Mechanisms of plant diversity-productivity relationships in complex ecological networks

Dissertation

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Georg Albert

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Reviewers:

Prof. Dr. Ulrich Brose, Friedrich Schiller University Jena

Prof. Dr. Nico Eisenhauer, Leipzig University

Prof. Dr. Eric Allan, University of Bern

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Now I'm a scientific expert; that means I know nothing about absolutely everything.

Arthur C. Clarke - 2001: A Space Odyssey

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Summary

The importance of biodiversity for providing ecosystem functions and services crucial to human well-being is well documented. However, despite an abundance of research on biodiversity-ecosystem functioning (BEF) relationships, their underlying mechanisms are insufficiently understood. While the relationships may suffice to support the argument for conserving biodiversity, the lack of a mechanistic understanding hampers the effectiveness of any future restoration efforts and prevents us from accurately predicting ecosystem responses to a changing world.

To identify the mechanisms driving BEF relationships, I combine theoretical and empirical approaches that address several underexplored aspects of the field. Specifically, I use theoretical models that focus on plant-resource dynamics, multi-trophic processes, and their joint effect on plant community composition and productivity. Additionally, I consider the spatial aspects of resource-based, animal-based, and generalized empirical interactions to adequately represent them. This also allows to scale local processes to responses observed at larger spatial scales.

I demonstrate that, when explicitly excluding animal interactions, positive effects of plant species richness on plant productivity can only emerge if plants have complementary resource requirements. However, to benefit from this complementarity, plants need to have an overlapping resource access in order to utilize otherwise unused resources. Benefitting from resource complementarity therefore comes with the cost of competition, which is larger the more similar resource requirements are. Given that resource interactions are small scale processes, local compositional shift can already suffice to maximize the productivity of single plants and the entire community, leading to strongly positive plant diversity-productivity relationships.

When embedded in complex food webs, positive plant diversity-productivity relationships can be further enhanced. This effect strengthens as animal diversity increases. A higher animal diversity has the additional benefit of fostering plant coexistence. Similarly, more animal species coexist when the plant community is diverse. However, I can show that an increased coexistence does not necessarily lead to positive plant diversity-productivity relationships. Instead, animal foraging movement can induce apparent competition between plants, leading to a reduced productivity of diverse plot communities. However, constraining animal home range sizes based on their body mass massively alters interactions in spatially explicit food webs, shifting competitive interactions to higher trophic levels. This leads to positive effects of plant diversity on productivity that tend to enhance the positive effects from complementary plant-resource interactions.

Positive plant diversity-productivity relationships are one of the most consistent findings of biodiversity experiments. This includes BEF-China, a large subtropical forest biodiversity experiment. By using its annual growth data and explicitly modelling pairwise interactions between neighbouring trees, I show that plants of different species generally compete less than plants of the same species, mirroring my theoretical work. Such local interactions can scale to positive plant diversity-productivity relationships observed at the community level. Additionally, a large share of the empirical interactions are positive, suggesting that competition is not the only mechanism at play. Given my theoretical work, multi-trophic interactions are therefore rendered as a likely candidate for driving positive plant diversity-productivity relationships.

My findings strongly suggest interactive effects between resource- and animal-based mechanisms, emphasizing the complexity and interdependence inherent to the mechanisms behind BEF relationships. However, my results also show clear differences in how either mechanisms assembles plant communities. Linking mechanisms and compositional shifts therefore presents itself as a potential way forward that allows a better understanding of what drives plant diversity-productivity relationships. Proceeding in this direction will not only allow us to focus conservation and restoration efforts to counteract the global biodiversity crisis, but also help to ensure the provisioning of ecosystem service that are crucial to human society.

Zusammenfassung

Die Notwendigkeit von Biodiversität für die Bereitstellung von lebenswichtigen Ökosystemfunktionen und –dienstleistungen ist gut dokumentiert. Trotz umfangreicher Untersuchungen der Zusammenhänge zwischen Biodiversität und Ökosystemfunktionen (BEF – biodiversity-ecosystem functioning), ist das Verständnis der zugrundeliegenden Mechanismen unzureichend. Auch wenn die bekannten Zusammenhänge ausreichen mögen um für den Artenschutz zu argumentieren, steht ein fehlendes mechanistisches Verständnis Restaurierungsbemühungen im Weg. Des Weiteren limitiert es unsere Fähigkeit, das Verhalten von Ökosystemen in einer sich ändernden Welt vorherzusagen.

Um die Mechanismen, die dem Zusammenhang zwischen Biodiversität und Ökosystemfunktionen zugrunde liegen, identifizieren zu können, kombiniere ich theoretische und empirische Ansätze um mehrere untererforschte Bereiche des Felds zu ergründen. Konkret fokussiere ich meine Arbeit auf Nährstoff-Dynamiken, multi-trophische Prozesse, und deren kombinierten Effekt auf die Zusammensetzung und Produktivität von Pflanzengemeinschaften. Des Weiteren ergründe ich räumliche Aspekte von nährstoffbasierten, tierbasierten und generalisierten Interaktionen zwischen Pflanzen, um diese adäquat zu repräsentieren. Dies ermöglicht mir außerdem lokale Prozesse in Muster auf höheren räumlichen Ebenen zu übersetzen.

Mit meiner Arbeit zeige ich, dass, wenn ich explizit Tiere ausschließe, eine erhöhte Artenvielfalt nur dann die Produktivität von Pflanzen erhöht, wenn diese einen komplementären Nährstoffbedarf haben. Um von dieser Komplementarität zu profitieren, müssen Pflanzen allerdings einen räumlich überlappenden Nährstoffzugang haben. Nur so können sie die ansonsten ungenutzten Nährstoffe auch nutzen. Die Vorteile einer komplementären Nährstoffnutzung bergen deshalb auch die Gefahr, konkurrieren zu müssen. Diese ist besonders hoch, wenn Pflanzen ähnliche Nährstoffansprüche haben. Da nährstoffbasierte Interaktionen räumlich lokale Prozesse sind, können bereits kleinräumige Veränderungen in der Artenzusammensetzung ausreichen, um die Pflanzenproduktivität zu erhöhen, was den positiven Zusammenhängen zwischen Pflanzendiversität und –produktivität bestärkt.

In komplexen Nahrungsnetzwerken können solche Zusammenhänge weiter verbessert werden, was positiv mit der Tierartenvielfalt skaliert. Zusätzlich ermöglicht eine erhöhte Tierartenvielfalt die Koexistenz von mehr Pflanzen, was auch umgekehrt der Fall ist. Dass mehr Pflanzen koexistieren hat aber nicht automatisch positive Effekte auf den Zusammenhang zwischen der Artenvielfalt der Pflanzen und deren Produktivität. Stattdessen kann die Mobilität von Tieren zu scheinbaren Konkurrenzeffekten zwischen Pflanzen führen, was sich negativ auf

die Produktivität, insbesondere in artenreichen Pflanzengemeinschaften, auswirken kann. Wenn man jedoch korrekterweise annimmt, dass die Mobilität von kleineren Arten eingeschränkt ist, verändern sich die Interaktionen in räumlichen Nahrungsnetzwerken massiv. Konkret verschieben sich die Konkurrenzbeziehungen auf höhere trophische Ebenen, was den positiven Zusammenhang von Artenvielfalt und Produktivität in Pflanzengemeinschaften mehr verstärkt als es ohne Tiere möglich wäre.

Positive Zusammenhänge zwischen Artenvielfalt und Produktivität in Pflanzengemeinschaften ist eines der konsistentesten Ergebnisse von Biodiversitätsexperimenten. So auch in BEF-China, einem großen, subtropischen Waldbiodiversitäts-Experiment. Unter der Verwendung von jährlichen Wachstumsdaten und der konkreten Modellierung von paarweisen Interaktion zwischen Nachbarbäumen kann ich zeigen, dass Pflanzen verschiedener Arten weniger konkurrieren als Pflanzen derselben Art, was auch meine theoretischen Ergebnisse wiederspiegelt. Solche lokalen Interaktionen skalieren zu den positiven Zusammenhängen zwischen Artenvielfalt und Produktivität die häufig in Pflanzengemeinschaften beobachtet werden. Viele der empirisch erfassten Interaktion sind positiv, was suggeriert, dass nicht nur Konkurrenzbeziehungen eine Rolle spielen. In Anbetracht meiner theoretischen Arbeit kann also vermutet werden, dass multi-trophische Interaktionen mit Tieren eine nicht zu verachtende Rolle bei dem positiven Zusammenhängen zwischen Artenvielfalt und Produktivität spielen.

Meine Ergebnisse zeigen ein deutliches Zusammenspiel von nährstoff- und tierbasierten Mechanismen. Die Komplexität und gegenseitige Abhängigkeit der Mechanismen, die hinter den Zusammenhänge zwischen Biodiversität und Ökosystemfunktionen stecken, wird daher deutlich. Nichtsdestotrotz gibt es klare Unterschiede in den Artenzusammensatzungen, die mit den jeweiligen Mechanismen assoziiert sind, was es ermöglicht kann, deren Effekte voneinander zu trennen. Wenn wir diesen Weg weiter verfolgen, wäre es uns demnach möglich, nicht nur dem globalen Artensterben entgegen zu wirken, sondern auch die Ökosystemsdienstleistungen zu erhalten, auf denen unsere Gesellschaft fußt.

General introduction

The importance of ecosystem functions

Against all odds, life was able to establish on Earth, evolving from the first simple organisms to a diversity of ecosystems containing a total estimate of 8.7 million species (Mora *et al.* 2011; but see Locey & Lennon 2016 who estimated 100 trillion microbial species alone). While the establishment of life on Earth is an intricate process that is still not fully resolved, one of its crucial steps is the transition from molecular building blocks to the first living organisms (Walker *et al.* 2017). Such organisms likely had to rely on chemosynthesis (i.e. using electrons from chemical reactions for obtaining energy) for primary production (Martin *et al.* 2018). Today, primary production is dominated by photosynthesis (i.e. using photons from light sources such as the sun for obtaining energy) but remains one of the most important ecosystem processes, not only for humanity but all other organisms that rely on biotic resources for food or other ecosystem functions (e.g. shelter, raw materials). With an estimated 450 gigatons in biomass, plants are the species kingdom contributing the largest share of around 82% to the total biomass of life on earth (measured in mass of carbon; Bar-On *et al.* 2018). It is thus not surprising that in the recent years, primary production became an even more relevant ecosystem function that can counteract climate change through carbon sequestration. It is therefore hard to deny the fundamental importance of conserving and facilitating plant primary production, rendering research on the mechanisms driving it an important endeavour.

In addition to plants, animals provide further ecosystem functions such as decomposition (Ebeling *et al.* 2014), or herbivore control (Barnes *et al.* 2020). However, given that primary production provides essential resources to animals, none of the animal-based ecosystem functions are entirely independent from plants. Similarly, plants are not independent of animal functions. For example, a better herbivore control will likely have positive effects on functions provided by primary producers as it elevates herbivory pressure (Barnes *et al.* 2020). Likewise, increased decomposition rates will have positive feedbacks on primary producers (Griffiths *et al.* 2021). The evident interdependence among animal- and plant-based ecosystem functions is rooted in the complex interactions between organisms (Barnes *et al.* 2018) and between organisms and their abiotic environments (e.g. Griffiths *et al.* 2021). Unravelling the mechanisms driving any ecosystem function therefore requires a deeper understanding of the co-occurring interactions that shape the ecosystem.

Positive effects of biodiversity

Ecosystems are changing globally as biodiversity is lost and community compositions are altered (Pereira *et al.* 2012). While ecosystems are naturally dynamic and change their compositions on their own (e.g. in response to changing seasons), the extreme changes observed globally are largely due to human impact, for example through land-use change, overexploitation, the introduction of exotic species, pollution, climate change, and human population as well as economic growth (IPBES 2019). While man-made biodiversity change may be ethically questionable at best, its effect on the provision of ecosystem functions that are crucial for human well-being and ultimately human survival is clearly the more pressing issue. Especially when considering the multitude of ecosystem functions provided, the value of biodiversity becomes apparent. Many biodiversity-ecosystem functioning (BEF) experiments could show that plant biodiversity is a major factor determining plant primary productivity (Cardinale *et al.* 2007) and its stability over time (Schnabel *et al.* 2021), as well as predation and herbivory rates (Barnes *et al.* 2020), decomposition rates (Ebeling *et al.* 2014), etc. While the positive effects usually saturate as biodiversity increases, suggesting some levels of redundancy of biodiversity, the saturation slows down as more ecosystem functions are considered (Hector & Bagchi 2007). In addition, redundancy is insurance, i.e. if more species are fulfilling the same function in an ecosystem, more species can be lost before ecosystem functioning is eroded (Loreau 2004). Conserving biodiversity is therefore, unsurprisingly, generally a great idea.

Biodiversity is a collective term describing different aspects of the diversity of life, most often of species but also genes, interactions, traits, functions, etc. In line with a large body of research investigating the effects of biodiversity on ecosystem functions, the original research presented in this thesis uses species richness (i.e. the number of different species) as the main measure of biodiversity for plants and animals respectively. However, I distinguish between biodiversity treatments and realized biodiversity. While the first captures the initial number of species, the latter is accounting for species interactions and therefore takes assembly processes in account. I additionally include Shannon diversity (sensu Jost 2006) and plant densities in some of my analyses to account for effects of plant abundances, allowing me to investigate more subtle shifts in community compositions. By combining different measures of biodiversity I can draw a careful picture of how biodiversity mechanisms structure communities and drive ecosystem functioning.

From interacting organisms to complex ecological networks

The positive effect of biodiversity for providing ecosystem functions is rooted in interactions. This is not surprising given that interactions between organisms such as animals and plants are an essential part of ecology. Two organisms interact if the presence of one influences the other. Usually, positive and negative interactions are related to a gain or loss in energy or biomass (i.e. trophic interactions), but recent studies highlight the importance of also considering non-trophic interactions such as predator-avoidance behaviour and competition for space, as they can severely alter the dynamics, composition, and functions of an ecosystem (Donohue *et al.* 2017). In addition, not all interactions are direct but instead mediated by other organisms or abiotic factors such as light or resource availability. For example, two organisms can compete for a resource and thereby indirectly interact via that resource (exploitative competition; Holt 1977). However, competition can also be consumer mediated (apparent competition; Holt 1977), where a shared consumer benefits from the presence of either competitor, which in turn can have negative feedbacks on the competitors. The outcome of apparent competition is not always trivial (Holt & Bonsall 2017) and may depend on prey quality in different patches (Hoogendoorn & Heimpel 2002). Moreover, the dynamics of trophic interactions also depends on interactions of other species within the food web (Woodward *et al.* 2008). In general, no interaction can be entirely understood in isolation as it is usually modified by other interactions.

To capture the complexity inherent to these interactions, ecologists adopted networks as a useful and flexible tool. They allow a summary of the interactions between the ecological entities of interest, which can be individuals but often encompass populations of different species represented as network nodes, with network edges connecting the nodes representing their interactions (e.g. networks in Fig.1A). Food webs emerged as the most well-known ecological networks that got considerable attention since the early days of ecology (Elton 1927). They link network nodes based on their feeding interactions, with feeding links describing energy and matter transitions from a resource to a consumer. Hence, food webs are directional, with primary producers at the base and consumer species occupying higher trophic levels, and are an integral part of larger biogeochemical cycles (Welti *et al.* 2017).

Despite the usefulness of ecological networks like food webs, a single network usually does not suffice to address the co-occurrence of multiple types of interactions or the temporal and spatial variation within networks. These shortcomings can be addressed in multi-layer network approaches, where networks are organized in layers that are interconnected by interlayer network edges (Pilosof *et al.* 2017). For example, food webs in a patchy landscape (i.e. each food web is a layer) may interact via dispersal (i.e. interlayer edge) which can drastically alter the dynamics of the system (e.g. depending on landscape structure; Ryser *et al.* 2021). Hence, multi-layer networks can help to understand how processes acting at one spatial resolution scale to and influence processes at other spatial resolutions. Similarly, multi-layer networks allow the investigation of scaling networks in time and between levels of organization (Pilosof *et al.* 2017), thus helping to solve some of the most difficult problems of current ecology (e.g. Chave 2013).

An alternative to dealing with the multitude of co-occurring interactions is to summarize them as net interactions. Such net interactions are often more phenomenological than the previously described and more strictly defined direct and indirect interactions. Especially when investigating the interaction between plants, net interactions are a common way to quantify them. For example, recent reviews highlight the prevalence of competitive (i.e. negative) over facilitative (i.e. positive) interactions (Adler *et al.* 2018; Yang *et al.* 2022) as average net interactions are negative. Since competition is an intricate process which is usually comprised of several trophic interactions (i.e. exploitative and apparent competition, Holt 1977), and facilitative interactions act in parallel, net interactions will be a combination of all those processes. A mechanistic interpretation of net interactions is therefore limited. However, estimating net interactions is far more feasible than separately describing each relevant process, and is therefore often the tool of choice in empirical studies.

Whether captured in food webs or net interaction networks, ecological interactions and their interaction networks can be used to investigate the drivers behind ecosystem functions. By differentiating between stocks (i.e. biomass densities of nodes) and fluxes (i.e. energy and matter transitions between nodes), different ecosystem functions can be quantified and related to food web properties (Thompson *et al.* 2012; Barnes *et al.* 2018). For example, fluxes from the abiotic environment to primary producers capture the primary productivity of an ecosystem as the turnover of primary producer biomass densities, thereby describing a concrete process. In contrast, stocks of primary producers are the cumulative result of several processes, including primary production, feeding pressure from herbivores, and primary producer's energy requirements (i.e. metabolism; Gauzens *et al.* 2019). While herbivory and metabolism can also have indirect feedbacks on primary production, primary production and primary producer stocks are not necessarily related (Schmid *et al.* 2009). Viewing ecosystem functions such as primary production in their food web context allows their clear definition, and thus can improve predicting their response to changes in the biotic environment, for example due a biodiversity loss. Further, using energy fluxes in BEF research can help linking ecosystem functions measured at one trophic levels with interactions spanning the entire food web, providing an ideal framework to investigate multiple drivers of BEF relationships.

Biodiversity mechanisms

Decades of research have produced mounting evidence for the importance of biodiversity across trophic levels for providing and maintaining ecosystem functions. While one line of research emphasizes the positive effects of biodiversity on a multitude of ecosystem functions (Tilman *et al.* 2014), another one reports human-induced global diversity change and loss (Ceballos *et al.* 2015). Together, they seem to draw a dire picture. However, our mechanistic understanding of how biodiversity affects ecosystem functions remains surprisingly limited (Barry *et al.* 2019; Wu *et al.* 2022). This constrains our ability to accurately scale BEF relationships measured locally and regionally to global patterns of diversity change (Gonzalez *et al.* 2020). Hence, predicting global consequences of diversity change is limited, and a sufficient guidance of conservation and restoration efforts is hampered.

While concrete processes driving biodiversity-ecosystem functioning pattern are hard to identify (Barry *et al.* 2019), two general types of mechanisms can be distinguished: complementarity and selection (Loreau 2000). Both are rooted in competition but capture different responses of plants to growing in a diverse community (i.e. a species mixture). Complementarity mechanisms collectively describe all mechanisms that emphasize the complementarity of species, i.e. making organisms of different species differ in their niches and therefore compete less than organisms of the same species with similar niches. Selection mechanisms are based on some species dominating the ecosystem functioning of a community due to having a competitive advantage over others. Complementarity and selection mechanisms can both lead to positive diversity effects, but while complementarity mechanisms lead to positive effects due to the ecosystem functions provided by a majority if not all species, selection mechanisms only require a few or single species. Interestingly, both types of mechanisms benefit from higher levels of diversity through sampling effects, i.e. if more species are available, there are higher chances for having complementary or dominant species. With competition at the heart of complementarity and selection mechanisms, they both deal with the effects of species interactions on species composition and coexistence mechanisms, and thus align with community assembly processes.

By utilizing a framework for disentangling patterns of complementarity and selection (Loreau & Hector 2001), many biodiversity-ecosystem functioning experiments could show that positive diversity effects are largely due to complementarity mechanisms (Hooper *et al.* 2005), whereas selection mechanisms tend to have weakly negative effects (e.g. Huang *et al.* 2018). Even though several processes have been proposed to create complementarity among species, including resource partitioning, multi-trophic interactions, and facilitative processes, all of them are difficult to quantitatively relate to biodiversity-ecosystem functioning relationships (Barry *et al.* 2019). This can be due to several reasons. First, multiple mechanisms acting in parallel and creating similar patterns of community composition can make a clear differentiation difficult. Second, some of the proposed mechanisms lack a clear, process-based definition and thus cannot be tested empirically. For example, differences in resource requirements between species only matter if the species compete for resources, which happens at a local scale that is rarely investigated (but see e.g. Fichtner *et al.* 2018). Third, to understand some mechanisms, a good understanding of the ecological context is required. For example, facilitative processes could be based on a few species which may not directly contribute to an increased ecosystem functioning, but support other species in doing so. To disentangle the contribution of different complementarity mechanisms to the positive biodiversity-ecosystem functioning relationships observed in natural communities, these problems need to be addressed in a systematic way, putting interactions at the centre of the research.

While my thesis will not be able to address this problem in its entirety, it can contribute to resolving the issue as it aims at advancing our mechanistic understanding of potential complementarity mechanisms by explicitly focusing on species interactions. I put a special emphasis on the integration of several complementarity mechanisms. Specifically, I focus on the joint effects of resource complementarity between plants and multi-trophic interactions in complex food webs. Additionally, I model mechanisms at appropriate spatial scales to accurately describe them and to connect local interactions between organisms and biodiversity-ecosystem functioning relationships observed at the community level.

Study outline

By focusing on the mechanisms behind the largely positive effects of plant diversity on plant productivity, I advance our ability to link patterns of biodiversity effects and biodiversity change while zooming in on one of the most prominent and supposedly best understood biodiversity-ecosystem functioning relationship. In doing so, I set out to answer the question: How do complex ecological interactions affect the often positive effects of plant biodiversity on plant productivity, and how can we disentangle the associated mechanisms? Hence, I put a special emphasis on the investigation and generalization of multi-trophic effects, expanding on the traditional view on biodiversity-ecosystem functioning relationships that puts plant communities at its core.

In the following three chapters, I take different perspectives on the mechanisms behind plant diversity-productivity relationships (Fig.1), as I investigate effects of (1) fundamental differences in plant resource requirements and multi-trophic diversity (chapter 1, Fig.1A), (2) local plant resource interactions and animal foraging movement (chapter 2, Fig.1B), and (3) generalized pairwise interactions in the neighbourhood of plant individuals (chapter 3, Fig.1C). The combination of theoretical (chapters 1-3) and empirical approaches (chapter 3) allows me to infer on the mechanisms underlying plant diversity-productivity relationships that are reported from field and experimental studies in natural ecosystems. Investigating processes across spatial scales, ranging from local (chapter 2 and 3) to the ecosystem level (chapter 1-3), additionally enables me to advance our understanding of the spatial scales at which different processes affect plant diversity-productivity relationships, contributing to a more complete picture of the drivers behind the patterns observed in BEF research.

