Julia. *J. Open Res. Softw.* , 5, 1–10.
- Ryser, R., Hirt, M.R., Haussler, J., Gravel, D. & Brose, U. (2021). Landscape heterogeneity buffers biodiversity of simulated meta-food-webs under global change through rescue and drainage effects. *Nat. Commun.* , 12, 1–9.
- Sabatini, F.M., Jimenez-Alfaro, B., Jandt, U., Chytry, M., Field, R., Kessler, M., *et al.* (2022). Global patterns of vascular plant alpha diversity. *Nat. Commun.* , 13, 1–16.
- Sapijanskas, J., Potvin, C. & Loreau, M. (2013). Beyond shading: litter production by neighbors contributes to overyielding in tropical trees. *Ecology* , 94, 941–952.
- Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). Ecological network assembly: How the regional metaweb influences local food webs. *J. Anim. Ecol.* , 91, 630–642.
- Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nat. Commun.* , 7, 1–8.
- Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimaraes-Steinicke, C., Bachmann, D., *et al.* (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nat. Commun.* , 10, 1–11.
- Tamburello, N., Cote, I.M. & Dulvy, N.K. (2015). Energy and the Scaling of Animal Space Use. *Am. Nat.* , 186, 196–211.
- Thebault, E. & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* , 329, 853–856.
- Thebault, E. & Loreau, M. (2003). Food-web constraints on biodiversity-ecosystem functioning relationships. *PNAS* , 100, 14949–14954.
- Tilman, D. (1982). *Resource competition and community structure* . Monographs in Population Biology. Princeton University Press, Princeton.
- Tilman, D., Isbell, F. & Cowles, J.M. (2014). Biodiversity and Ecosystem Functioning. *Annu. Rev. Ecol. Evol. Syst.* , 45, 471–493.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997). Plant diversity and ecosystem productivity: Theoretical considerations. *PNAS* , 94, 1857–1861.
- Tucker, M.A., Ord, T.J. & Rogers, T.L. (2014). Evolutionary predictors of mammalian home range size: body mass, diet and the environment: Home range-body mass patterns: are all mammals equal? *Glob. Ecol. Biogeogr.* , 23, 1105–1114.
- Valdovinos, F.S., Hale, K.R.S., Dritz, S., Glaum, P.R., McCann, K.S., Simon, S.M., *et al.* (2022). A bioenergetic framework for aboveground terrestrial food webs. *Trends Ecol. Evol.* , 1–12.
- Wang, S. & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecol. Lett.* , 32, 9–20.

## Figure captions

**Fig. 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. (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.

**Fig. 2:** Plant diversity-productivity relationships for the three food web scenarios considered, i.e. without food web ('none'), with spatially nested food web ('nested'), and with spatially non-nested food web ('non-nested'). 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 not included.

**Fig. 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, i.e. without food web ('none'), with spatially nested food web ('nested'), and with spatially non-nested food web ('non-nested'). 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.