In chapter 1 (Fig.1A), I integrate plant-resource models with dynamic food web simulations to investigate how differences in plant's resource requirements, measured as resource-use dissimilarity, and multi-trophic animal diversity jointly drive plant diversity-productivity relationships. I show that resource-use dissimilarity is a good approximation for plant's resource-use complementarity, which increases the positive effects of plant diversity on productivity. Similarly, introducing multi-trophic interactions and increasing animal diversity leads to more positive diversity-productivity relationships. The relationships are particularly strong when plant and animal-based mechanisms act together, suggesting synergistic effects that are reflected in high levels of species coexistence and associated complementarity effects. Resource and animal-based effects are largely due to altering the productivity of low diversity plant communities, whereas the most diverse plant communities show little response to changes in resources-use dissimilarity and animal diversity. While resource-use dissimilarity and animal diversity seem to align in their effects on diversity-productivity relationships through species complementarity, I find clear differences in how they affect plant community composition. In particular, resource-use dissimilarity can favour species that access more resources and are thereby more productive, whereas an increasing animal diversity tends to shift the community towards supporting less productive species with low resistance to herbivore pressure, allowing them to persist in diverse communities. These contrasting patterns highlight how different mechanisms, while creating similar patterns of complementarity and plant diversity-productivity relationships, may be based on fundamentally different assembly processes.

In chapter 2 (Fig.1B), I take a closer look at the resource- and animal-based processes behind plant diversity-productivity relationships by modelling them at their appropriate spatial scale. Specifically, I simulate growth of plant individuals assembled in spatially explicit communities of different species diversity and embedded in complex food webs. By spatially constraining resource-based interactions to neighbouring plants, I demonstrate that such local interactions suffice to create positive plant diversity-productivity relationships at the ecosystem scale. When excluding such local interactions by removing the spatial overlap in resource-use of neighbouring plants ('spatial resource overlap'), exploitative competition between plants is nullified, but so are the potential effects of resource complementarity. As a result, plant diversity-productivity relationships are neutral, and even negative in the presence of animals. The effects of animals without a spatial resource overlap between plants do not differ qualitatively between the two types of food web models I consider. However, when spatially constraining animal home range sizes based on their body masses, creating spatially nested food webs, a spatial resource overlap between plants leads to the most positive effects of plant diversity on productivity. When assuming well-mixed animal populations, creating spatially non-nested food webs, diversity-productivity relationships are negative in the majority of cases. The striking difference between spatially nested and non-nested food webs finds an explanation in the differences of how animals induce apparent competition between plant individuals and animal populations. In particular, spatially nested food webs induce less apparent competition between plants than spatially non-nested food webs, as fewer plants are integrated in the constrained home range sizes of herbivores. Additionally, stronger apparent competition between herbivores reduces the top-down control on plants and stabilizes the dynamics of the simulated ecosystems. This is mirrored in the highest levels of maintained plant diversity in spatially nested food webs. Together, the synergistic effects of resource- and animal-based mechanisms for plant diversity and its relation with productivity confirms the findings of chapter 1. However, chapter 2 additionally highlights the spatial specificities of both mechanisms, and the importance to consider them at an appropriate spatial scale.

In chapter 3 (Fig.1C), I move away from process-based simulations of the potential mechanisms behind plant diversity-productivity relationships, and dive into the analysis of phenomenological tree interaction networks based on local compositions in a large tree diversity experiment in subtropical China, BEF-China. Specifically, I fit tree growth models that include species-specific pairwise interactions between neighbouring trees whose strength scale with the body mass of the interacting trees. Surprisingly, more than 50% of all net interactions between species are positive, contrasting the widespread notion of the prevalence of competitive interactions between plants. I demonstrate the non-randomness of the species interaction network by comparing predicted community mean net interactions and productivity (i.e. mean annual tree growth) of the empirical interaction network with networks with reshuffled interaction coefficients. When reshuffling interaction coefficients without constraints, mean net interactions and hence productivity show relationships with plant diversity ranging from positive to negative but are on average neutral. The positive relationships from the empirical interaction networks can be reproduced, however, by constraining the reshuffling to intra- and interspecific interactions respectively. Hence, differences between intra- and interspecific interactions give rise to positive diversity-productivity relationships. Specifically, more positive inter- than intraspecific interactions are required for positive relationships to emerge, aligning with classic theoretical predictions of species coexistence. This presents evidence for the prevalence of diversity maintenance mechanisms, most prominently competitive reductions due to species complementarity, being a fundamental driver of BEF relationships.

Overall, this thesis investigates how interactions within and across trophic levels shape plant communities and their diversity-productivity relationships. Instead of focusing on single interactions or simplified networks, I embrace the complexity inherent to naturally occurring ecological networks and investigate their effects as a whole. By analysing theoretical and empirical biodiversity experiments, I can compare the potential processes and their phenomenological outcomes while taking a fresh perspective on BEF research that explicitly puts species interactions at its core. Together, my findings highlight the importance of multi-trophic processes in driving the positive effects of plant diversity on productivity, contributing to the ongoing shift away from pattern recognition to a more mechanistic understanding of BEF relationships.

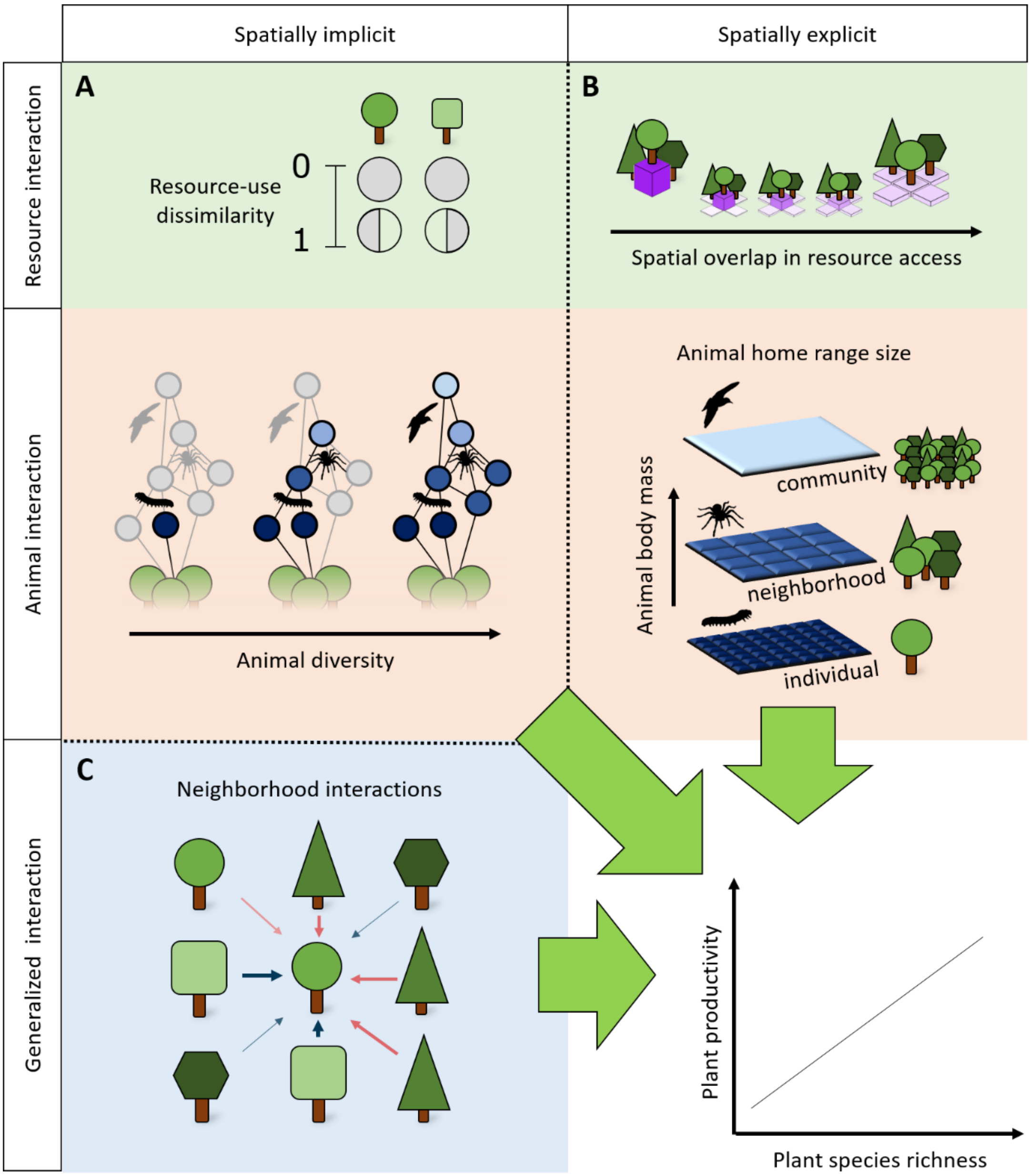

Fig.1: Overview of the research chapters in this thesis, taking different perspectives on plant diversity-productivity relationships. (A) In chapter 1, resource- and animal-based interactions are modelled as resource-use dissimilarity and by manipulating the multi-trophic diversity of the animal community respectively. (B) In chapter 2, resource- and animal-based interactions are modelled spatially explicit. Resource-based interactions between neighbouring plants are based on spatial overlaps in resource-access. For animal-based interactions, different scenarios of animal home ranges are considered. (C) In chapter 3, generalized interactions between neighbouring trees are fitted in an empirical model.

Research chapters

Overview

Chapter 1: The hidden role of mulit-trophic interactions in driving diversity-productivity relationships

Bibliographic information: 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

Short summary: In the first chapter, I investigate the interactive effects between resource-use dissimilarity and multi-trophic interactions in a simulated biodiversity experiment. I show the interactive effects of both mechanisms, as well as their ability to create complementarity plant communities that yield positive diversity-productivity relationships. I further show differences in the selection mechanisms associated with either mechanism.

Chapter 2: Animal movement and plant space-use drive plant diversity-productivity relationships

Bibliographic information: Albert, G., Gauzens, B., Ryser, R., Thébault, E., Wang, S. & Brose, U. (in prep.) Animal movement and plant space-use drive plant diversity-productivity relationships.

Short summary: In my second chapter, I again investigate resource- and animal-based mechanisms, but consider their underlying spatial processes. I can show that local resource-interactions between neighbouring plants are necessary for positive diversity-productivity relationships to emerge. Additionally, my findings display strong effect of different animal movement models, indicating its potential to drive diversity-productivity relationships.

Chapter 3: Pairwise interaction networks link species coexistence with positive biodiversity-productivity relationships in tree communities

Bibliographic information: Yu, W., Albert, G., Rosenbaum, B., Schnabel, S., Bruelheide, H., Connolly, J., Härdtle, W., von Oheimb, G., Rüger, N., Trogisch, S. & Brose, U. (in prep.) Pairwise interaction networks link species coexistence with positive biodiversity-productivity relationships in tree communities.

Short summary: In my final chapter, I investigate empirical interactions between neighboring trees from a large subtropical BEF experiment. I find clear differences between inter- and intraspecific interactions as well as a large proportion of positive interactions, indicating the prevalence of complementarity mechanisms beyond resource-interactions. Scaling the local interactions to community level effects allows me to recreate the often confirmed positive plant diversity-productivity relationships, highlighting the importance of local processes.

Chapter 1: The hidden role of mulit-trophic interactions in driving diversity-productivity relationships

Manuscript No. (sequence number in the dissertation):

1

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Authors:

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■ First author, ☐ Co-first author, ☐ Corresponding author, ☐ Co-author.

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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

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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

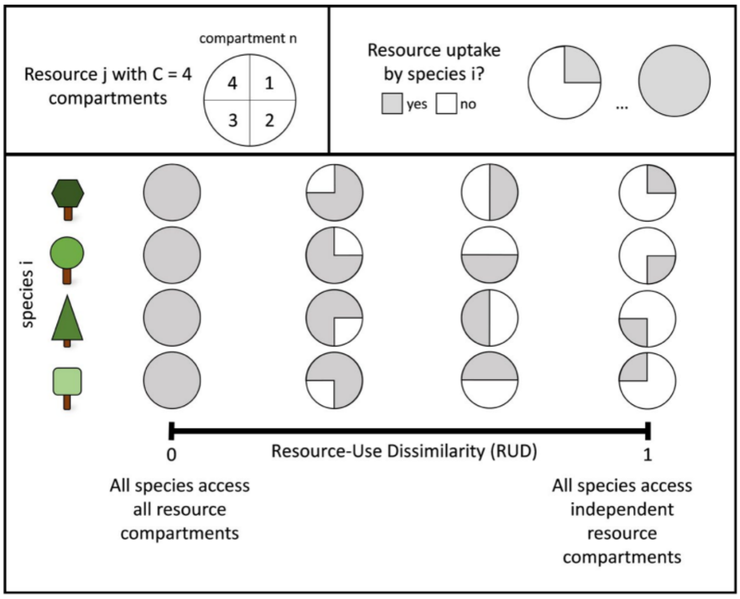

FIGURE 1 Conceptual figure of a gradient of resource-use dissimilarity (RUD) as a measure of resource-use complementarity, exemplified for a primary producer community with four tree species in the species-pool. We assume that each resource has as many compartments C as there are species in the species-pool. 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

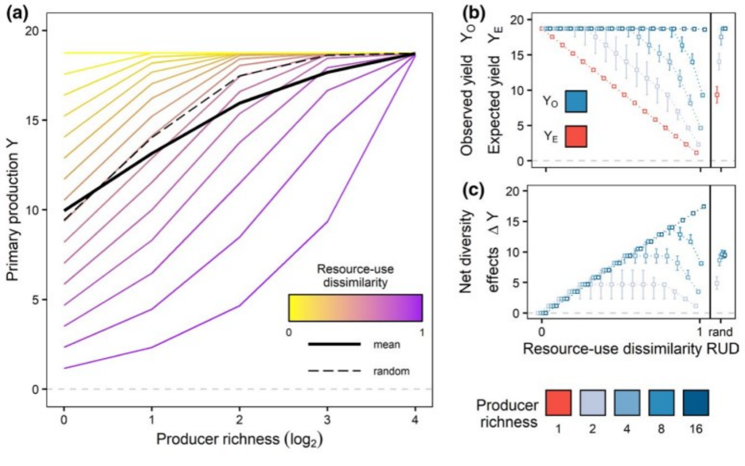

FIGURE 2 Diversity effects and resource-use dissimilarity (RUD) without multi-trophic interactions. (a) Mean diversity–productivity relationships at different levels of the RUD gradient (coloured lines), their overall average (thick black line), and the random RUD scenario (black dashed line). (b) Observed 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)

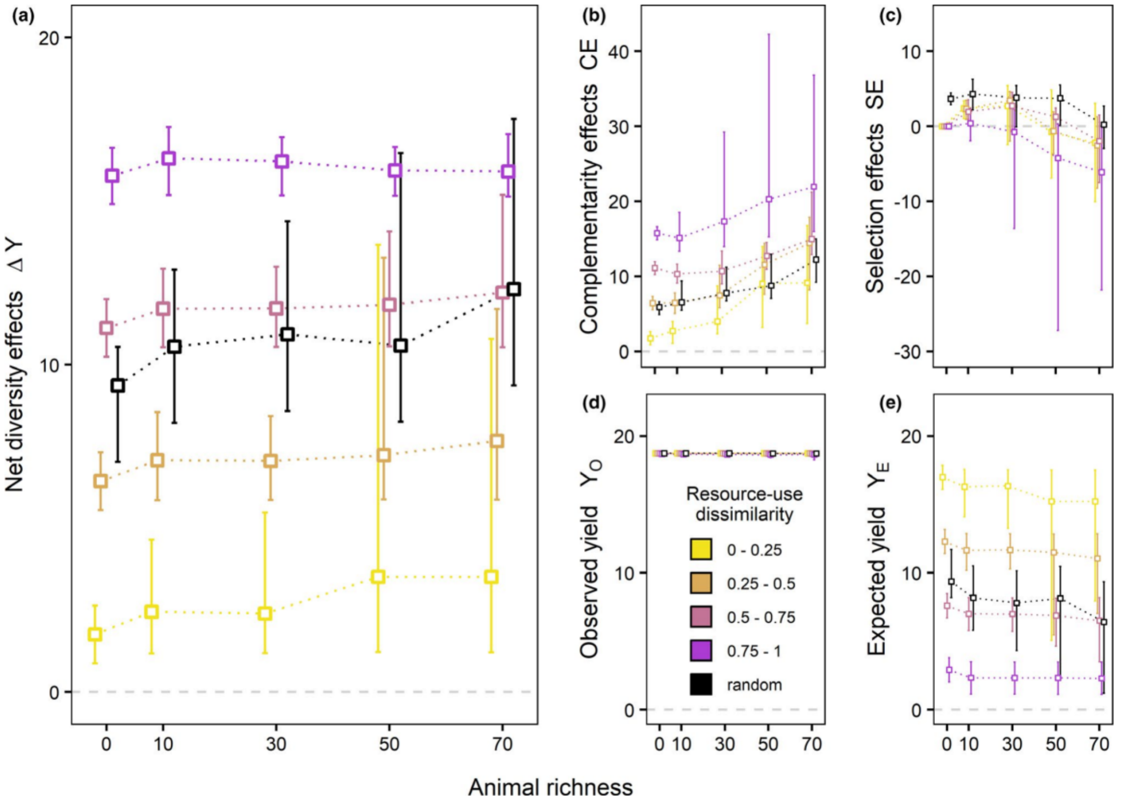

FIGURE 3 Effects of animal richness (i.e. multi-trophic animal richness of 0, 10, 30, 50 and 70) on (a) net diversity effects $\Delta Y = Y_O - Y_E = \mathrm{CE} + \mathrm{SE}$, (b) complementarity effects CE and (c) selection effects SE, as well as (d) observed yield Y_O and (e) expected yield Y_E. 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

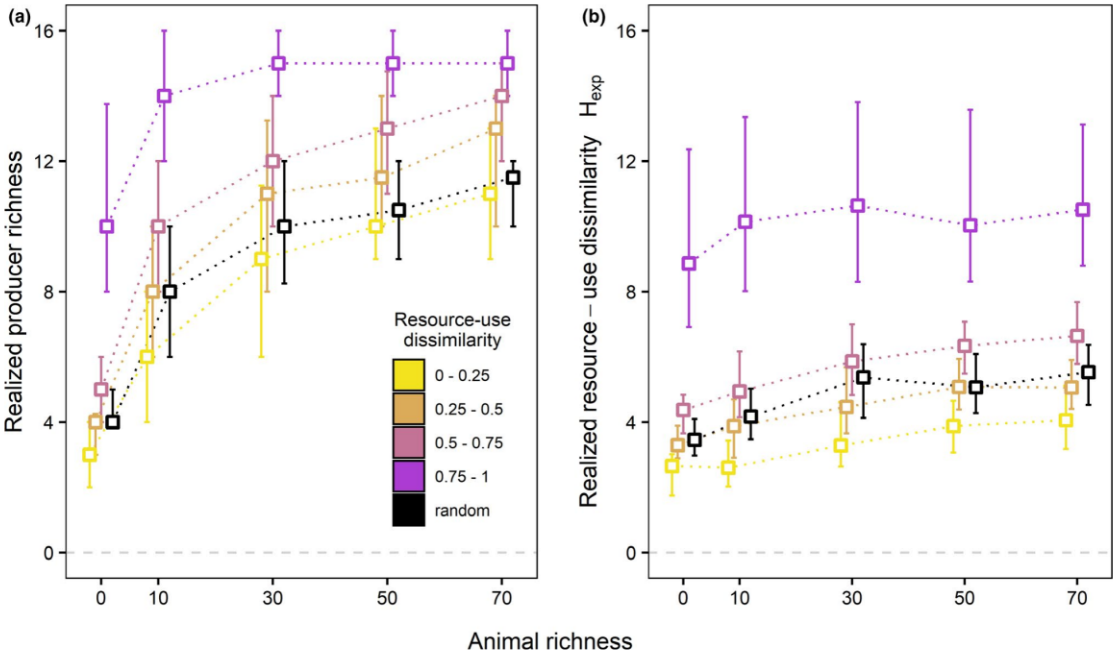

FIGURE 4 Effects of animal richness (i.e. multi-trophic animal richness of 0, 10, 30, 50 and 70) on (a) realised species richness and (b) realised resource-use dissimilarity H_{exp} of the producer community. Summarised at primary producer richness of 16 for different ranges of the resource-use dissimilarity (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 intraguild 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.

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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

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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

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Georg Albert, Benoit Gauzens, Remo Ryser, Elisa Thébault, Shaopeng Wang, Ulrich Brose

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Author	Conceptual	Data analysis	Experimental	Writing the manuscript
Georg Albert	50 %	70 %	100 %	65 %
Ulrich Brose	20 %	10 %	0 %	20 %
Shaopeng Wang	20 %	5 %	0 %	5 %
Others	10 %	15 %	0 %	10 %
Total:	100%	100%	100%	100%

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

Georg Albert[1,2], Benoit Gauzens[1,2], Remo Ryser[1,2], Elisa Thébault[3], Shaopeng Wang[4], Ulrich Brose[1,2]

1 EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany.

2 Institute of Biodiversity, Friedrich Schiller University Jena, 07743 Jena, Germany.

3 Institute of Ecology and Environmental Science (iEES), CNRS, Sorbonne University, 75005 Paris, 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, 100871 Beijing, China.

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, allometrically scaling animal home range sizes spatially limits herbivore effects and allows top predators to integrate 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 to local biodiversity and productivity patterns.

Key words: foraging range, BEF, multi-trophic, coexistence, primary production

Introduction

To quantify the impact of biodiversity loss on human well-being, ecological research has measured plant 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), which calls 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 and 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, the potential interactions between animal- and resource-based mechanisms, as well as their different spatial scales, raise the question: How do they interact and scale to 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 scale (Cardinale *et al.* 2007). Only recently there is a shift towards investigating the implications of interactions between plant individuals at a much smaller scale that comprises only the immediate neighbours (hereafter: neighbourhood scale; Fig.1; Sapijanskas *et al.* 2013; Fichtner *et al.* 2018). 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 a 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 the relationship between plant diversity and productivity.

While plants can interact through a local spatial resource overlap, animal movement spatially 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 and apparent competition emerging among herbivores (Fig. 1C). This spatial structure of natural food webs opposes the wide-spread 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 calls 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 to 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) animal-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 integrated both in a simulated biodiversity experiment. It is based on a well-established model of food web dynamics (Schneider *et al.* 2016; Albert *et al.* 2022) but explicitly includes the spatial position of plant individuals and associated local resource pools as well as animal populations with varying home range sizes. To assess the effects of local resource-competition between neighbouring plants, we manipulate the focus of plants on using resources from their local resource pools in relation to their neighbouring resource pools. This allows us to 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). 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.

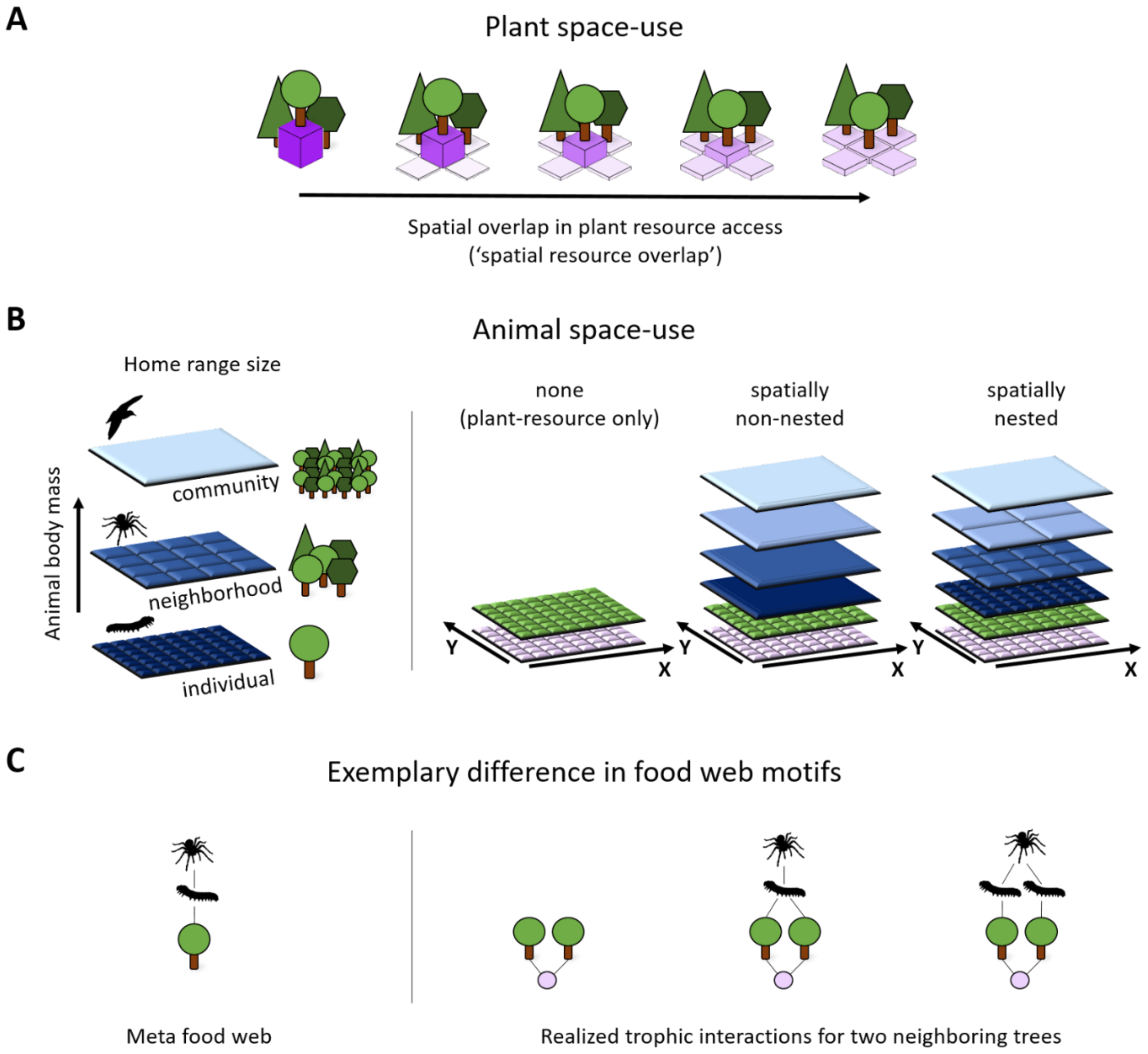

Fig. 1: Overview of the considered spatial processes of plant and animal interactions within a plant community. (A) Differences in plant space-use are captured by a gradient of spatial overlap in plant resource access ('spatial resource overlap'), ranging from no overlap, where each plant is limited to its own local resource-pool and exploitative competition is impossible, to an even overlap with neighbouring plants that maximizes 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.

Defining a meta food web topology

To create food web topologies, we use allometrically scaled carnivorous interactions where larger predators consume smaller prey species (following Schneider *et al.* 2016), which is common to terrestrial aboveground ecosystems (Brose *et al.* 2019). However, herbivorous interactions do not follow this pattern. Thus we define herbivorous interactions to mimic network properties of real world plant-herbivore interactions (following Thébault & Fontaine 2010).

We define carnivorous interactions based on allometric relationships between animals. Hence, we assign each animal species i with a body mass m_i, which is defined as $m_i = 10^{a_i}$ with a_i being randomly drawn from a uniform distribution on [0, 8]. As a result, body masses of animals span eight orders of magnitude. Based on their body masses, we define feeding likelihoods L_{ij} between animals as

$$L_{ij} = \left(\frac{m_i}{m_j R_{opt}} e^{1-\frac{m_i}{m_j R_{opt}}}\right)^{\gamma} \tag{1}$$

with R_{opt} being the optimal predator-prey body mass ratio set to 100, and γ describing the width of a Ricker curve that captures a species niche breadth, which we set to 2 (Schneider *et al.* 2016). Weak feeding likelihoods where $L_{ij} < 0.01$ are set to zero.

A common drawback when using synthetic food web topologies is that plant-herbivore interactions are rarely representative of terrestrial above-ground ecosystems (Valdovinos *et al.* 2022). Given the strong focus on such ecosystems in BEF research, we aim at solving this issue by mimicking empirical network properties. Thus, we used an algorithm introduced by Thébault & Fontaine (2010) that utilizes a stochastic model to generate networks of varying levels of nestedness and modularity depending on two parameters, p_{nest} and p_{mod}. We set them to 0.2 and 0.7 respectively to mimic the low nestedness and high modularity known from empirical terrestrial above-ground plant-herbivore interactions. With this algorithm, we first assign each plant and herbivore species to one among four feeding modules, leading to four modules of equal sizes in a modular network. Each species is also assigned a relative weight based on values drawn from a power law distribution with an exponent of -2. This weight defines the probability of interaction of a species in a nested bi-partite network, leading to a large number of weakly connected species nested within a few highly connected species (Santamaría & Rodríguez-Gironés 2007). Second, starting with a network without any interactions, the algorithm adds links iteratively until we reach a target connectance of the network, which we set to 0.2 in accordance with empirical values for similarly sized networks (Thébault & Fontaine 2010). To add new links we first select a target plant. The probability of selecting a plant based on its weight is defined by a Bernoulli trial with parameter p_{nest}, otherwise the target plant is randomly selected. The set of potential herbivores is either herbivores from the same module as the selected plant species (with a probability p_{mod}), or all herbivores (with a probability $1-p_{mod}$). Then, a link is added between the selected plant species and one herbivore species randomly selected from the set of potential herbivore species, either according to the relative herbivore weights (with a probability p_{nest}) or from a uniform distribution (with a probability 1-p_{nest}). We discard plant-herbivore networks in cases where the algorithm yields unconnected species. A more in-depth description of the algorithm can be found in Thébault & Fontaine (2010) and in the code provided at https://github.com/GeorgAlbert/SpatialFoodWebBEF.

Our food webs initially have 16 plant and 60 animal species. To integrate the plant-herbivore interactions with the allometrically scaled carnivorous interactions, we randomly select 32 animal species to be herbivorous. Other than in allometrically scaled food webs (e.g. Williams & Martinez 2000; Schneider *et al.* 2016), herbivorous species are thus not constrained to specific prey body mass ranges. From the 32 herbivorous species, we select half of them to be strict herbivores, setting all carnivorous feeding interactions to zero irrespective of their feeding likelihood L_{ij}. Those strict herbivores also comprise any basal animal species that otherwise lack feeding interactions, assuring that there is no isolated species. Herbivorous feeding likelihoods L_{ij} are set to their maximum value of one.

Represent food webs in space

The spatially-explicit representation of meta food webs is done by (1) defining local patches with associated plant individuals and resource pools, (2) capturing the interactions between neighbouring plants by manipulating the access to neighbouring resource pools ('spatial resource overlap', Fig. 1A), and (3) defining animal space-use by either assuming unconstrained movement (i.e. spatially non-nested food webs), or allometrically scaled home range sizes (i.e. spatially nested food webs; Fig. 1B).

To explicitly model plant populations in space, we define plant communities that consist of 64 evenly spaced plant individuals arranged on an 8x8 grid of local patches. Each patch has its own local resource pool. Other than animal populations that can be characterized by an average adult body mass, plants grow throughout their entire life span, thus changing their body mass continuously. Hence the body mass of plant species i, m_i, in patch k is equal to its biomass density, B_{ik}. This leads to plant growth rates, r_{ik}, and metabolic demands, x_{ik}, that change dynamically (see below).

Plants interact with each other as they compete for resources with their neighbouring plants. To investigate the importance of this interaction, we manipulated the strength of it by using a gradient of spatial resource overlap (Fig. 1A). Specifically, we scale the relative effort a plant of species i at patch k puts in taking up resources from its accessible resource pools k', $n_{(ik)(k')}$. We distinguish between the relative effort put in taking up resources from the local patch $n_{(ik)(k)}$ and neighbouring patches $n_{(ik)(k')}$. Starting with 100% effort ($n_{(ik)(k)} = 1$) put into acquiring resources from its own and 0% ($n_{(ik)(k')} = 0$) from its neighbouring patches, effectively avoiding resource competition, we decrease the effort put into its own patch by 20% over 4 steps, ending with an effort of 20% ($n_{(ik)(k')} = 0.2$) for all five patches. By making sure that the spatial resource overlap is consistent within a plant community, differences in resource exploitation only emerge dynamically during community assembly. Further, we use periodic boundary conditions to avoid edge effects in the resource interaction.

We consider two scenarios of animal space-use in addition to a null model where we exclude animals entirely (Fig. 1B). In the first scenario, we assume spatially well-mixed animal populations in accordance with the classic food web perspective (i.e. spatially non-nested food webs). Each animal population can therefore access the entire ecosystem without any constraints. The second scenario introduces home range sizes that increase with the animal species' body mass (Tucker *et al.* 2014). We thus define four size classes of animals, each spanning a body mass range of two orders of magnitude (i.e. [10^0, 10^2], (10^2, 10^4], (10^4, 10^6], (10^6, 10^8]). Each of the size classes is associated with a home range size, ranging from the scale of plant individuals, over the scale of a plant neighbourhood, to the scale of the entire plant community (Fig. 1B). This creates local sub-food webs that are nested within the home ranges of larger predators, yielding spatially nested food webs. Since spatially non-nested and spatially nested food webs differ in how they integrate space, animal mediated interactions between neighbouring plants differ between them (Fig. 1C). Comparing both scenarios therefore allows us to investigate the effects of apparent competition and spatial integration in complex food webs.

Feeding rates

Feeding interactions between a consumer species i in patch k and its resource species j in patch k' are driven by feeding rates $F_{(ik)(jk')}$,

$$F_{(ik)(jk')} = \frac{\omega_i b_{ij} B_{jk'}^{1+q_{ij}}}{1+c_i B_{ik}+\omega_i \sum_{j,k'} b_{ij} h_{ij} B_{jk'}^{1+q_{ij}}} \cdot \frac{1}{m_i} \qquad (2)$$

Feeding rates $F_{(ik)(jk')}$ are based on the biomass densities of consumer species i in patch k, B_{ik}, and its resource species j in patch k', $B_{jk'}$. Additionally, they include species specific capture coefficients b_{ij}, handling times h_{ij}, and hill exponents $1+q_{ij}$, as well as consumer species specific relative consumption rates ω_i and time lost due to consumer interference, which is scaled by c_i. By dividing per capita feeding rates of species i by its body mass m_i, feeding rates $F_{(ik)(jk')}$ are scaled to be relative to one unit of biomass.

Capture coefficients b_{ij} describe the success rate of consumer species i to capture resource species j by scaling feeding likelihoods L_{ij}. They are calculated as

$$b_{ij} = b_0 m_i^{\beta_i} m_j^{\beta_j} L_{ij} \qquad (3)$$

The capture coefficient b_{ij} is based on the assumption that encounter rates increase with a species' movement speed, which themselves scale with its body mass. Capture coefficients are therefore a function of body mass of consumer species i, m_i, and resource species j, m_j, each scaled with a species and feeding type specific exponent β_i and β_j respectively (carnivore: N(0.42, 0.05), omnivore: N(0.19, 0.04), herbivore: N(0.19, 0.04), plant: N(0, 0); Hirt *et al.* 2017). Similarly, the scaling constant b_0 depends on the type of feeding interaction (carnivorous: 50, omnivorous: 100, herbivorous: 400).

The time necessary for species i to attack, ingest, and digest resource species j is captured by the handling time h_{ij}, which again scales with the body mass of both resource and consumer species (η_i : N(-0.48, 0.03), η_j: N(-0.66, 0.02)) and a scaling constant $h_0 = 0.4$,

$$h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j} \tag{4}$$

Since herbivores rarely handle an entire organism, handling times of herbivore species i do not scale with body mass. Instead, we use the inverse of its maximum feeding rate $F_{max,i} = y_i * x_i * m_i$, which is a multiple ($y_i$: N(6, 1)) of its per-capita metabolic demands $x_i * m_i$.

The Hill-exponent, $1+q_{ij}$, that determines the functional response type of a feeding interaction, is assumed to be close to 1 when predators are as big as their prey, leading to a saturating increase of feeding rates as the densities of the resource species increases (i.e. type II functional response). As predator-prey body mass ratios R_{ij} increase, the Hill exponent gets closer to 2, leading to feeding rates that increase following a logistic curve (i.e. type III functional response). To achieve that, we calculate

$$q_{ij} = \frac{q_{max} R_{ij}^2}{q_0^2 + R_{ij}^2} \tag{5}$$

where $q_{max} = 1$ and $q_0 = 100$. For herbivorous interactions, we assume a functional response type III and set $q_{ij} = 1$ accordingly.

To account for the generality of species i, we use relative consumption rates ω_i, which are the inverse of a species' number of resource species. Additionally, we consider the time lost due to consumer interference, which increases with densities B_{ik} and a species-specific scaling parameter c_i (N(0.8, 0.2)).

Food web dynamics

To capture food web dynamics, we use three different types of ordinary differential equations (ODE) for animals (equation 6), plants (equation 7), and abiotic resources (equation 8) respectively.

$$\frac{dB_{ik}}{dt} = e_j B_{ik} \sum_{j,k'} F_{(ik)(jk')} - \sum_{j,k''} B_{jk''} F_{(jk'')(ik)} - x_i B_{ik} \tag{6}$$

$$\frac{dB_{ik}}{dt} = r_{ik} G_{ik} B_{ik} - \sum_{j,k''} B_{jk''} F_{(jk'')(ik)} - x_{ik} B_{ik} \tag{7}$$

$$\frac{dN_{lk}}{dt} = D(S_l - N_{lk}) - \sum_{j,k''} v_{lj} r_{jk''} G_{jk''} B_{jk''} \frac{N_{lk}}{\Pi_{jlk''}} \tag{8}$$

Animal populations of species i at patch k change their biomass densities B_{ik} as they feed on other species j in patches k' and are consumed by other species j in patches k'', and due their metabolic demands, which scale allometrically with $x_i = 0.141 * m_i^{-0.305}$ (Ehnes *et al.* 2011). Since not all of the consumed biomass can be converted into tissue, we use a conversion efficiency e_j that depends on the organism consumed (animal: 0.906, plant: 0.545; Lang *et al.* 2017).

Similar to animals, plants of species i in patch k decrease their biomass B_{ik} in response to being consumed and because of their metabolic demands, which scales allometrically with $x_{ik} = 0.138 * B_{ik}^{-0.25}$ (Ehnes *et al.* 2011). Plants increase their biomass B_{ik} as they grow, which is determined by their intrinsic growth rate that gets more efficient as the plant grows bigger, with $r_{ik} = B_{ik}^{-0.25}$. Additionally, growth is limited by one of two limiting resources l, captured in the plants' growth factor G_{ik}

$$G_{ik} = \min\left(\frac{\Pi_{i1k}}{K_{i1}+\Pi_{i1k}}, \frac{\Pi_{i2k}}{K_{i2}+\Pi_{i2k}}\right) \tag{9}$$

where K_{il} is the half saturation density of plant species i for resource l (U(0.1, 0.2)), and Π_{ilk} is the total of either of the two resources l that plant i in patch k can access. The total resource l accessible by this plant is calculated as

$$\Pi_{ilk} = \sum_{k'} n_{(ik)(k')} N_{lk'} \tag{10}$$

with $n_{(ik)(k')}$ capturing the relative effort a plant of species i at patch k puts in extracting resources from a resource pool at patch k'. It is used to define the spatial resource-use scenarios described above, with $n_{(ik)(k')}$ being zero at all but a plant's local and neighbouring patches. Each scenario has its own combination of values where local patches can have the values 1.0, 0.8, 0.6, 0.4, or 0.2 and neighbouring patches 0.0, 0.05, 0.1, 0.15, or 0.2 (Fig. 1A, scenarios from left to right).

Resource densities of resource l in patch k N_{lk} decrease as they are used by plants, and increase with a constant turnover rate D = 0.25, and a resource specific supply concentration S_l, which is set to 50 for resource 1 and to 25 for resource 2. We include plant stoichiometric requirements with v_{li}, where v_{1i} is the content of resource 1 in plant species i (N(2/3, 0.05)) and $v_{2i} = 1 - v_{1i}$. We make sure that the loss of a local resource l in patch k is relative to its contribution to the growth of a plant species i in patch k'' by adding $N_{lk} / \Pi_{ilk''}$.

Food web dynamics are calculated for each sub-population of animals, individuals of plants, and local resource pools. Animal sub-populations or plant individuals of the same species i but in different patches k share the same parameters and may only differ in their biomass densities B_{ik}. We considered animals and plants with densities $B_{ik} < 10^{-6}$ per patch as extinct. In spatially nested food webs, animal species occupy patches of different sizes. Thus we adapt their populations' extinction threshold accordingly (10^{-6}, $4*10^{-6}$, $1.6*10^{-5}$ and $6.4*10^{-5}$ as home range sizes increase from the size of plant individuals to the size of plant communities; Fig.1B). In spatially non-nested food webs, all animal species i use the extinction threshold of the plant community level (i.e. $6.4*10^{-5}$). We use randomly assigned starting densities for animal and plant species (U(0,10)), as well as the resources ($U(S_l/2, S_l)$). Whenever parameters are drawn from normal distributions, we make sure that values fall within the range of three standard deviations. An overview of all the parameters used is given in the appendix (Tab. S1).

Experimental setup and simulation

To investigate the effects of plant biodiversity, we manipulated the plant communities of 20 different food webs. In each food web, we simulate the dynamics of 64 plants of 16 species i that are randomly distributed over the 64 patches k (4 plants per species, one plant per patch; mixtures). Additionally, we simulate the dynamics in single species communities (monocultures) for each of the 16 species. For monocultures, we remove all animal populations that cannot feed on the selected plant species prior to simulating. We simulate the dynamics for 50,000 time steps, where the communities usually reach equilibrium. Together with the animal and plant space-use scenarios (Fig. 1), we simulate a total of 5,100 food webs. 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.

Response variables

We measure plant productivity and diversity at the scale of plant communities. We define plant productivity as the joined resource uptake of all plants of species i in patches k

$$P = \sum_i P_i = \sum_{i,k} P_{ik} = \sum_{i,k} r_{ik} G_{ik} B_{ik} \qquad (11)$$

To account for cyclic dynamics at the end of simulations, we use each plant's productivity P_{ik} as an average over the last 1,000 time steps.

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_{exp} to compare to species richness and thereby quantify plant dominance patterns (Jost 2006)

$$H_{exp} = \exp\left(-\sum_i p_i \ln(p_i)\right), \text{with } p_i = \frac{P_i}{P} \qquad (12)$$

Shannon diversity H_{exp} is calculated using the proportion p_i of plant species i's productivity P_i to the productivity P of the entire community.

Results

Plant diversity-productivity relationships

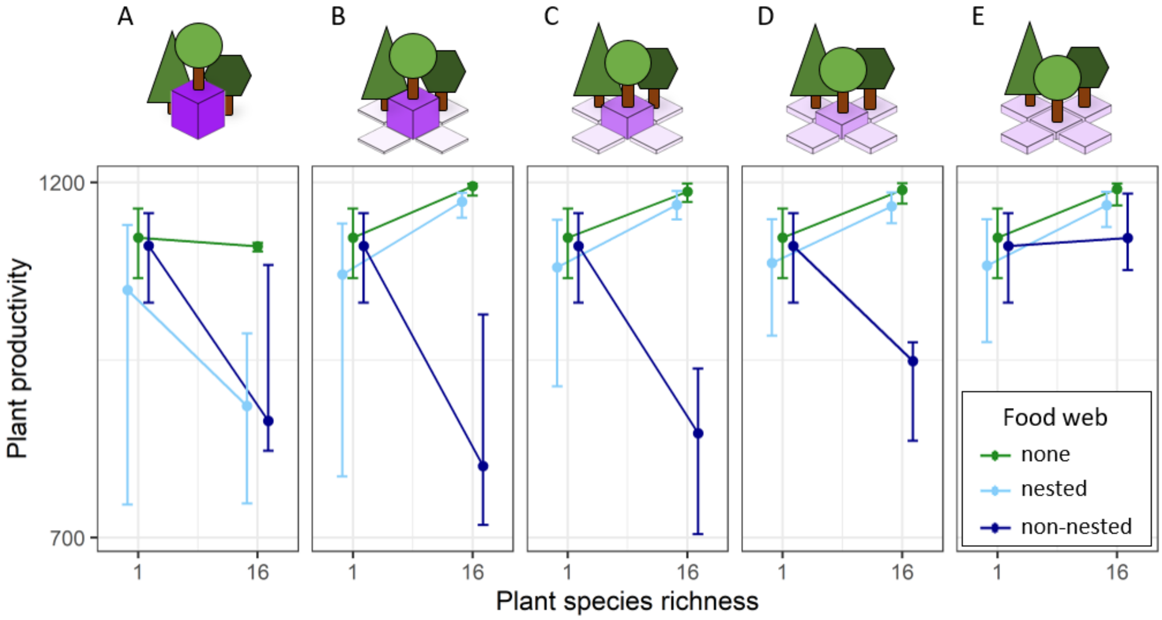

Fig. 2: Plant diversity-productivity relationships for the three food web scenarios considered, i.e. without food web ('none'), with spatially nested food web ('nested'), and with spatially non-nested food web ('non-nested'). Plant productivity is measured for the entire community. (A-E) Effects of increasing 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.

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 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 lowest on average but also 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 the response of productivity to species richness in plant communities without animals depends on whether or not plants have access to resources of neighbouring patches at all, but not on the strength of this spatial resource overlap.