# Figures

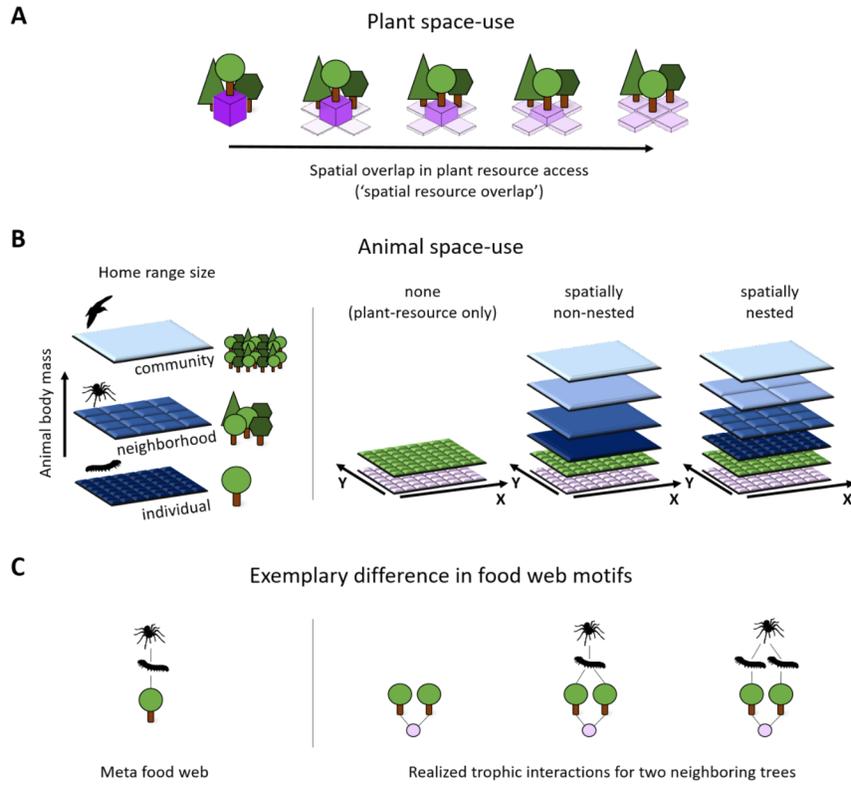


Fig. 1

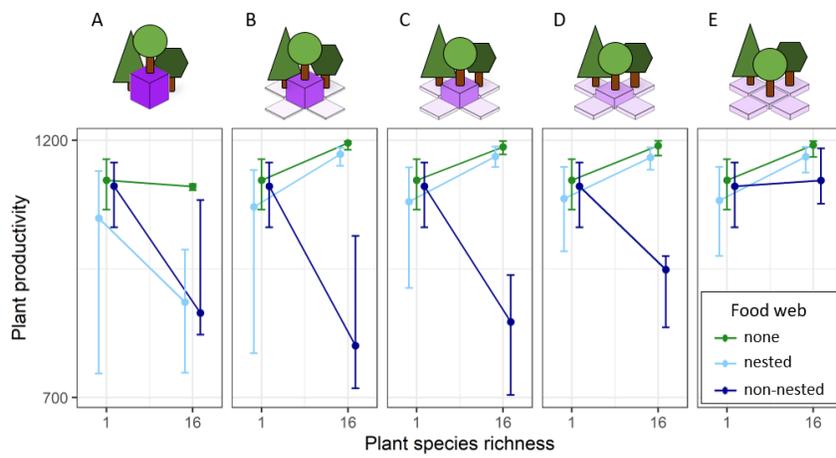


Fig. 2

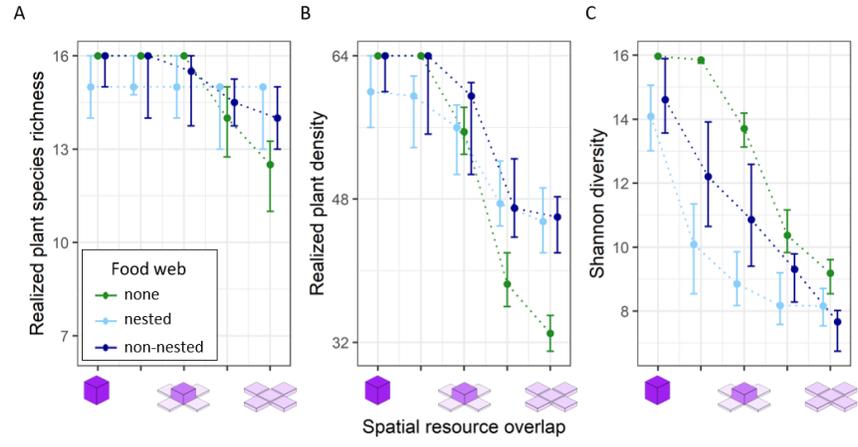


Fig.3