In spatially non-nested food webs, plant communities show a strong decrease in productivity in most resource-use scenarios as their richness increases (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

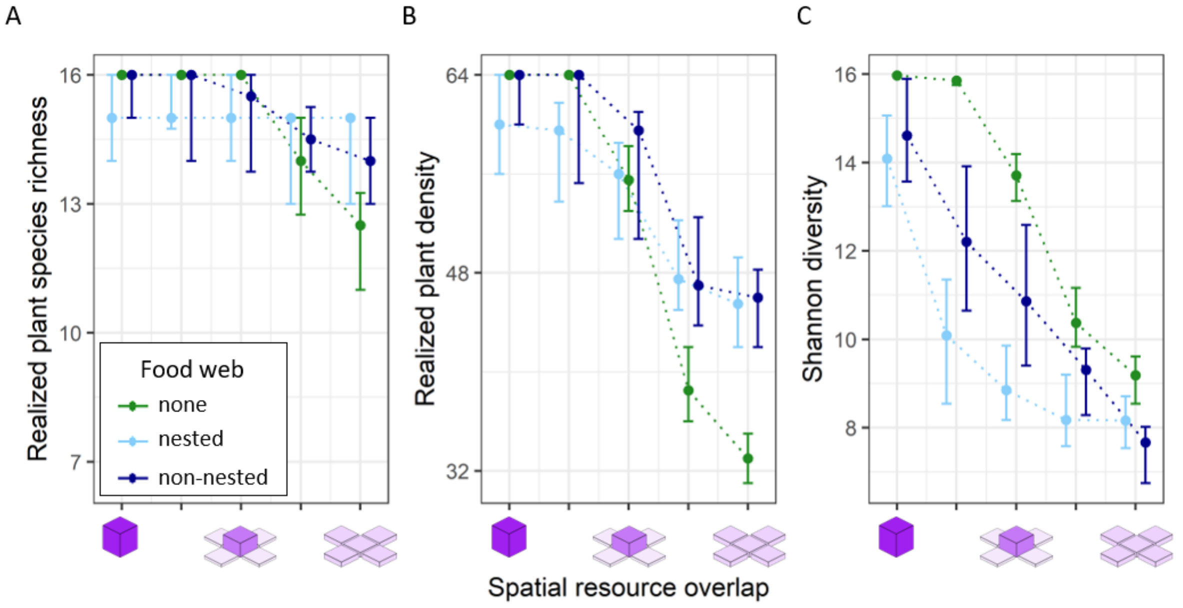

Fig. 3: Effects of increasing the spatial overlap in plant resource access ('spatial resource overlap') on plant community composition in plant communities assembled from 16-species and in three different food web scenarios, i.e. without food web ('none'), with spatially nested food web ('nested'), and 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.

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 to 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 is 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 showed 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. For plants growing in monocultures, this has no effect since all their neighbours share common resource requirements. Additionally, exploitative competition between equally well adapted plants will have little effect without external processes (e.g. environmental stochasticity) that can introduce and emphasize performance differences among organisms of the same species. 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. In the absence of animals, we show that even a weak spatial resource overlap is enough to maximize productivity due to stoichiometric complementarities, suggesting that giving each plant access to only small amounts of otherwise inaccessible resources suffices to create positive diversity-productivity relationships.

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. 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 stoichiometric complementarity whereas selection (sensu Loreau 2000) due to competitive differences shift the community to be more energy efficient, 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 higher biomass density, leading to higher herbivore densities, which in turn has a negative top-down effect on the other plant species with a lower resource acquisition efficiency (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 the local biomass densities of the 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 a local habitat on a grid cell) 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 yielded strongly positive diversity-productivity relationships due to the positive effects of an apparent competition shift up the food chain (i.e. from being between plants to being between herbivores) and the spatial integration of sub food webs by top predators.

It is undeniable that assuming a realistic space-use of plants and animals is a more accurate representation of the processes that drive ecosystems when compared to the more commonly used approaches that assume well-mixed systems (Schneider *et al.* 2016; Albert *et al.* 2022). 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 are most affected by differences in animal movement. This renders animal movement, 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.* 2021) 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). So far, the most prominent among the proposed mechanisms driving these patterns is a complementarity in how plants use resources (Barry *et al.* 2019). While it is possible to emerge due to fundamental niche differences, multi-trophic drivers can produce similar effects (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.

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Chapter 3: Pairwise interaction networks link species coexistence with positive biodiversity-productivity relationships in tree communities

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Authors:

Wentao Yu, Georg Albert, Benjamin Rosenbaum, Florian Schnabel, Helge Bruelheide, John Connolly, Werner Härdtle, Goddert von Oheimb, Nadja Rüger, Stefan Trogisch, Ulrich Brose

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Author	Conceptual	Data analysis	Experimental	Writing the manuscript
Wentao Yu	20 %	40 %	5 %	50 %
Georg Albert	35 %	30 %	10 %	20 %
Benjamin Rosenbaum	20 %	20 %	5 %	5 %
Ulrich Brose	20 %	10 %	0 %	20 %
Others	5 %	0 %	80 %	5 %
Total:	100%	100%	100%	100%

Pairwise interaction networks link species coexistence with positive biodiversity-productivity relationships in tree communities

Wentao Yu[1, 2, †], Georg Albert[1, 2, †], Benjamin Rosenbaum[1, 2], Florian Schnabel[1, 3], Helge Bruelheide[1, 4], John Connolly[5], Werner Härdtle[6], Goddert von Oheimb[1, 7], Nadja Rüger[1,8], Stefan Trogisch[1, 4], Ulrich Brose[1, 2]

[†] authors contributed equally

[1] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany.

[2] Institute of Biodiversity, Friedrich Schiller University Jena, 07743 Jena, Germany.

[3] Systematic Botany and Functional Biodiversity, Leipzig University, Leipzig, Germany

[4] Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

[5] School of Mathematics and Statistics, University College Dublin, Dublin 4, Ireland

[6] Leuphana University of Lüneburg, Institute of Ecology, Lüneburg, Germany

[7] Technical University Dresden, Institute of General Ecology and Environmental Protection, Tharandt, Germany

[8] Department of Economics, Institute of Empirical Economic Research, University of Leipzig, Leipzig, Germany

Abstract

Studies focusing on the local neighbourhood of trees demonstrated that species diversity and tree density influence the productivity of trees. However, the underlying mechanisms that drive the positive effects of diversity on individual tree productivity remain elusive, hampering our mechanistic understanding of the diversity-productivity relationships. We use data from a large-scale biodiversity experiment in a subtropical forest to show that changes in individual tree productivity are driven by species-specific pairwise interactions. By scaling up individual-based results to the community level, we show that less negative interspecific interactions than intraspecific interactions are the critical determinant for the emergence of positive diversity effects. Hence, our results suggest a fundamental consistency between the conditions for species coexistence at the neighbourhood scale and diversity-productivity relationship at the community scale, providing an avenue whereby neighbourhood diversity effects can be translated into community diversity effects. Altogether, our results highlight the importance of tree-tree interactions in understanding community productivity and the consequences of biodiversity change.

Key words: tree-tree interactions; facilitation; BEF-China; interspecific interactions; species interaction network;

Introduction

Forests provide a wealth of ecosystem functions and services, such as biomass production, carbon sequestration, climate regulation, water filtration, and prevention of soil erosion (Durieux *et al.* 2003; Bala *et al.* 2007; Quijas *et al.* 2012; Pan *et al.* 2013). However, globally, forests are under siege from increasing land-use conversion to agriculture, associated fragmentation, pollution as well as climate change (Sala *et al.* 2000; Malhi *et al.* 2008; FAO 2012; FAO and UNEP 2020). The unprecedented rate of biodiversity loss in forests (Naeem *et al.* 2012) could considerably compromise the capacity of the world's forests to deliver essential ecosystem functions and services (Cardinale *et al.* 2012; Isbell *et al.* 2015). Therefore, it is crucial to understand the consequences of species loss on the functioning and services of forest ecosystems. To this end, manipulative experiments have been carried out in the past two decades and it has been well established that forests with diverse species are generally more productive than monocultures (Chisholm *et al.* 2013; Tilman *et al.* 2014; Huang *et al.* 2018). Nonetheless, the fundamental mechanisms that give rise to the positive diversity-productivity relationship (DPR) are still obscure.

As mixed-species forests are aggregates of individual trees, mechanisms that influence the productivity of individual trees could hold the key to unlocking the mechanisms underlying positive diversity-productivity relationships. The few studies that explicitly investigated the effects of the neighbourhood diversity, which were generally characterised by species richness and competitive intensity (i.e total basal area of neighbouring trees), demonstrated that overall a more diverse neighbourhood enhanced individual tree growth (Potvin & Dutilleul 2009; Pretzsch & Schütze 2009; Fichtner *et al.* 2018; Schnabel *et al.* 2019). However, using sheer diversity (species richness) to capture the neighbourhood effect has drawbacks as the neighbourhood species composition could be more important for individual tree growth than the neighbourhood diversity (Ratcliffe *et al.* 2015). Interestingly, this suggests that observed changes in individual tree growth could be driven by divergent interactions due to the identity and relative abundance of neighbouring trees (Potvin & Dutilleul 2009). We thus hypothesise that varying community composition affects productivity via changes in tree-tree interactions at the local neighbourhood (Fig. 1a), a scale at which plant interactions emerge (Stoll & Weiner 2000; Trogisch *et al.* 2021).

The local neighbourhood is characterised by the focal tree and the pairwise tree-tree interactions with all of its immediate neighbours, forming an intricate local interaction network. The productivity of a focal individual tree can be boosted by the dominance of positive (e.g. resource partitioning, facilitation, indirect trophic interactions controlling herbivory) over negative (e.g. strong competition) interactions in the network depending on the diversity, size, density and identity of its neighbours (Callaway & Walker 1997; Callaway *et al.* 2002; Schnabel *et al.* 2019). Conversely, the productivity of a focal individual tree can also be decreased by the dominance of negative over positive interactions. By extension, the interaction network composed of all the pairwise tree-tree interactions in the community should impact productivity at the community scale unless their aggregation is a zero-sum game. As a consequence, the nature and intensity of interactions in the network could play a key role in determining the diversity-productivity relationship. This species-pair specificity is thus particularly pertinent to unravelling the general pattern of interactions and their role in inducing positive diversity-productivity effect. Specifically, we expect that positive effects of tree diversity on community productivity require that interspecific interaction strengths are less negative, or even positive, compared to intraspecific interaction strengths that govern monoculture productivity, which is similar to conditions for coexistence (Fig. 1b, Chesson 2000).

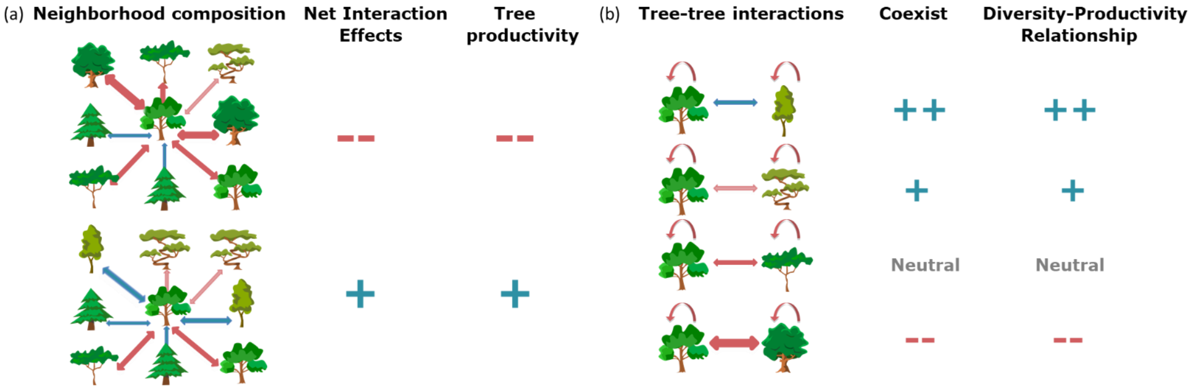


Fig. 1: Conceptual illustration of mechanisms through which local neighbourhoods can affect productivity-diversity relationships. Red and blue colour denote negative and positive interactions respectively, with the thickness indicating the intensity of interactions. (a) illustrates that the same species richness in the neighbourhood but different species compositions can either promote or diminish the productivity of individual trees through the combined net interaction effects determined by pairwise interactions. (b) demonstrates the hypothesised correspondence between species coexistence and diversity-productivity relationships. Curved arrows denote intraspecific interactions, whilst straight arrows represent interspecific interactions.

Despite the attempts made to explore diversity effects at the neighbourhood scale, studies focused on pairwise tree-tree interactions are scarce (Sapijanskas *et al.* 2013). This scarcity finds an explanation in the thorny issues hampering the discovery of the above-mentioned mechanisms. First of all, resolving multiple pairwise tree-tree interactions of a focal tree demands specific experimental design that ensures the systematic representation of all pairwise tree-tree interactions across a diversity gradient including monocultures. Secondly, the typically low replication of pairwise tree combinations and the simultaneous effects of multiple pairwise interactions on focal tree productivity impose serious challenges on the statistical modelling. Therefore, we are missing systematic interaction-network approaches to investigate how characteristics of the interaction network, such as the distribution of positive and negative interactions among different tree species pairs and the difference between inter- and intra-specific interactions, link to the diversity-productivity relationship. An in-depth knowledge of tree-tree interactions underpinned by concomitantly operating mechanisms, competition for resources and facilitation, with an interaction-network perspective would facilitate our mechanistic understanding of diversity effects at the community scale.

Here, we used annual tree growth data spanning seven years from a large-scale biodiversity-ecosystem functioning (BEF) experiment. The random planting scheme of the experiment yielded sufficient pairwise tree-tree interaction data, coupled with the equal distance between all planted trees allowing us to adequately assess the interactions between all immediate tree neighbours. We employed a Bayesian approach to partition individual tree growth into the intrinsic growth rate and effects of interactions with its immediate neighbours. We start with predictions by the Metabolic theory of ecology describing the allometric relationship between intrinsic growth rate of an organism and its biomass (West *et al.* 1997, 1999; Enquist *et al.* 1999), which provides a solid theoretical ground for modelling the intrinsic growth rate. Interactions with neighbouring trees were described by the sum of each pairwise tree-tree interaction between a tree and its immediate neighbours. Each unique pairwise tree-tree interaction is characterised by a distinct species-specific interaction coefficient, all of which constitute the tree-tree interaction network. With this modelling framework, we set out to test the following hypotheses: (1) species-specific pairwise tree-tree interaction coefficients are required to accurately predict individual tree growth; (2) the specific characteristics in the distribution of interaction coefficients are in congruence with the conditions for coexistence; (3) the specific characteristics in the distribution of interaction coefficients across the links of the tree-tree networks are responsible for the positive diversity-productivity relationships at the community level.

Materials and Methods

To test for the necessity of pairwise interactions in determining individual tree productivity, we formulated three models, 1) a null model without interactions, 2) a neutral model that assumes interactions are independent of the species involved, and 3) a pairwise interaction model that incorporates species identity. We then fitted these models to field data from a large-scale BEF experiment (Bruelheide *et al.* 2014) whose specific experimental design enabled us to examine interactions between various tree species over a 7-year time series with sufficient replicates, both of which are central for our model fitting. Lastly, we carried out simulation experiments based on the empirical interaction coefficient matrices to unravel the specific characteristics in the distribution of interaction coefficients in shaping the positive diversity-productivity relationship.

Experimental design

In this study, we used data from site A (29.125°N, 117.908°E) of the BEF-China tree diversity experiment (Bruelheide *et al.* 2014). The experimental site was located in southeast subtropical China (29.08°–29.11° N, 117.90°–117.93° E) between 105 and 275 m above sea level with an average slope of 27.5°. The predominant soil types in the area are Cambisols, Regosols and Colluvissols (Scholten *et al.* 2017). The mean annual temperature is 16.7 °C whereas the mean precipitation is 1821 mm per year (Yang *et al.* 2013). In total, 155 study plots (25.8 × 25.8 m^2) were included with a diversity gradient ranging from monoculture, to 2, 4, and 8 species mixtures. Species of the mixtures were randomly assigned to plots following a “broken-stick” design. Within a plot, species were planted randomly. All species were equally represented along the diversity gradient. In March 2009, each plot was planted with 400 1- to 2-year-old tree saplings (20 × 20 individuals) with equal projected distance of 1.29 m. All saplings that died during the first growing season were replanted in November 2009 (deciduous species) and March 2010 (evergreen species). Weeding was carried out twice a year from 2009 to 2011, and later once a year during the growing season (May–October). More detailed description of the experimental design is provided by Bruelheide *et al.* (2014). The 155 plots are distributed over two datasets with no overlap in tree species. They each have a high number of replicates of various species pairs and a diversity gradient from monocultures to mixtures of 8 species.

Tree data

To avoid edge effects, we focused our analyses on core areas (central planting position) of 6x6 trees for monocultures and 2 species mixtures and 12x12 trees for 4 and 8 species mixtures. For all trees within these core areas of the plots, species identity, stem diameter (measured 5 cm above-ground) and tree height (measured from the stem base to the canopy top) were recorded once per year over the 7-year study period (2010–2016). Within a plot, trees that were located at the core were documented as focal trees. For each focal tree, the location and identity of its neighbouring trees were also recorded. One sample consists of one focal tree and its immediate neighbouring trees in a given year. Above-ground biomass of each tree was calculated as the product of its above-ground volume and its species-specific wood densities, which were collected from a comparative study plot near BEF-China experimental site that covers all the species used in BEF-China (Kröber *et al.* 2014; Bongers *et al.* 2021). Above-ground wood volume of each tree was calculated by multiplying the arithmetic product of tree basal area and tree height with a factor of 0.5 (Fichtner *et al.* 2017, 2018) to account for the discrepancy between actual tree volume and the volume of a cylinder (Pretzsch 2009). In the case of missing biomass data of one or more neighbouring trees in a certain year, the sample was removed from the dataset. Annual biomass growth rates were calculated as the biomass difference between two consecutive years. Trees that exhibited negative growth rates were excluded to avert potential bias. The negative growth rates could be attributed to measurement errors or stochastic processes (e.g. large branches were cut off by natural forces) which were not accounted for in our model. Moreover, the likelihood of aforementioned processes increases with time (Fichtner *et al.* 2020), further confounding the model estimates when using time series data. In the end, 1948 and 1352 focal trees from dataset 1 and 2 from 74 and 81 plots respectively were included in this study, with a total number of data points of 7700 and 4585 over the 7-year study period.

Pairwise tree-tree interaction model

We decomposed the observed individual growth rate into its intrinsic growth rate and interactions with its immediate neighbouring trees, assuming the effects of higher order interactions are negligible (Simberloff 1982). Metabolic theory predicts the relationship between intrinsic growth rate and body mass can be described by a three-quarter power allometric scaling. It is predicated on the assumption that the metabolic rate of an organism is constrained by the rates of resources uptake across surfaces and rates of nutrient distribution through branching networks of vessels within the organism (West *et al.* 1997, 1999; Enquist *et al.* 1999). Although metabolic theory received some empirical support (Hatton *et al.* 2019), the empirical data from plants used for testing the three-quarter exponent were usually obtained from natural stands, which already included the biotic interactions. Here, we employed this allometric relationship between biomass and intrinsic growth rate while retaining the flexibility of the exponent to test the validity of three-quarter scaling in metabolic theory, which formed our *null model* described by:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)} B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) \quad (1)$$

where $B_{t,i}$ and $B_{t+1,i}$ denote the biomass of tree i in year t and t+1 respectively. Following metabolic theory, $\beta_{s(i)}$ is a species-specific coefficient, whereas θ is a general exponent for allometric scaling. We accounted for plot effects and annual environmental changes by incorporating them as random effects (ε_p, ε_t), while allowing them to have species-specific effects (ε_{ps}, ε_{ts}) as tree species may respond differentially to similar environmental conditions.

We then factored in the interaction effect between the focal tree and its neighbouring tree which was defined by the product of interaction coefficient α and the biomass of the neighbouring tree with a scaling exponent. This assumes the strength of interactions scales with body size since larger trees seize disproportionally more resources relative to their size (Yodzis & Innes 1992; Freckleton & Watkinson 2001). Additionally, the exponent of the biomass of the neighbouring tree allowed us to test whether the scaling relationship is linear (exponent = 1) or nonlinear. If the species identities of interacting trees have no bearings on the interaction strength (Hubbel 2001), an average interaction coefficient (which is identical across species) would suffice, resulting in the *neutral model* which is described as follows:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)} B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) + \alpha_{ave} \sum_{j \in n_j}^{n_j} B_{t,j}^{b} \quad (2)$$

where the α_{ave} represents an average interaction coefficient and $B_{t,j}$ denotes the biomass of neighbouring tree j with a scaling exponent b. n_j denotes the number of neighbouring trees, which could be smaller than eight due to mortality.

Contrary to equation (2), if the species identity of the neighbouring trees is necessary for accurately characterising individual tree productivity, then a *pairwise interaction model* is needed, which can be expressed by:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)} B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) + \sum_{j \in n_j}^{n_j} \alpha_{s(i),s(j)} B_{t,j}^{b} \quad (3)$$

where the interaction coefficient $\alpha_{s(i),s(j)}$ encapsulates the effects of species identity $s_{(j)}$ of tree j on species identity s(i) of tree i. When $s_{(i)} = s_{(j)}$, $\alpha_{s(i),s(j)}$ stands for intraspecific interaction coefficient, whilst when $s_{(i)} \neq s_{(j)}$, $\alpha_{s(i),s(j)}$ represents interspecific interaction coefficient. We tested different formulations of the random effect structure and found the formulation in which only intrinsic growth rates are affected generally fits best (see Appendix S1). Distances between focal tree and neighbouring trees were not considered in our study, because in plots where the spacing is well controlled, additional spatial information may not improve the performance of the model to characterise tree-tree interactions (Biging & Dobbertin 1995).

To ensure it is theoretically possible to estimate unique parameters given the data and our model structure, we performed a parameter identifiability analysis (Guillaume *et al.* 2019). We simulated tree growth data of eight species in monoculture, 2, 4, and 8 species mixture over 7 years 10 times using assigned parameter values following Equation (3). The distributions used for randomly generating the parameters can be found in Appendix Tab. S1. We then fitted the model to the 10 independent simulated datasets and calculated the difference between the posterior mean and the true value of each parameter. This allowed us to ensure that we are able to recover true parameter values (see Appendix S2). We then fitted the null, neutral, and pairwise interaction models to the two independent empirical datasets using the Rstan package (Stan Development Team 2020) in R version 4.2 (R Core Team 2022). Each model was fitted using three Markov chains and 4000 iterations with 2000 as warm-up. To ensure that the HMC sampler effectively explored the parameter space and the model convergence, we graphically checked the trace plots of Markov chains and the R-hat metric (Gelman *et al.* 2013). We used posterior predictive checks (Conn *et al.* 2018) to inspect the goodness-of-fit for each model via visually comparing the predictions from the model to the observed data. Bayesian leave-one-out cross-validation (LOO-CV) was chosen to evaluate the model performance based on its out-of-sample predictive ability, for LOO-CV is known to produce nearly unbiased estimate of the predictive power of a given model (Watanabe 2010). We implemented the computation of LOO-CV in loo package for R (Vehtari *et al.* 2016), which utilises an efficient and stable importance sampling procedure (Vehtari *et al.* 2022). The set of models fitted with two independent datasets allowed us to robustly evaluate the model performances.

Reshuffling the interaction coefficient matrix

To uncover the specific characteristics in the tree-tree interaction network that are responsible for positive diversity-net interaction relationships, we performed randomization experiments on the interaction coefficient matrix obtained from the pairwise interaction model. We defined the second term in equation (3) as the net interaction effect, which can directly boost or diminish the growth of individual trees. We first reshuffled the whole interaction coefficient matrix to test whether the estimated interaction coefficient matrix emerged by chance. We then investigated how the difference between inter- (off-diagonal elements in interaction matrix) and intraspecific (diagonal elements) interaction coefficients shaped the diversity-productivity relationship by constraining the reshuffling to the off-diagonal and diagonal elements respectively. For each scenario, we sampled 100 times. With the generated interaction coefficient matrices under each scenario, we computed the net interaction effects and productivity for each focal tree. We then scaled up the individual-based effects to the community level and examined the diversity-net interaction and diversity-productivity relationships, thereby establishing the link between the diversity effect at the local level and the diversity effect at the community level (see Appendix S4 for detail). We hypothesised that the interspecific interactions should be less negative than the intraspecific interactions for a positive diversity-productivity relationship to emerge. To test this hypothesis, we calculated the mean difference of inter- and intraspecific interaction for each of the randomly reshuffled matrices and tested for the relationship between the difference in inter- and intraspecific interaction and the slope of the emergent diversity-productivity relationships.

Results

Model Fitting and Model Performance

To assess the importance of explicitly modelling pairwise tree-tree interactions, we compared the pairwise interaction model (i.e. the model assigning specific interaction parameters to all tree species pairs) with a null model without interactions and a neutral model where interaction terms are constant across species (i.e. interactions are neutral concerning species identities). In a parameter identifiability analysis, all parameters of the pairwise models were accurately retrieved using simulated data with relatively low deviations between the estimated and assigned true values (Appendix Fig. S1). All models showed good convergence with R-hat values of 1.0 for almost all estimates. Across both datasets, the pairwise model was invariably ranked the best in terms of its predictive power (Tab. 1).

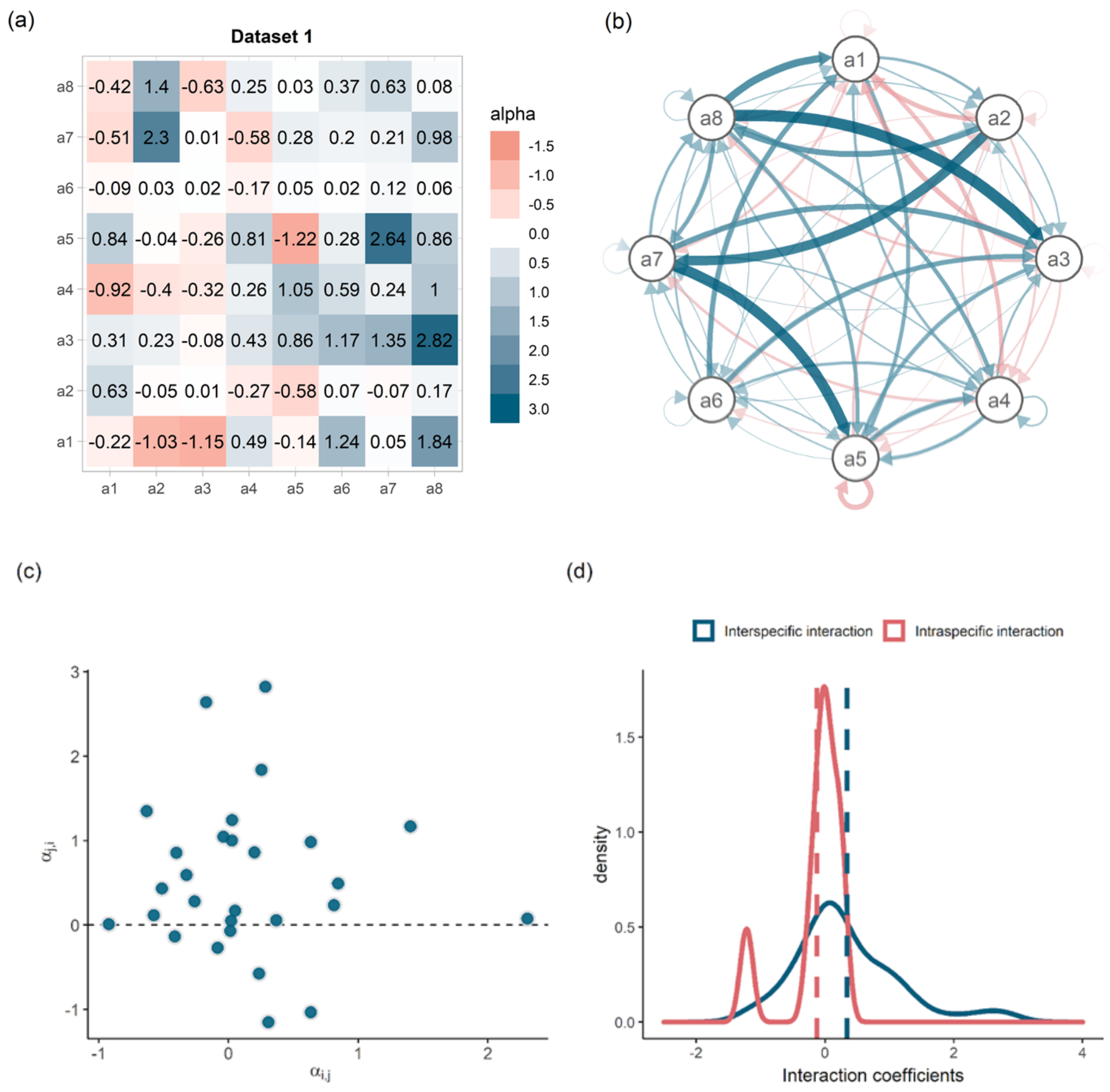
The estimated scaling exponent of the intrinsic growth term stands at 0.8 from the pairwise model and it is the largest in comparison with that of the null and the neutral model for dataset 1. For dataset 2, a similar scaling exponent parameter of 0.81 was found for both pairwise and neutral models, whereas a slightly larger exponent of 0.82 was estimated for the null model. The interaction strength scales with the biomass of the neighbouring tree non-linearly, with exponents of 0.19 and 0.14 for the two datasets, respectively.

Tab. 1: Results of scaling exponents (mean and 95% credible interval) and model comparison for the null, neutral, and pairwise model with best to worst performed model listed from top to bottom.

		elpd_diff	se_diff	Metabolic exponent	Exponent of neighbouring tree’s biomass
Dataset 1	pairwise	0	0	0.80 (0.78, 0.81)	0.19 (0.14, 0.25)
	null	-63.80	46.89	0.77 (0.76, 0.78)	/
	neutral	-64.37	45.35	0.78 (0.77, 0. 80)	0.13 (0.09, 0.36)
Dataset 2	pairwise	0	0	0.81 (0.79, 0.83)	0.14 (0.09, 0.19)
	null	-47.77	41.40	0.82 (0.80, 0.83)	/
	neutral	-55.15	41.05	0.81 (0.80, 0.83)	0.21 (0.02, 0.55)

The estimates of interaction coefficients

We obtained the full interaction coefficient matrices from both datasets to examine the characteristics of the pairwise tree-tree interactions. Given that the results from both datasets are qualitatively the same, we only show figures from the dataset 1 (see Appendix S2 for dataset 2). The estimates of interaction coefficients in the pairwise model show values ranging from -1.22 to 2.82 and -1.44 and 1.56 for dataset 1 and dataset 2, respectively (Fig. 2a, Fig. S3a). Out of the 64 interaction coefficients estimated, about half (dataset 1: 33; dataset 2: 32) had 90% credible intervals that did not overlap with zero, indicating those interaction effects are clearly positive or negative. The two interaction coefficients between specific tree pairs were neither reciprocal nor inverse in magnitude (Fig. 2c), which is mirrored by the links with different thickness or/and colour between the connecting species, depicted in the network (Fig. 2b). From the two interaction networks, we found that the majority of the tree-tree interactions were positive, with an incidence of 67.2% [43/64] and 51.6% [33/64] in dataset 1 and 2, respectively. When separating intra- (diagonal values in Fig. 2a) and interspecific (off-diagonal values) coefficients, a similar trend emerged from the two independent model fittings, with intraspecific interaction coefficients tightly clustered around zero, whereas interspecific interaction coefficients spanned across a wider range (Fig. 2d). Moreover, the mean values of the inter-specific interaction coefficients (0.34±0.82 and 0.08±0.63 for dataset 1 and data 2, respectively) are consistently larger than those of the intraspecific interaction coefficients (-0.13±0.47; -0.03±0.22). These results demonstrate two related patterns: (1) interspecific interaction strengths were generally higher (i.e. less negative) than intraspecific interaction strengths, and (2) interspecific interactions tended to be positive, whereas intra-specific interactions are on average negative.



	a1	a2	a3	a4	a5	a6	a7	a8
a8	-0.42	1.4	-0.63	0.25	0.03	0.37	0.63	0.08
a7	-0.51	2.3	0.01	-0.58	0.28	0.2	0.21	0.98
a6	-0.09	0.03	0.02	-0.17	0.05	0.02	0.12	0.06
a5	0.84	-0.04	-0.26	0.81	-1.22	0.28	2.64	0.86
a4	-0.92	-0.4	-0.32	0.26	1.05	0.59	0.24	1
a3	0.31	0.23	-0.08	0.43	0.86	1.17	1.35	2.82
a2	0.63	-0.05	0.01	-0.27	-0.58	0.07	-0.07	0.17
a1	-0.22	-1.03	-1.15	0.49	-0.14	1.24	0.05	1.84

Fig. 2: Overview of estimated interaction coefficients. (a) shows interaction coefficients matrices for dataset 1, i.e. row a1 and column a4 denote interaction coefficient $\alpha_{1,4}$, representing the effect that species 4 has on species 1. (b) depicts the interaction networks for dataset 1 with blue and red colour denote positive and negative interaction coefficients respectively. The thickness and colour saturation correspond to the magnitude of interaction coefficients. The arrows point to the species which is affected by the connecting species. (c) demonstrates that there is no pattern between the two interaction coefficients of a specific tree pair. (d) depicts the density distribution of intra- (red) and interspecific (blue) interaction coefficients for dataset 1 with dashed lines representing the means.

Difference between inter- and intraspecific interactions

To further uncover the specific characteristics in the interaction networks that are responsible for the positive diversity-net interaction relationship, we performed several simulation experiments by reshuffling the empirical interaction coefficient matrices and calculated the community-level net interaction effects. Reshuffling the whole interaction coefficient matrix gave us a wide variety of relationships between net interactions and diversity, ranging from negative to neutral and positive relationships (Fig. 3a, unconstrained). Compared to the positive relationship observed in the empirical data (Fig. 3a, green lines), the average across all the simulated communities led to a flat line of both community mean net interaction and productivity with respect to diversity (Fig. 3a, unconstrained, blue lines). This suggests that the empirical emergence of the positive relationship does not necessarily arise from a random distribution of interaction strengths across the matrix. In contrast, reshuffling the diagonal (intraspecific interactions) and off-diagonal (interspecific interactions) values in their respective subsets greatly constrained the relationships between community mean productivity and diversity to be positive (Fig. 3a, constrained), although the positive trend was still more pronounced in the empirical data than the community mean net interaction and productivity averaged across all the simulated communities. This indicates that characteristic differences between intraspecific and interspecific interaction strengths largely explain the constraint that the relationship between mean community productivity and diversity is positive. By analysing the emergent diversity-productivity relationships in relation to the difference of inter- and intraspecific interactions, we found that positive relationships emerge only if interspecific interactions are on average higher (i.e. more positive or less negative) than intraspecific interactions (Fig.3b). Conversely, when intraspecific interactions have more positive or less negative effects than interspecific interactions, we found negative relationships between diversity and productivity. Collectively, these results indicate the significance of the difference in sign as well as magnitude of the inter- and intraspecific interactions in determining the strength and direction of the diversity-productivity relationship.

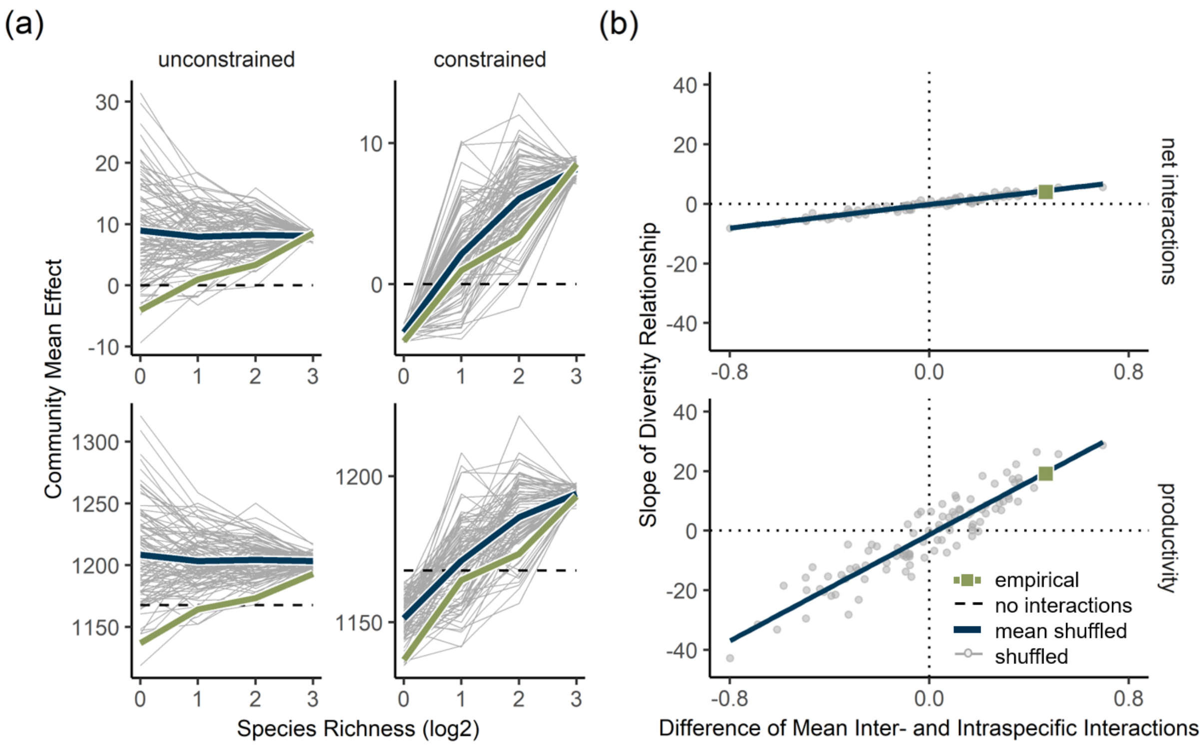


Fig. 3: Results from reshuffling the interaction matrix. (a) illustrates the simulated diversity-net interaction (top) and diversity-productivity (bottom) relationships at the community level for dataset 1 under two different scenarios: completely random reshuffling of interaction matrix (unconstrained) and reshuffling within inter- and intraspecific interactions (constrained). Grey lines show community mean effects for each reshuffled interaction matrix, with thick blue lines showing their average. Green lines show values based on empirical interactions. (b) shows the relationship between the difference between inter- and intraspecific interactions and the slopes of the simulated diversity-net interaction and diversity-productivity relationships (grey lines in (a) unconstrained scenario). The slopes based on empirical data are shown in green squares.

Discussion

By explicitly modelling the pairwise interactions at the neighbourhood scale of individual trees, we show that the sign and strength of an interaction depends on the species involved. It is essential for predicting tree growth when compared to models without and with species-independent interaction terms. Contrary to our expectations, our results show that the species interaction network is dominated by positive rather than negative interactions. Through reshuffling the interaction coefficients in the network, we demonstrate that the positive difference between average inter- and intraspecific interactions in the community is a critical determinant of the positive diversity-productivity relationships. Taken together, our study elucidates the mechanisms underlying positive diversity-productivity relationships.

Species identities are essential

To identify whether modelling pairwise tree interactions is important for predicting tree growth, we utilised two independent datasets, both leading to the pairwise model being the best performing one. This strongly suggests that the identity of neighbours is an indispensable factor in shaping individual tree productivity. A population-level analysis of European forests showed that the identities of neighbouring trees drive the variation in community-level productivity (Baeten *et al.* 2019). Studies at the neighbourhood scale usually characterised the local neighbourhood by the size of neighbouring trees (i.e. the total basal area of neighbouring trees) or the richness of neighbouring species (Potvin & Dutilleul 2009; Pretzsch & Schütze 2009; Fichtner *et al.* 2018). Their results showed that neighbourhood diversity and density are central for regulating community scale productivity. Nevertheless, studies that explicitly model pairwise interactions in the neighbourhood, which allow a better inference on the underlying competitive and facilitative mechanisms, are scarce. Sapijanskas *et al.* (2013) using data from a tropical forest BEF experiment showed that the inclusion of pairwise interactions through the neighbours' litter production in addition to shading improved the prediction of individual tree growth. Our model takes a phenomenological approach, assuming the pairwise interaction term captures the total impact of competitive (negative) and facilitative (positive) interactions between distinct species pairs. The sum of pairwise interaction effects of the focal tree then constitutes the net interaction effect, which captures the overall local neighbourhood interaction effects, allowing for scaling up to the interaction effects at the community level. This model framework thus not only enhances our ability to discern the pairwise interactions, but also provides a means to decipher the mechanisms through which local pairwise interactions shape the diversity-productivity relationships.

Positive interactions were detected more often than negative interactions in the network

Surprisingly, we found that positive interaction coefficients were dominant in the interaction networks. The high frequency of positive interactions indicates facilitation and stress amelioration among trees, which could be accompanied by reduced competition due to resource partitioning or biotic interaction (Barry *et al.* 2019) so that the positive effects are not offset by strong competition. Our findings therefore stand in contrast to recent meta studies that suggest competition to be the prevalent form of plant-plant interactions globally (Adler *et al.* 2018; Yang *et al.* 2022), with only about 25% of the recorded interactions being positive (Adler *et al.* 2018). Generally, the ecological literature postulates that positive interactions are prevalent in stressful environments (stress gradient hypothesis; (Gómez-Aparicio *et al.* 2004; Brooker 2006; Callaway 2007; Mazía *et al.* 2016). In moderately or weakly stressful environments, positive interactions are thought to be generally outweighed by the relatively larger negative effect of competition (Brooker & Callaghan 1998; Callaway *et al.* 2002). In contrast, our results show that positive interactions eclipse competition in the majority of interactions, even in a moderately stressful environment (Wu *et al.* 2015). We ascribe this discrepancy primarily to the fact that prior studies with a focus on positive interactions usually isolated species pairs (Brooker *et al.* 2007; Yang *et al.* 2022) and investigated how the strength of positive interactions changes from stress-free to an extremely stressful environment (Brooker *et al.* 2007) rather than examining the relative importance of positive interaction and competition across species in more diverse communities. Moreover, our results also point to a potential mismatch between two paradigms in the literature: (1) the dominance of negative interspecific interactions and (2) positive diversity-productivity relationships. Based on our empirical analysis and simulations, we show that the positive diversity-productivity relationship that emerges at the community level (Huang *et al.* 2018) requires that interspecific interactions are positive or less negative than intraspecific interactions. While a dominance of weakly negative interspecific interactions cannot be completely ruled out, these results also suggest that the occurrence or dominance of positive interspecific interactions, as in our study, makes the occurrence of positive diversity-productivity relationships much more likely. Our results thus highlight the significance of understanding the relative importance and intensity of the positive interaction in relation to the net interaction effect as well as how the positive interaction links to the positive diversity-productivity relationship.

Non-linear scaling with the size of neighbouring tree

Our results reveal that interaction strength scales sub-linearly with the biomass of the neighbouring tree, reflecting the disproportionate capacity of larger plants to compete for resources (Schwinning & Weiner 1998; Freckleton & Watkinson 2001; Weiner *et al.* 2001). While there is a general agreement that competition scales with size [ref], how positive interactions relate to the size of the neighbouring tree is often overlooked. For instance, plants with deep roots can make water available to plants with shallow roots through hydraulic lift (Dawson 1993; Emerman & Dawson 1996) and some plant species can shelter their direct neighbours from harsh microclimate conditions by physically mediating wind, heat, or light (Wright *et al.* 2017). As is the case of competition, those positive interactions likely scale with the size of the neighbouring tree, with larger trees providing more readily accessible water or a more suitable microclimate. Furthermore, negative and positive interactions could scale with the size of the neighbouring tree differentially, resulting in a non-linear scaling for the net interaction. Thus, the scaling relationship between positive interaction and the size of the neighbouring trees is worth exploring further.

Difference between inter- and intraspecific interactions

From the interaction networks, we discover that interspecific interactions are on average more positive or less negative than intraspecific interactions, which is consistent with findings of a recent synthesis study (Adler *et al.* 2018). A field study on Borneo forest (Stoll & Newbery 2005), which found a differing effect of conspecific versus heterospecific neighbours with conspecific neighbours reduced the growth of the focal tree considerably more than heterospecific neighbours, also offers indirect support to our result. To further uncover the specific characteristics in interaction networks that are responsible for the positive effects of diversity on productivity, we reshuffled the species interaction network to show that the difference between inter- and intraspecific interaction coefficients is the principal driver. The competitive network is considered as a key driver for species coexistence and maintaining biodiversity (Maynard *et al.* 2017). The magnitude and direction of competitive interactions within the network can either boost or diminish the individual growth. Consequently, the characteristics of the competitive network among species could be central for determining the diversity-productivity relationships (Huston *et al.* 2000; Hooper *et al.* 2005; Becker *et al.* 2012). Our results corroborate this notion and expand the competitive network to a general interaction network which incorporates the effect of often overlooked positive interactions, demonstrating that the positive difference between inter- and intraspecific interactions is a key driver for the emergence of positive diversity-productivity relationships.

This finding also echoes with the general principle of coexistence theory, which predicts that intraspecific competition should be stronger than interspecific competition for any pair of stably coexisting species (Chesson 2000). The mechanisms underlying coexistence are frequently invoked to explain how and why mixtures outperform monocultures and there certainly is, to some extent, correspondence between coexistence and BEF studies (Turnbull *et al.* 2013). Indeed, (Loreau 2004) provided a theoretical proof that a stably coexisting mixture would inevitably overyield and create a diversity effect. Hence, when interspecific competition is on average less intense than intraspecific competition, it is indicative of the presence of complementarity (including resource partitioning, abiotic facilitation, and biotic feedback; Barry *et al.* 2019). As this pattern of interaction strengths is prerequisite for avoiding competitive exclusion and fostering species coexistence (Huston *et al.* 2000), this may provide an explanation for the dominance of positive diversity effects in diversity-productivity studies. By establishing the connection between coexistence theory and BEF studies in an interaction network context, our research therefore offers novel insights into the preconditions for a positive diversity-productivity relationship. On top of that, our results show that the positive diversity-productivity relationship becomes steeper as the difference between inter- and intraspecific interaction increases. This finding could have practical implications for forest restoration as it implies the possibility of selecting an optimal composition of tree species from local pools to maximise productivity.

Scaling exponent in Metabolic Theory

Next to the findings concerning the links between interaction network and diversity-productivity relationships, our model formulation allowed us to simultaneously test the three-quarter scaling predicted by metabolic theory (West *et al.* 1997, 1999; Enquist *et al.* 1999). The estimated metabolic exponents were 0.80 and 0.81 respectively, suggesting a higher intrinsic growth rate than three-quarter. This disparity is conceivable because our individual model factored in the interactions with neighbours whereas previous studies that retrieved the three-quarter exponent usually conducted at community scale implicitly included the interactions (Hatton *et al.* 2019). Another explanation for the disparity is that trees at distinct life stages could scale differentially with biomass. Enquist *et al.* (2007) demonstrated that the metabolic exponent for saplings was one instead of three-quarter. Hence, our results could be attributable to the fact that we predicted growth from the first year until seventh year without separating life stages. Future studies with large data sets consisting of more tree species and pronounced variations in individual biomass will facilitate the test of the exponent predicted by metabolic theory when accounting for the interactions with surrounding plants.

Future directions

In our *pairwise interaction model*, the interaction strength scales with the biomass of the neighbouring tree, reflecting an intensified interaction strength over time as the biomass of the neighbouring tree increased over the years (Reich *et al.* 2012). With data spanning a longer period becoming available, it could be profitable to explicitly examine the temporal variation in pairwise interactions. Moreover, the interaction coefficients in our model quantitatively reflect the ecological strategies of species pairs, paving the way to relate functional traits to the interaction coefficients. Functional traits linking essential biological processes to biotic interactions can act as common currency, facilitating the removal of species identity (McGill *et al.* 2006; Westoby & Wright 2006; Kunstler *et al.* 2016). By substituting species identities with functional traits, the number of parameters needed to be estimated will be markedly reduced. As a consequence, this trait-based approach could assist in unravelling the general relationship between functional traits and biotic interactions across the forest ecosystems worldwide, thereby improving our predictive power of the effect of biodiversity loss on ecosystem functioning at the global scale.

We accounted for environmental heterogeneity by using plots and years as random factors and allowing interactions between them and species identity. Given the large number of plots with randomly assigned species and species compositions, it is not likely that the interactions were confounded with the variations in the abiotic environment (Healy *et al.* 2008). This interpretation is supported by Kröber *et al.* (2015), whose findings demonstrated that environmental variations in slopes, aspect and soil conditions jointly explained only 4% of crown width growth rate in the BEF-China experiment. Nonetheless, we should not rule out the potential of environmental conditions to modify interactions. Previous studies showed that plant interactions exhibited differential response across environmental gradients, in which the combination of specific species pairs and the stress type could play major roles (Bertness & Ewanchuk 2002; Soliveres *et al.*

2015). Thus, further research should consider identifying environmental factors that influence plant interactions. Whenever the local environmental variables do not have an apparent impact, microclimate, which could also modify the interactions, warrants further investigation (Yang *et al.* 2022).

Furthermore, local biodiversity effects could result from processes beyond pairwise interactions (Levine *et al.* 2017; Li *et al.* 2021). Although our approach was predicated on the assumption that higher-order interactions were negligible, our individual-based pairwise model can serve as a foundation to disentangle the community-level diversity effect in a mixture from local diversity effects. For example, our model can be scaled up to the stand level through simulations, the resulting stand level biomass can then be compared with observed biomass to detect the diversity effects that have not been captured by pairwise interactions.

Conclusion

Our analyses have revealed the importance of species-specific pairwise interactions for tree productivity. Scaling up these results to the community level supported our prediction that interspecific interactions need to be less negative than intraspecific interactions to yield a positive relationship between diversity and tree community productivity. Together, these results show a fundamental consistency between the conditions for species coexistence at the neighbourhood scale and positive diversity-productivity relationships at the community scale. They also highlight that implications of biodiversity change for forest productivity differ depending on species identity, which can be predicted by simulations of forest interaction networks. Tree-tree interaction networks may thus provide critically important information for understanding constraints on species coexistence, community productivity and the consequences of biodiversity change.

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General discussion

Biodiversity-ecosystem functioning (BEF) research has highlighted the importance of biodiversity for providing ecosystem functions crucial for human well-being. However, while there is no shortage of attempts at capturing the mechanisms driving the positive effects of biodiversity (e.g. Oram *et al.* 2018), it remains surprisingly difficult to clearly identify them (Barry *et al.* 2019). This shortcoming can have several reasons, but is most likely rooted in the complexity of ecological mechanisms and their interactions. Instead of investigating them in isolation, a holistic approach can therefore be advantageous, allowing to simultaneously account for multiple interacting mechanisms. In this thesis, I therefore investigated plant diversity-productivity relationships in process-based simulation models that integrate animal- and resource-mediated plant interactions, showing clear interactive effects between them. Additionally, I use an empirical model that estimates net interaction effects between neighbouring plants, showing that positive effects of biodiversity on ecosystem functions emerge from local interactions between organisms. A large proportion of positive net interactions further indicate that mechanisms beyond resource competition (e.g. multi-trophic interactions) are involved in shaping plant communities and their diversity-productivity relationships. While my findings highlight the complex interactions between entangled mechanisms, they also indicate systematic differences in how either mechanism affects plant community composition, thereby hinting at possible ways to disentangle them.

Complementarity through different mechanisms

In this thesis, I showed evidence for the interactive effects of resource- and animal-based mechanisms, which both have largely positive effects on plant diversity-productivity relationships when integrated in process-based theoretical models. In chapter 1, resource-use dissimilarity and multi-trophic interactions independently created positive diversity-productivity relationships, but their joint effects usually exceeded their individual ones. Additionally, multi-trophic effects were particularly pronounced when resource-based effect were weak. The results from chapter 2 demonstrate that a spatial overlap in plants' resource access is a requirement for positive diversity-productivity relationships. The strength of this overlap moderates the response of the three different food web scenarios considered. It is not surprising that the results from chapter 1 and 2 suggest a general bottom-up control of multi-trophic effects by resource-based processes, given that resources are ultimately limiting the considered food webs (Schneider *et al.* 2016). However, multi-trophic effects could often strengthen positive diversity-productivity relationships and, more importantly, maintain complementary communities of coexisting plant species. In addition to the positive effects of diversity on productivity, this can further affect the temporal stability of plant and animal productivity positively (Eschenbrenner & Thébault 2022), and likely contributes to an increased ecosystem multifunctionality (Hector & Bagchi 2007) that could not be maintained with resource-based processes alone.

My findings confirm previous research that showed a prevalence of complementarity mechanisms as the main cause of positive plant diversity-productivity relationships (Hooper *et al.* 2005; Barry *et al.* 2019). I found different complementarity mechanisms depending on the processes involved. Specifically, a dissimilarity in resource-use of plant species showed strong positive effects on plant diversity-productivity relationships in chapter 1. In chapter 2, I additionally found signals of a stoichiometric complementarity between neighbouring plants that differed in their resource requirements (González *et al.* 2017). In comparison to resource-use dissimilarities that are based on accessing different parts of a resource pool (e.g. due to using different forms of nitrogen, Ashton *et al.* 2010), stoichiometric complementarity requires an overlap in resource access, aligning with classic theoretical descriptions of resource complementarity (Tilman *et al.* 1997). My findings therefore show that resource complementarity can have different aspects acting in parallel to affect diversity-productivity relationships.

Apart from resource-based complementarity mechanisms, I found positive effects of multi-trophic interactions on plant species complementarity in chapter 1, and hints of similar mechanisms in chapter 2. This indicates that not only resource but also trophic complementarity (Poisot *et al.* 2013) will simultaneously affect the plant community. More positive interspecific than intraspecific net interactions found in chapter 3 align with increased complementarity effects found in the same experiment (Huang *et al.* 2018). A sole role of resource complementarity can again be ruled out given the large proportion of positive interaction coefficients, which indicates that processes beyond resource competition act on the plant community. Instead, the positive interactions hint at facilitative processes but cannot differentiate whether they emerge through resource related processes (i.e. abiotic facilitation), in response to multi-trophic interactions (i.e. biotic facilitation; Wright *et al.* 2017), or are related to other complementarity mechanisms entirely. My findings thus demonstrate the interactive and entangled nature of the drivers of plant diversity-productivity relationships, potentially explaining why their identification has proved to be such a challenge (Barry *et al.* 2019).

Complementarity mechanisms are based on niche differentiation that reduces competition and thus promotes coexistence (Loreau 2000). In chapter 1, niche differences due to resource-use dissimilarity of plant species showed very similar effects. Multi-trophic effects from chapter 1 and 2 also fostered coexistence as they limit competitive exclusion by preventing plant species from dominating (Brose 2008; Mortensen *et al.* 2018). In most cases, animal- and resource-based coexistence were clearly associated with complementarity mechanisms leading to positive plant diversity-productivity relationships. However, despite relatively consistent effects of animals on plant coexistence, their associated plant diversity-productivity relationships can vary substantially. In chapter 2, I show that differences in animal movement can cause a lot of the observed variation, even leading to negative plant diversity effects. Animal and plant diversity (results from chapter 1; see also Wu *et al.* 2022), the generalism of herbivores (Thébault & Loreau 2003) and other network properties can play a role in explaining the variability as well. Despite the positive association between complementarity and coexistence, neither can explain diversity-productivity relationships entirely, suggesting that more subtle compositional patterns of the multi-trophic community may hold the key to understanding what drives them (Leibold *et al.* 2017; Bannar-Martin *et al.* 2018).

Investigating selection to identify BEF mechanisms

When investigated closer, animal- and resource-based mechanisms assemble some strikingly different plant communities. While both tend to foster coexistence, plant species differ in how they benefit from the different mechanisms. In chapter 2, animal-based processes tend to show that some plant species dominate ecosystem functioning (i.e. low Shannon diversity despite high species richness), especially when spatial overlaps in plants' resource access were high. The large variability of empirical net interactions found in chapter 3 show species-specific compositional effects that similarly indicate the benefitting of some species over others. In both cases, selection mechanisms are implied. In chapter 1, however, this becomes clearer as I could capture selection mechanisms using selection effects (Loreau & Hector 2001). The selection effects indicate that differences in plant's resource-use seem to favour productive, or no particular monoculture species in the random and non-random scenarios, respectively. In comparison, multi-trophic effects tend to only favour productive monoculture species when the diversity of the animal community and therefore the complexity of feeding interactions (Riede *et al.* 2010) is low. As animal diversity increases, less productive monoculture species are favoured disproportionally, leading to negative selection effects. Those species specifically benefit from dilution effects (i.e. reduced host-plant abundances in mixtures leading to reduced herbivore pressure; Otway *et al.* 2005), which are associated with positive plant diversity-productivity relationships (Barnes *et al.* 2020). Despite this and animal-based species selection not being a new phenomenon (Paine 1966), multi-trophic selection processes have rarely been object to BEF research (but see Cappelli *et al.* 2022). Their investigation therefore presents itself as an exciting opportunity for shedding some light on the processes involved in driving plant diversity-productivity relationships.

My call for a better understanding of multi-trophic selection mechanisms aligns with recent calls for investigating how multi-trophic interactions alter plant community assembly processes (Münkemüller *et al.* 2020) and how the resulting plant community composition affects ecosystem functions and BEF relationships (Leibold *et al.* 2017; Bannar-Martin *et al.* 2018). A typical approach used in BEF research partitions diversity in complementarity and selection effects (Loreau & Hector 2001). It is best known for reinforcing the idea that complementarity mechanisms drive plant diversity-productivity relationships (Hooper *et al.* 2005; Barry *et al.* 2019), and is an application of the Price equation originally developed to mathematically describe natural selection (Price 1970). One version of the Price equation allows to partition selection effects (sensu Loreau & Hector 2001) in abundance- and ecosystem functioning-based selection effects (Fox 2005). It has been used to show that negative selection effects often observed in BEF experiments may actually be related to species providing higher ecosystem functions when grown in a mixture without increasing in abundance (Wagg *et al.* 2017). This can be partially related to stronger effects of herbivore and pathogens (Cappelli *et al.* 2022), aligning with my findings of multi-trophic selection mechanisms affecting BEF relationships. An extension of the Price equation allows a more flexible comparison of communities, fostering the investigation of relations between compositional shifts and changes in ecosystem functions (Fox & Kerr 2012). In a globally distributed fertilization experiment in grasslands, this approach could show that an increased productivity in response to fertilization was due to an increased productivity of persistent species. The few gained and the many lost species had only weak effects on productivity, highlighting the dominance of resident species (Ladouceur *et al.* 2022). The Price equation can thus be utilized to investigate how changes in ecosystem functioning are related to compositional and environmental changes, potentially allowing a more in-depth understanding of multi-trophic selection processes and diversity mechanisms in general.

Include processes at appropriate scales

The research presented in this thesis uses a combination of spatially implicit (chapter 1 and 3) and spatially explicit approaches (chapter 2). Despite being spatially implicit, the mathematical formulation of the relationships investigated in chapter 3 describes interactions between neighbouring plants, and thus a process at a concrete spatial scale. Therefore, only chapter 1 is entirely based on assuming well-mixed systems, whereas chapter 2 and 3 describe processes at different spatial scales, aiming at their correct spatial representation. The decision of modelling plant individuals in chapter 2 and 3 has the advantage of describing ecological processes such as competition more accurately (DeAngelis & Grimm 2014). This can help to disentangle local effects of competition for belowground resources and light (Sapijanskas *et al.* 2013), and scale effects of local interactions to community responses, as demonstrated in chapter 3 (see also Fichtner *et al.* 2018). Modelling processes at an appropriate scale may also help to further scale up BEF relationships observed in local communities to global patterns of biodiversity change (Gonzalez *et al.* 2020). Additionally, local variations of ecosystem functions can be related to processes such as dispersal that act at larger spatial scales (Furey *et al.* 2022). However, as demonstrated for foraging related to animal home range sizes in chapter 2, finding the correct spatial scale of a process can be difficult and may differ between taxa, size classes, etc. Describing and capturing drivers of BEF relationships may therefore require multi-scale analyses and considerable advancement in understanding the involved processes. The work presented in this thesis can only scratch the surface of this issue, but sheds light on the difficulties associated with scaling feeding and local plant interactions, contributing to the ongoing endeavour of scaling BEF relationships (Gonzalez *et al.* 2020).

Outlook

Decades of research have highlighted the often positive effects of biodiversity for providing ecosystem functions. However, identifying the underlying mechanisms has proven difficult. By describing the interplay of co-occurring mechanisms, my thesis can help solving some of the challenges related to BEF mechanisms, but also provides a perspective on promising research directions.

One of the biggest challenges of the research presented in the thesis lies in the difficulties in associating empirical findings with process-based theoretical descriptions. I designed the spatially explicit simulations presented in chapter 2 with the BEF-China planting design in mind. Accordingly, the prediction of local net interaction effects in chapter 3 have a very similar underlying data structure as the output of the simulations. The problem of not being able to say with certainty which processes give rise to the observed net interactions estimated in chapter 3 can therefore be solved by bringing both approaches together. By using a virtual ecologist approach (Zurell *et al.* 2010) and manipulating processes in theoretical models, I can test how different mechanisms acting at different spatial scales collapse to local net interaction effects estimated by statistical models, and how they scale to the entire plant community. This framework is also flexible to include processes that were not investigated in this thesis but contribute to biodiversity effects (e.g. abiotic facilitation) or adapt to global change (e.g. due to drought stress or environmental stochasticity). The integration of process-based and predictive models can therefore serve as an important tool to identify current and future drivers of BEF relationships.

Many BEF experiments have shown that the positive effects of diversity on ecosystem functions such as productivity establish over time (e.g. Huang *et al.* 2018). This is often interpreted as niche adaptations of plant species to their biotic and abiotic environment (Cardinale *et al.* 2007). There is two ways by which plants can adapt. Either their niches move in niche-space, or their niches change in size. One expected response of species to co-occurring in the same habitat is a narrowing of their niches (Violle *et al.* 2012). This will result in a reduced interspecific competition due to a reduced niche overlap, and hence describe a process associated with complementarity mechanisms. However, a narrow species niche also indicates high intraspecific competition, which can be problematic, especially when diversity is low. Hence, niche adaptations should depend on the diversity of the community, but also on the local composition, as plants growing next to plants with similar niches would need to adapt more. While a high spatial and temporal turnover in grasslands allows plants to adapt over several generations, trees will need to adapt throughout their lifecycle, rendering an inter-individual adaptation a likely outcome (e.g. Proß *et al.* 2021).

To capture a plant's niche, functional traits have been repeatedly used (e.g. Blonder 2018). However, the data and associated effort required to test how inter-individual and inter-specific niches adapt to local diversity and species composition is demanding. Predicting values of leaf traits using spectroscopic methods is therefore a useful approach to make such investigations feasible (Burnett *et al.* 2021). Using this method, nine leaf traits from 480 trees in varying biotic and abiotic environments were recorded in the BEF-China experiment, yielding over 2000 trait values per trait (Davrinche & Haider 2021). Utilizing this data to test the sources of trait variation and accordingly understand species but also individual adaptation to local diversity and composition allows to better understand how trees utilize niche spaces, giving valuable insights into the mechanisms behind diversity effects. Expanding on this by relating leaf trait variation and ecosystem functions, such as productivity, can additionally help to establish the link between niche adaptation and BEF relationships.

Just like with the research presented in this thesis, accompanying these empirical investigations with theoretical models that describe processes explicitly can help to guide their interpretation and test our understanding of the underlying mechanisms. In an ongoing project I therefore help to integrate different scenarios of niche adaptation (i.e. niche shifts and niche contraction) with an algorithm of multi-trophic assembly processes (Bauer *et al.* 2022) to specifically investigate how those processes can explain establishment effects in BEF experiments. An underlying assumption of the multi-trophic assembly is that trophic similarities between animal species should reduce over time (i.e. limiting similarities; MacArthur & Levins 1967), reducing the redundancy of the species involved. Plant niche adaptations and multi-trophic assembly should therefore lead to a reduction of competition throughout the food web, maximizing the productivity of the entire system.

To properly describe niche adaptations of plants, describing the processes defining a niche more realistically is necessary. A recent study highlights different ways by which facilitative processes can expand a species' realized niche (Koffel *et al.* 2021), hinting at the potential effects on BEF relationships. An increased utilized niche space suggests that productivity increases. However, it can also increase interspecific niche overlaps comparable to the spatial resource overlaps simulated in chapter 2, leading to competitive interactions. It is therefore not unlikely that facilitative interactions, despite being largely associated with positive interactions, may have at least some negative consequences. This will be especially likely when complex multi-trophic processes are involved (Wright *et al.* 2017), and calls for a systematic investigation.

The research presented in this thesis highlights some of the difficulties associated with defining appropriate scales to describe processes involved in driving plant diversity-productivity relationships. However, capturing processes at appropriate scales allows to assess the heterogeneity associated with them, and can thus contribute to spatially scaling their effects on ecosystem functions (Thompson *et al.* 2021). Following this idea, I contribute to a project that predicts local litter decomposition in forests with a fixed species richness but differing planting schemes. Preliminary findings show that a more heterogeneous planting scheme will diversify the litter composition, leading to increased decomposition rates throughout the ecosystem. Hence, this work can demonstrate how scaling up ecosystem functioning patterns is possible once scaled down to the driving processes.

Conclusion

The aim of the thesis was to investigate how complex ecological interactions affect the often positive effects of plant biodiversity on plant productivity, and how to disentangle the associated mechanisms. My findings are in line with previous studies indicating the prevalence of complementarity mechanisms as the driving force in simulation and field experiments. When modelled explicitly, resource- and animal-based mechanisms similarly assembled diverse plant communities of complementary producer species, showing clear interactive effects. Resource-based limitations could cascade through the system and constrain the ability of multi-trophic mechanisms to modify plant diversity-productivity relationships. In general, animal-based processes could introduce a large variability in the response of plant diversity-productivity relationships, some of which can be explained by differences in animal movement. This highlights that modelling mechanisms at an appropriate spatial scale is necessary to understand their effects on plant diversity-productivity relationships fully, but will also help to successfully scale them. My findings further show that, regardless of the spatial context, animal- and resource-based mechanisms equally fostered coexistence, but favoured different plant species. I thus propose that investigating compositional differences resulting from different mechanisms will help to disentangle their effects, ultimately allowing better predictions of their response to changing biotic and abiotic environmental conditions. Finally, this work will help to conserve and restore ecosystems and their functions, potentially creating a sustainable future for humanity in which we can coexist with the uncountable richness of species and ecosystems that started evolving so many billion years ago.

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Appendix A: Supplementary – Chapter 1

S1: Detailed description of simulation model

We used an allometric-trophic-network model to simulate the complex trophic dynamics of ecosystems in a controlled environment (Schneider et al. 2016). It defines trophic interactions between different species based on their body-mass ratios and utilizes a set of differential equations that describes density changes of two limiting abiotic resources, and varying numbers of producers and animal consumers over time.

Simulating producer-resource interactions

The change in biomass density P_i of primary producer species i is calculated as

$$\frac{dP_i}{dt} = r_i G_i P_i - \sum_k A_k F_{ki} - x_i P_i \qquad [\text{mass area}^{-1}\ \text{time}^{-1}]\ (1)$$

with the first term describing resource-dependent growth, the second describing mortality due to predation by animals, and the third describing metabolic demands. Both the intrinsic growth rate r_i of species i, which defines its maximum possible growth rate, and the metabolic demands x_i of species i scale allometrically with body mass (Enquist et al. 1998) as $r_i = m_i^{-0.25}$ and $x_i = x_P m_i^{-0.25}$, respectively. The specific body-mass $m_i = 10^{\mu_P}$, where μ_P follows a uniform distribution on [0, 6], was randomly assigned to any producer species i. Metabolic demands were rescaled by $x_P = 0.138$ (Brose 2008). Growth of primary producer species i was further limited by the species specific growth factor G_i, defined by two limiting resource $j \in \{1, 2\}$ as

$$G_i = \min\left(\frac{\theta_{i1}}{K_{i1}+\theta_{i1}}, \frac{\theta_{i2}}{K_{i2}+\theta_{i2}}\right) \qquad (2)$$

where K_{ij} is the half-saturation density of resource j at which the resource uptake rate of primary producer i is half of its maximum, and follows a uniform distribution on [0.1, 0.2]. θ_{ij} is the concentration of resource j accessible by primary producer i.

To simulate different scenarios of resource-use dissimilarity (RUD; see methods in main text), we split both resources j in 16 compartments and spread resource concentrations of each considered resource j across C = 16 resource compartments. The change in resource concentrations N_{jn} of resource j in resource compartment n was defined as:

$$\frac{dN_{jn}}{dt} = D\left(\frac{S_j}{C} - N_{jn}\right) - v_j \sum_i r_i G_i P_i \frac{N_{jn}}{\theta_{ij}} \qquad [\text{mass area}^{-1}\ \text{time}^{-1}]\ (3)$$

The first term describes the rate at which resources are renewed. It is limited by the turnover rate D, which was set to 0.25. The supply concentration S_j represents the maximum concentration of resource j. It was set to 50 and 25 for resources 1 and 2, respectively. As we defined each compartment n to be quantitatively the same, we split the supply concentration S_j equally between compartments. The second term captures the loss of resources due to primary production, which is similar to the resource-dependent growth term used to calculate the change in primary producer densities but separated for each resource compartment. The relative content of resource j in the biomass of primary producers is described as v_j and was set to 1 and 0.5 for resources 1 and 2, respectively. By keeping the ratio between S_j and v_j the same for both resources j, all resources considered can limit the growth of primary producers and consequently play a role in determining competitive advantages while contributing differently to primary production. The pool of resource j accessible by producer species i corresponds to the sum of resource concentrations in the compartments it has access to:

$$\theta_{ij} = \sum_n \vartheta_{in} N_{jn} \qquad (4)$$

with $\vartheta_{in} = 1$ if species i can access resource compartment n, $\vartheta_{in} = 0$ otherwise.

At the end of the simulations, we quantified primary production in equilibrium as the summed up resource uptake rate of both resources j, in all compartments n, and for all primary producer species i:

$$Y = \sum_i Y_i = \sum_j \sum_n v_j \sum_i r_i G_i P_i \frac{N_{jn}}{\theta_{ij}} \qquad [\text{mass area}^{-1}\ \text{time}^{-1}]\ (5)$$

Creating network topology and simulating animal consumers

Similar to primary producer species, each animal species k was characterized by its specific body-mass $m_k = 10^{\mu_A}$ with the exponents drawn randomly from a uniform distribution on [2, 12]. To create a viable network topology, we calculated the probability of animal consumer species x to feed on an encountered animal or producer resource species z as

$$L_{xz} = \left(\frac{m_x}{m_z R_{opt}} e^{1 - \frac{m_x}{m_z R_{opt}}} \right)^{\gamma} \tag{6}$$

which describes a feeding kernel that is maximized at the optimal consumer-resource body-mass ratio R_{opt} = 100. The width of the kernel is defined by γ = 2, and constrains generalism. Low probabilities with $L_{xz} \leq 0.01$ were set to be zero. We only considered animal communities where each species had at least one resource species at maximum producer richness (i.e., 16 producer species). When lowering producer richness (see main text), animal species that lost their resource species were removed before simulations.

The change of biomass densities of species k, A_k over time, was simulated as

$$\frac{dA_k}{dt} = e_P A_k \sum_i F_{ki} + e_A A_k \sum_l F_{kl} - \sum_l A_l F_{lk} - x_k A_k \qquad \text{[mass area}^{-1}\text{ time}^{-1}\text{]} \ (7)$$

with the first term describing increases due to the summed up herbivorous feeding on primary producer species i, with a conversion efficiency e_P = 0.545 (Lang et al. 2017). Similarly, the second term describes the summed up carnivorous feeding on animal species i, with a conversion efficiency of e_A = 0.906 (Lang et al. 2017). The third term captures mortality due to predation by animals i in the same way as for primary producers. The last term represents metabolic demands of animal species k, which scales allometrically with body-mass (Ehnes et al. 2011) as $x_k = x_A {m_k}^{-0.305}$, with a scaling constant x_A = 0.141 (Ehnes et al. 2011). All trophic interactions include feeding rates

$$F_{xz} = \frac{\omega_x b_{xz} Z_z^{1+q_{xz}}}{1 + cX_x + \omega_x \sum_\zeta b_{x\zeta} h_{x\zeta} Z_\zeta^{1+q_{x\zeta}}} \cdot \frac{1}{m_x} \qquad \text{[time}^{-1}\text{]} \ (8)$$

as a function of the biomass densities X_x and Z_z of the consumer species x and resource species z, respectively. Feeding rates capture the proportion of biomass of resource species z consumer species x consumes. By dividing by body-mass, the per-capita feeding rate is transformed to be relative to one unit biomass. Consumers with multiple resource species have to split their feeding efforts, captured in the relative consumption rate ω_x, defined as the inverse of the number of prey species of consumer x. Apart from spending time on searching and handling resources, consumers lose time due to consumer interference c (e.g. to territorial behaviour or reproduction) which acts as a self-regulation mechanism and was drawn from a normal distribution ($\mu_c = 0.8$, $\sigma_c = 0.2$) for each food-web independently. Further, we used an interaction-specific, allometric Hill-exponent $1 + q_{xz}$ (Kalinkat et al. 2013), which determines the functional response type of the interaction. It was calculated as:

$$q_{xz} = \frac{q_{max} R_{xz}^2}{q_0^2 + R_{xz}^2} \qquad (9)$$

with R_{xz} being the consumer-resource body-mass ratio of consumer species x and resource species z. By setting $q_{max} = 1$, we assure that the functional response varies between the classic type II ($q_{xz} = 0$) and type III ($q_{xz} = 1$). At optimal consumer-resource body-mass ratio $R_{opt} = 100$ we wanted q_{xz} to be at intermediate levels. Therefore, we also set $q_0 = 100$. At higher consumer-resource body-mass ratios, the functional response gets closer to the classic type III, which lowers the feeding rates at low resource densities. The feeding rate was further determined by the capture coefficient:

$$b_{xz} = b_0 m_x^{\beta_x} m_z^{\beta_z} L_{xz} \qquad [\text{area time}^{-1}] \ (10)$$

which describes the success rate of consumer species x to capture resource species z. It is based on the assumption that an encounter is more likely with higher movement speeds of both consumer and resource species. Since movement speed scales allometrically and based on feeding type (Hirt et al. 2017), we drew β_x and β_z from according normal distributions (carnivore: $\mu_\beta = 0.42$, $\sigma_\beta = 0.05$, omnivore: $\mu_\beta = 0.19$, $\sigma_\beta = 0.04$, herbivore: $\mu_\beta = 0.19$, $\sigma_\beta = 0.04$, primary producer:

$\mu_\beta = 0$, $\sigma_\beta = 0$). Similarly, we assumed different values for b_0 based on the feeding type of the consumer (carnivore: $b_0 = 50$, omnivore: $b_0 = 100$, herbivore: $b_0 = 200$). The handling time:

$$h_{xz} = h_0 m_x^{\eta_x} m_z^{\eta_z} \qquad \text{[time] (11)}$$

scales with the body-mass of consumer and resource species to the power of η_x ($\mu_{\eta_x} = -0.48$, $\sigma_{\eta_x} = 0.03$) and η_z ($\mu_{\eta_z} = -0.66$, $\sigma_{\eta_z} = 0.02$) respectively. It captures the time spent attacking, ingesting, and digesting the resource species. The scaling constant h_0 was set to 0.4. All parameters drawn from normal distributions had to fall within the inclusive limits of $\mu \pm 3\sigma$ or be redrawn otherwise.

Simulation setup

Initial biomass densities of primary producer and animal species were randomly drawn from uniform distributions on [0, 1]. Resource densities were initialized for the whole resource-pool with random values drawn from uniform distributions on $[S_j / 2, S_j]$, which were then evenly split between compartments. We ran simulations until $t = 150.000$. Species that reached biomass densities $< 10^{-6}$ during simulations were assumed to be extinct, and their values were set to 0. For an overview of the parameters used in the simulation, see Tab. S1.

We ran all simulations in Julia 1.2.0 (Bezanson et al. 2017) using the DifferentialEquations package (Rackauckas & Nie 2017) and utilizing a stiffness detection algorithm that automatically switched between the solvers Vern7 for non-stiff problems and Rodas4 for stiff problems.

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Tab. S1: Parameters, their explanation and values used in the simulation.

Parameter	Explanation	Value
b_0	scaling constant of capture coefficient	carnivore: 50 omnivore: 100 herbivore: 200
β_x	capture coefficient's allometric scaling exponent of consumer species x	carnivore: N(0.42, 0.05^2) omnivore: N(0.19, 0.04^2) herbivore: N(0.19, 0.04^2)
β_z	capture coefficient's allometric scaling exponent of resource species z	carnivore: N(0.42, 0.05^2) omnivore: N(0.19, 0.04^2) herbivore: N(0.19, 0.04^2) primary producer: 0
C	number of resource compartments n	16
c	time lost due to consumer interference	N(0.8, 0.2^2)
D	turnover rate of resources	0.25
e_A	conversion efficiency of animal to animal biomass	0.906
e_P	conversion efficiency of primary producer to animal biomass	0.545
η_x	handling time's allometric scaling exponent of consumer species x	N(-0.48, 0.03^2)
η_z	handling time's allometric scaling exponent of resource species z	N(-0.66, 0.02^2)
γ	constant that scales width of probability curve given by L_{xz}	2
h_0	scaling constant of handling time	0.4
K_{ij}	half-saturation densitiy of resource j	U(0.1, 0.2)

Table S1 - continued

Parameter	Explanation	Value
m_i	body-mass of primary producer species i	$10^{U(0, 6)}$
m_k	body-mass of animal species k	$10^{U(2, 12)}$
q_{max}	maximum value of Hill-exponent	1
R_{opt}	optimal consumer-resource body-mass ratio	100
S_j	maximum concentration of resource j	for j=1 S_j=50
		for j=2 S_j=25
v_j	relative content of resource j in primary producers	for j=1 v_j=1
		for j=1 v_j=0.5
x_A	scaling constant of metabolic demands of animals	0.141
x_P	scaling constant of metabolic demands of primary producers	0.138

S2: Statistical analysis

We analysed the independent and the interactive effects of resource-use complementarity and multi-trophic interactions on complementarity effects using a linear model. To deal with the skewness of the data without overemphasizing values < 1, we log(x+1)-transformed complementarity effects prior to analysis. The statistical analysis was performed in R 4.1.0 (R-Core-Team 2021).

Tab. S2: Results of linear regression of animal richness, resource-use dissimilarity, and their interaction on complementarity effects in 16-species mixtures. Adjusted $R^2 = 0.50$. See supplementary 2 for further description of the method.

Coefficient	Estimate	SE	t-value	p-value
(Intercept)	0.951	0.038	25.190	< 0.001
animal richness	0.019	0.001	18.025	< 0.001
resource-use dissimilarity	2.260	0.064	35.100	< 0.001
animal richness * resource-use dissimilarity	-0.017	0.002	-9.191	< 0.001

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Fig. S1: Effects of resource-use dissimilarity RUD on the realized resource-use dissimilarity of primary producers H_{exp}. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

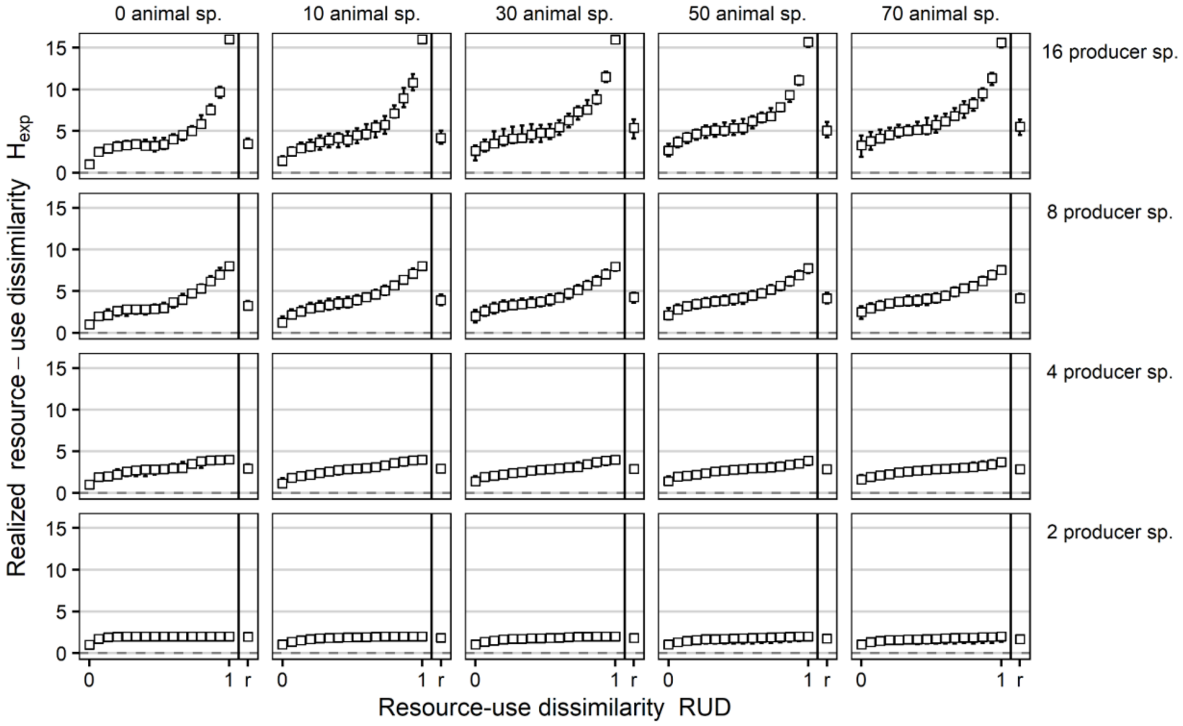


Fig. S2: Effects of resource-use dissimilarity RUD on net diversity effects ΔY of the primary producer community. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

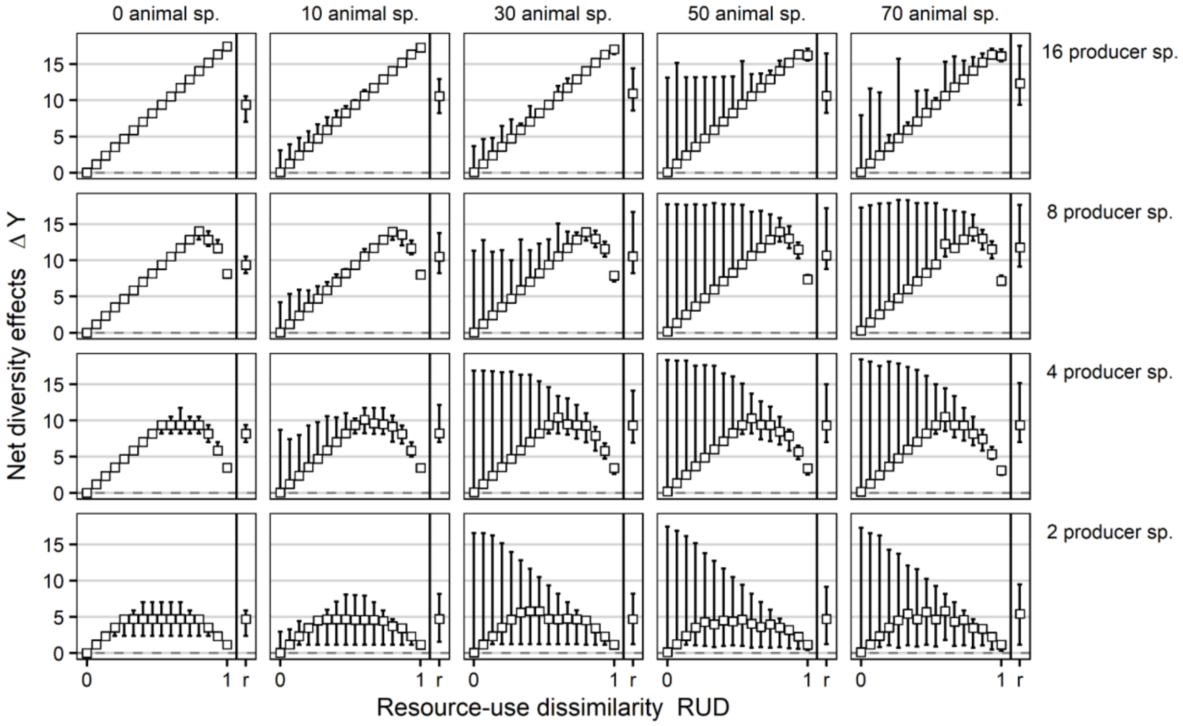


Fig. S3: Effects of resource-use dissimilarity RUD on complementarity effects CE of primary productivity. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

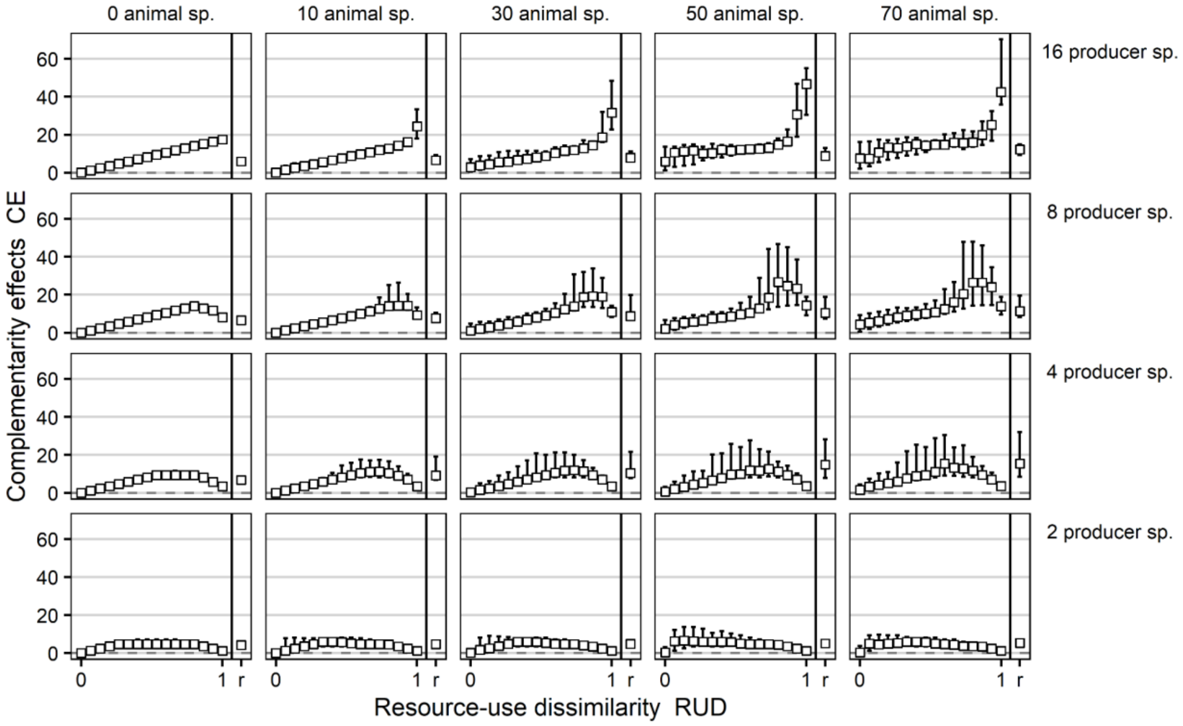


Fig. S4: Effects of resource-use dissimilarity RUD on selection effects SE of primary productivity. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

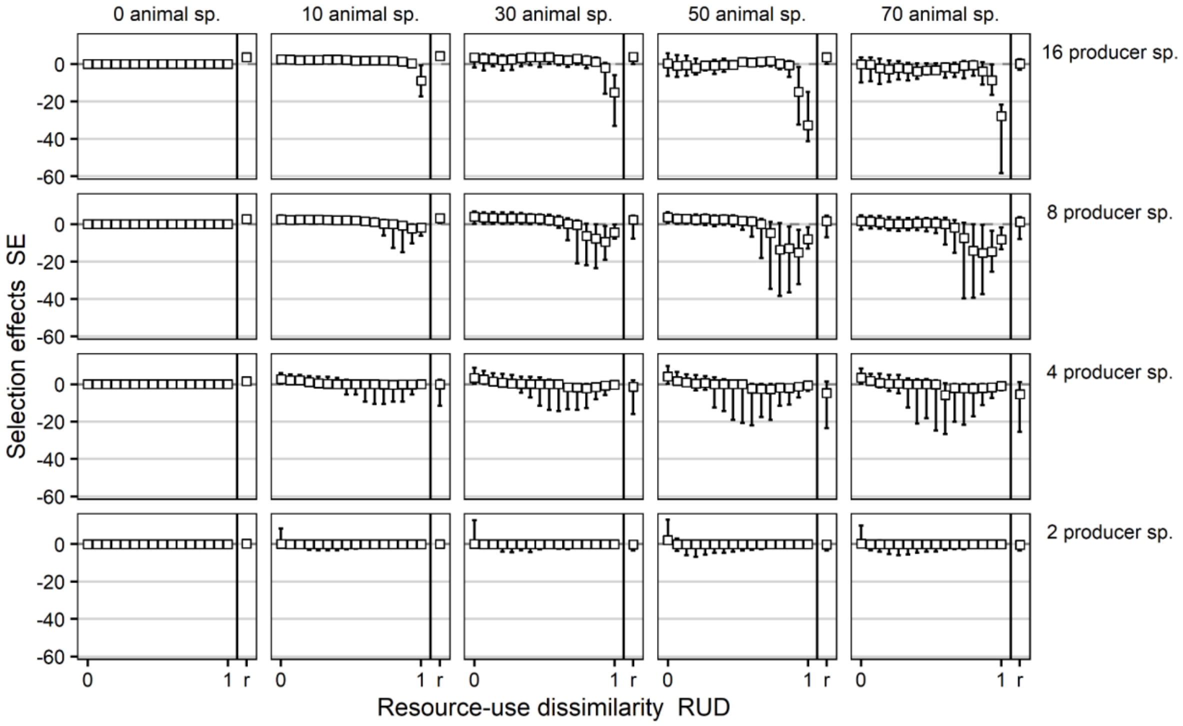


Fig. S5: Effects of resource-use dissimilarity RUD on the relative survival of the primary producer community. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

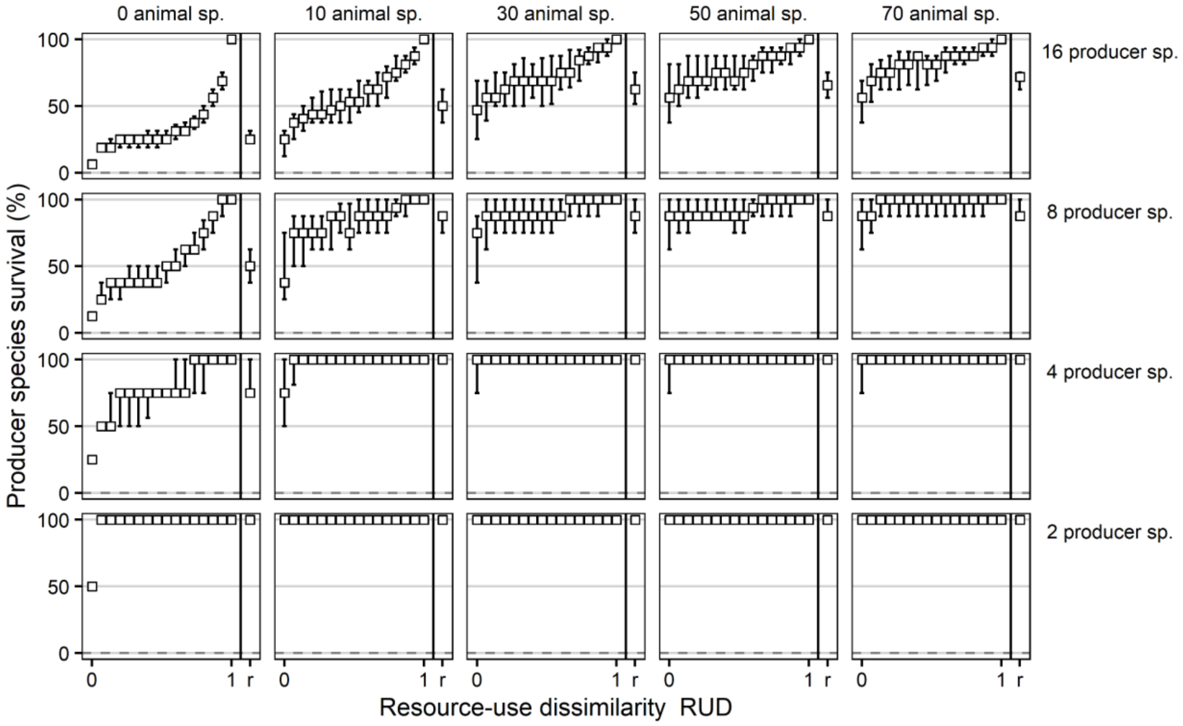


Fig. S6: Effects of resource-use dissimilarity RUD on observed yield Y_O (blue) and expected yield Y_E (red) of the primary producer community. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).

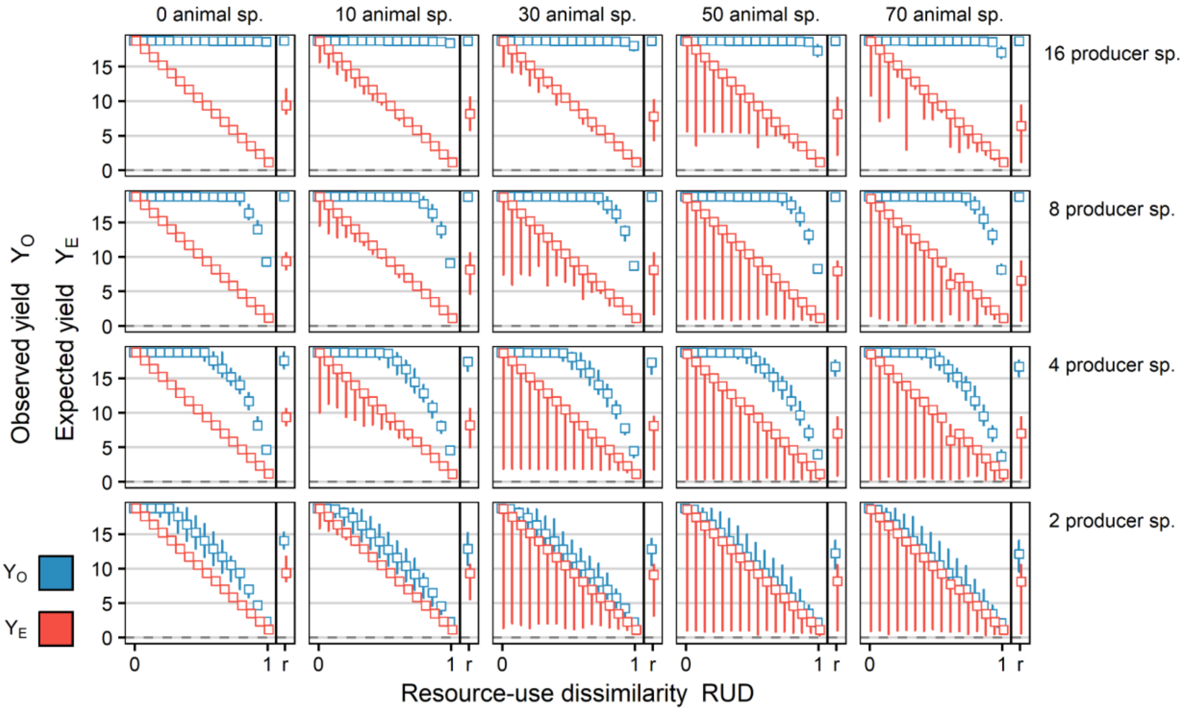


Fig. S7: Effects of $\log_2$ producer richness on producer biomass densities. Effects are shown for different levels of multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line.

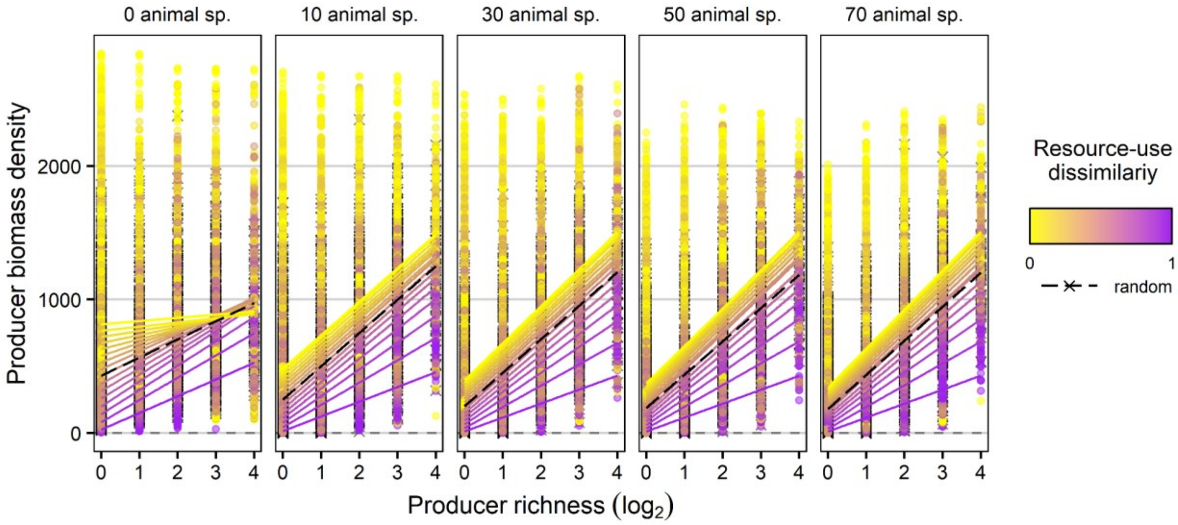


Fig. S8: Effects of relative primary producer species survival on the $\log_{10}$ biomass of the surviving producer species. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line.

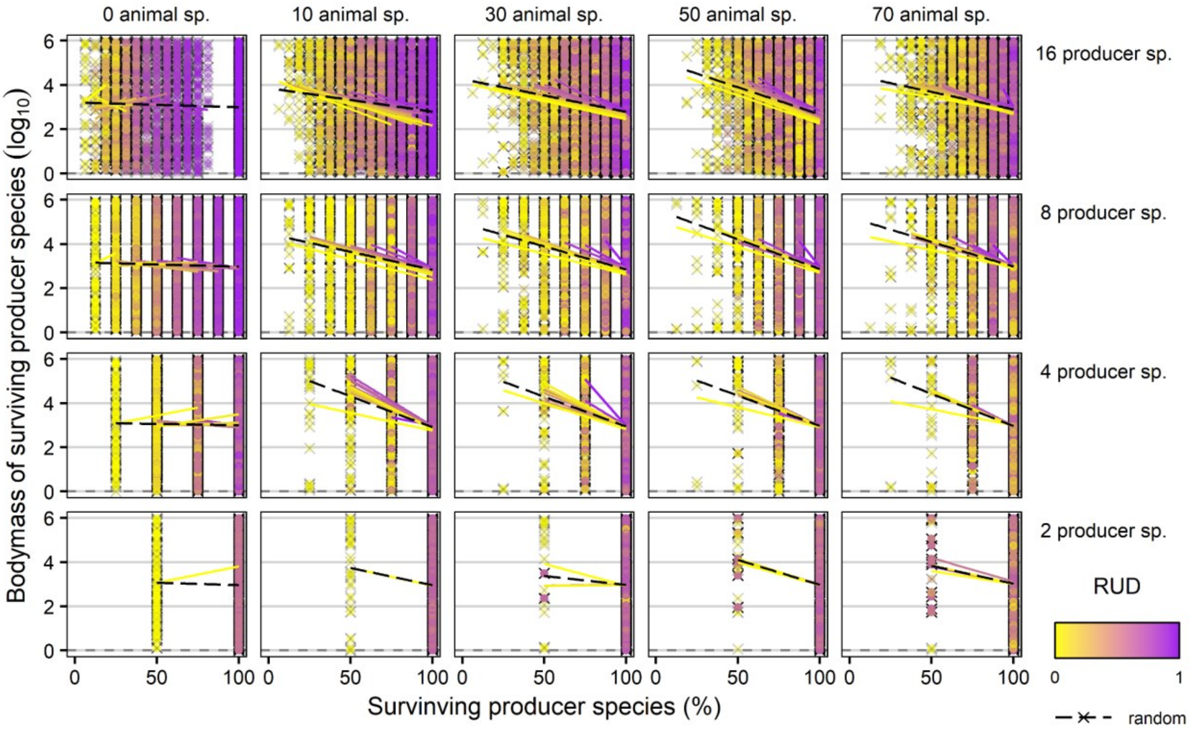


Fig. S9: Effects of $\log_{10}$ biomass of the surviving producer species on their productivity relative to their maximum possible productivity (i.e., used resources / accessible resource). Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line.

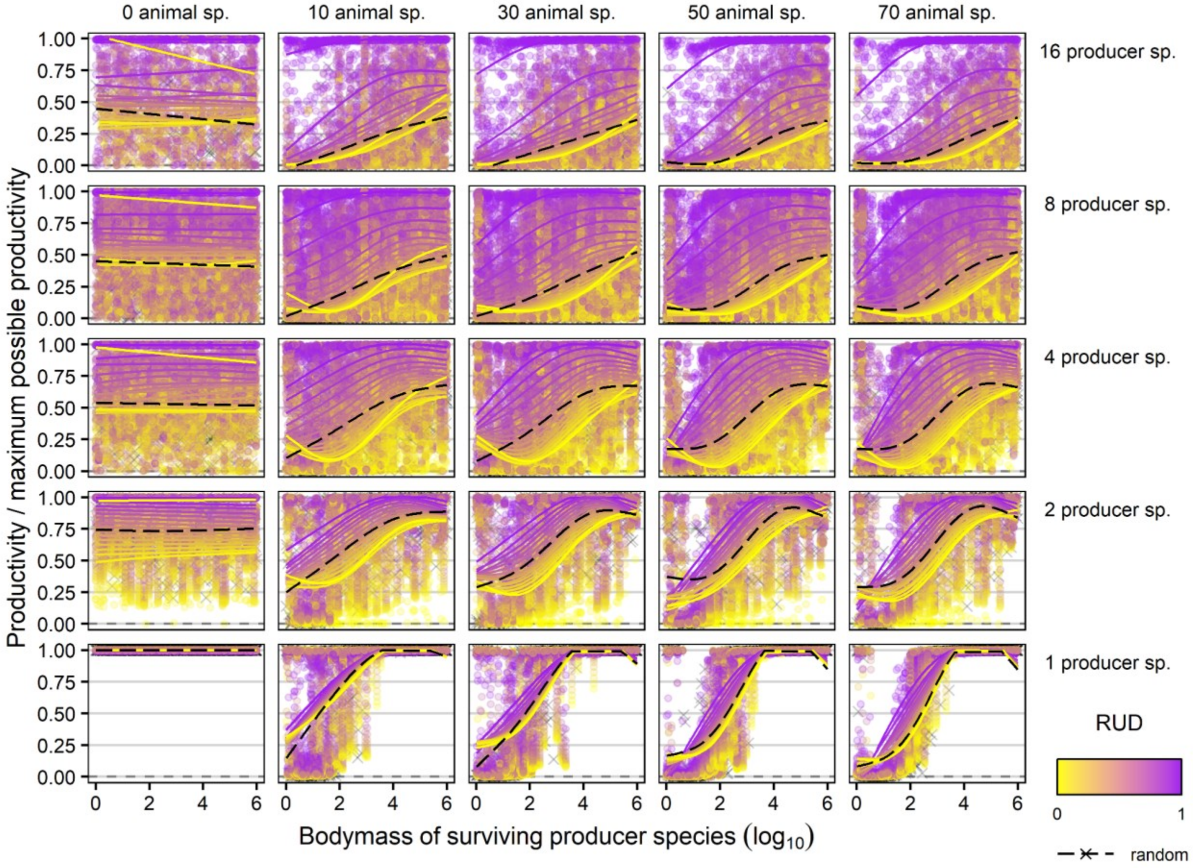


Fig. S10: Effects of relative primary producer species survival on complementarity effects CE. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line. To improve readability, only 95% of the simulated food-webs are shown.

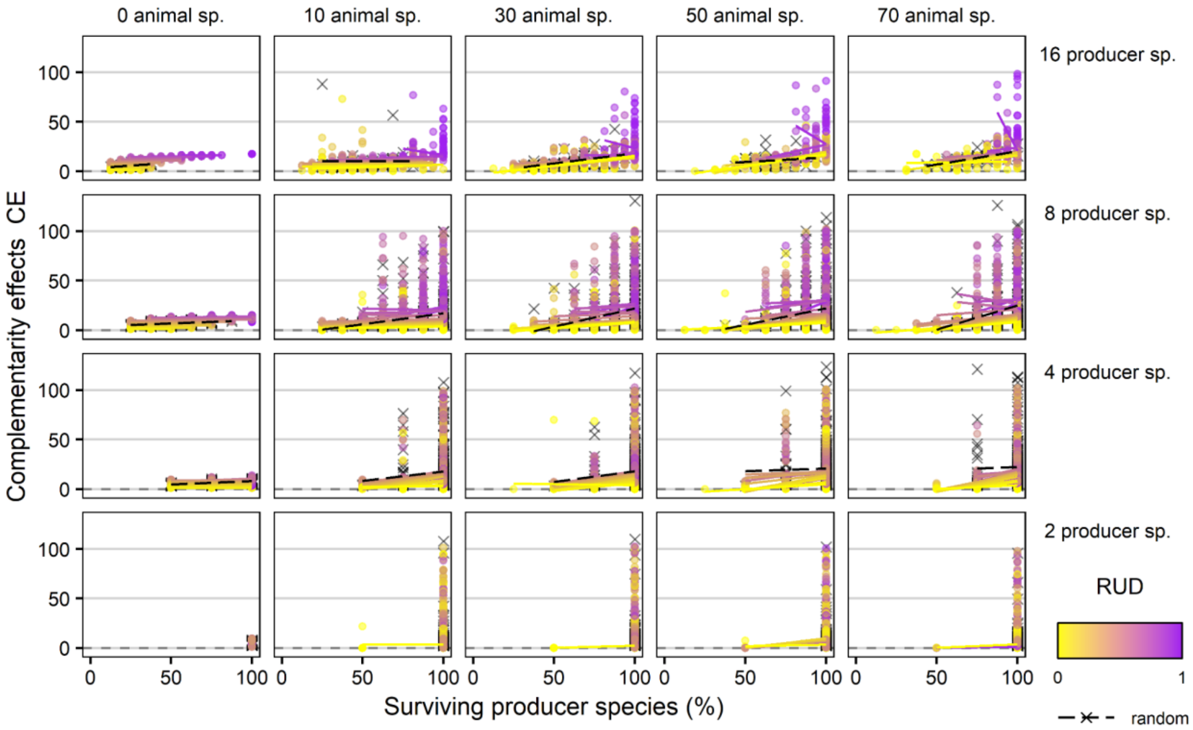


Fig. S11: Effects of relative primary producer species survival on selection effects SE. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line. To improve readability, only 95% of the simulated food-webs are shown.

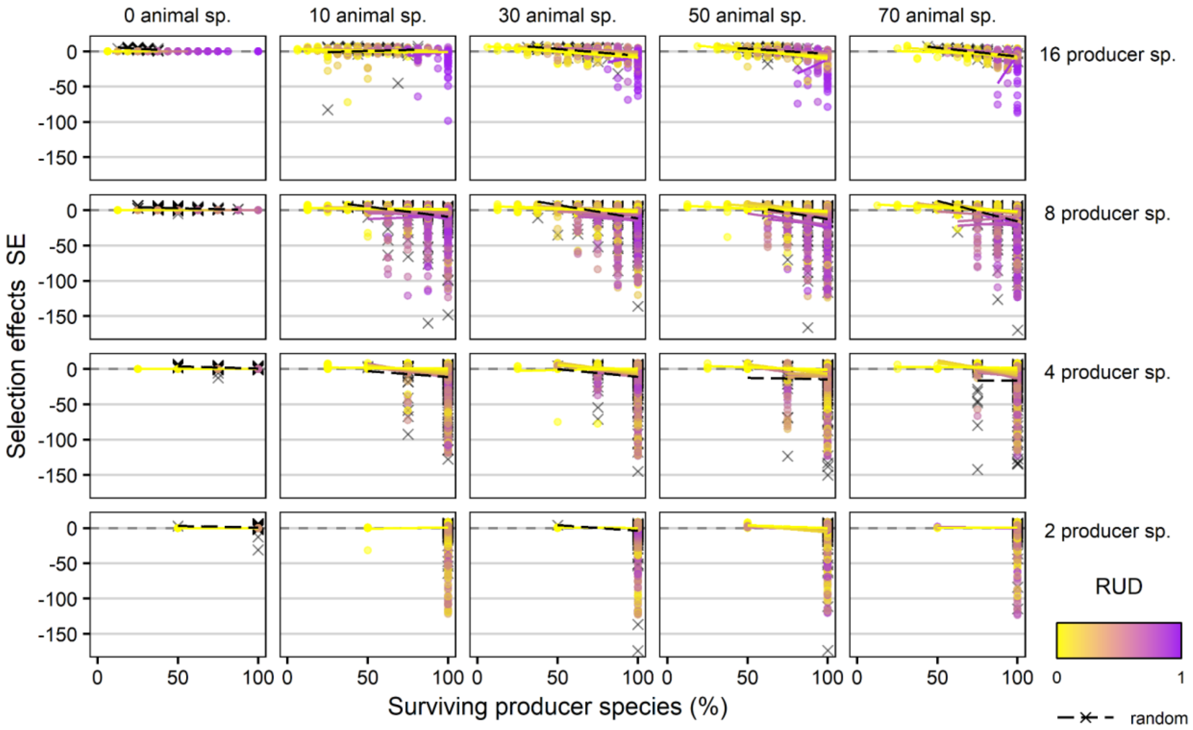


Fig. S12: Effects of relative primary producer species survival on net diversity effects ΔY. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). The level of the resource-use dissimilarity (RUD) gradient is indicated by the coloured points and lines (yellow: low, purple: high). The random RUD scenario is indicated by black crosses and the dashed line. To improve readability, only 95% of the simulated food-webs are shown.

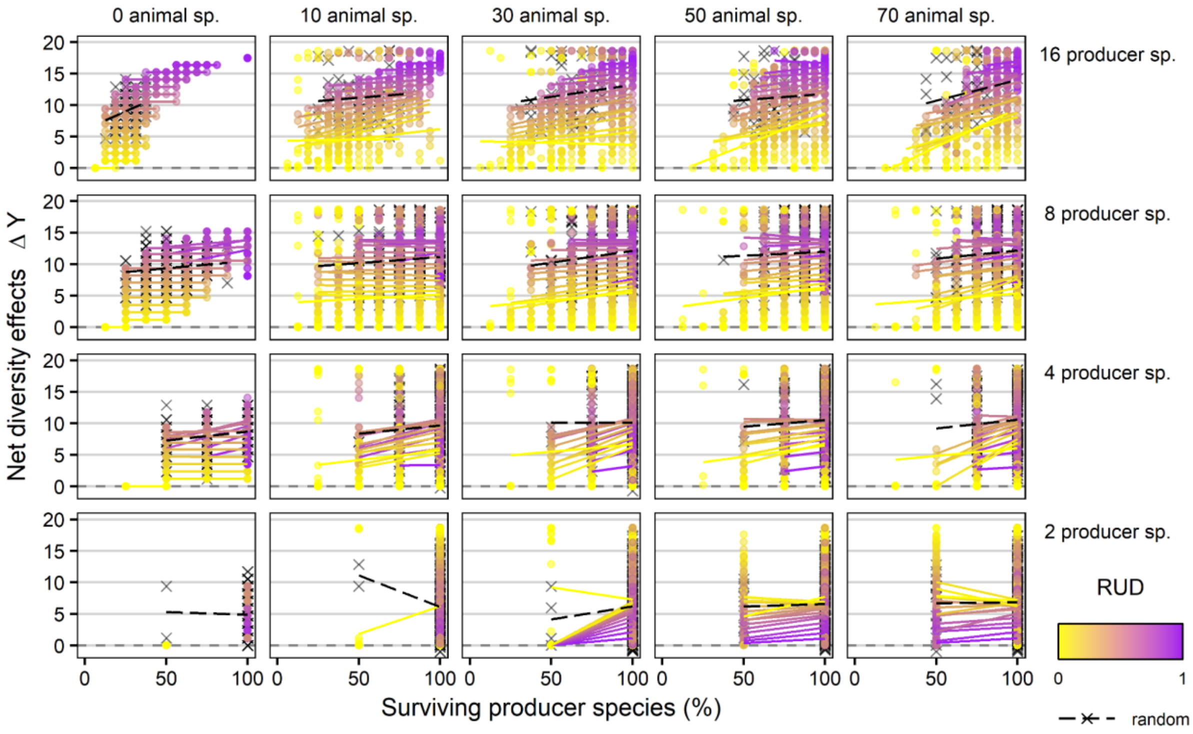
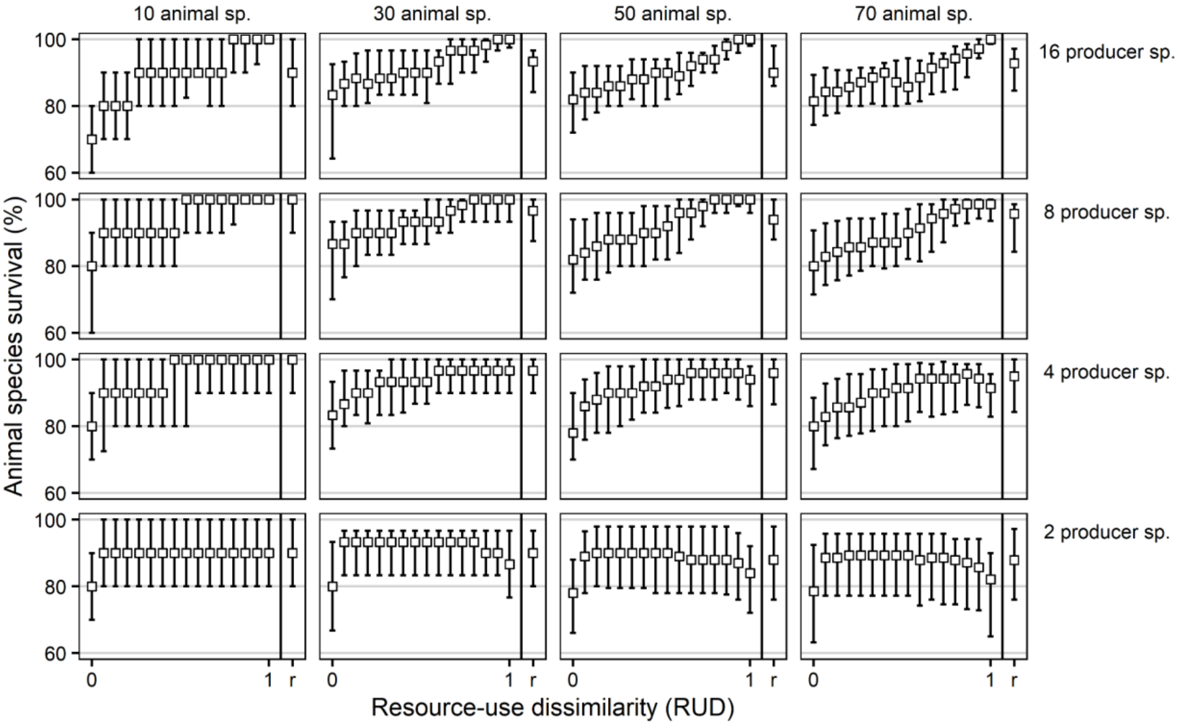


Fig. S13: Effects of resource-use dissimilarity RUD on the relative survival of the animal community. r denotes the random RUD scenario. Effects are shown for different levels of producer (rows) and multi-trophic animal richness (columns). Error bars show 25th and 75th; squares show 50th percentile (i.e., median).



Appendix B: Supplementary – Chapter 2

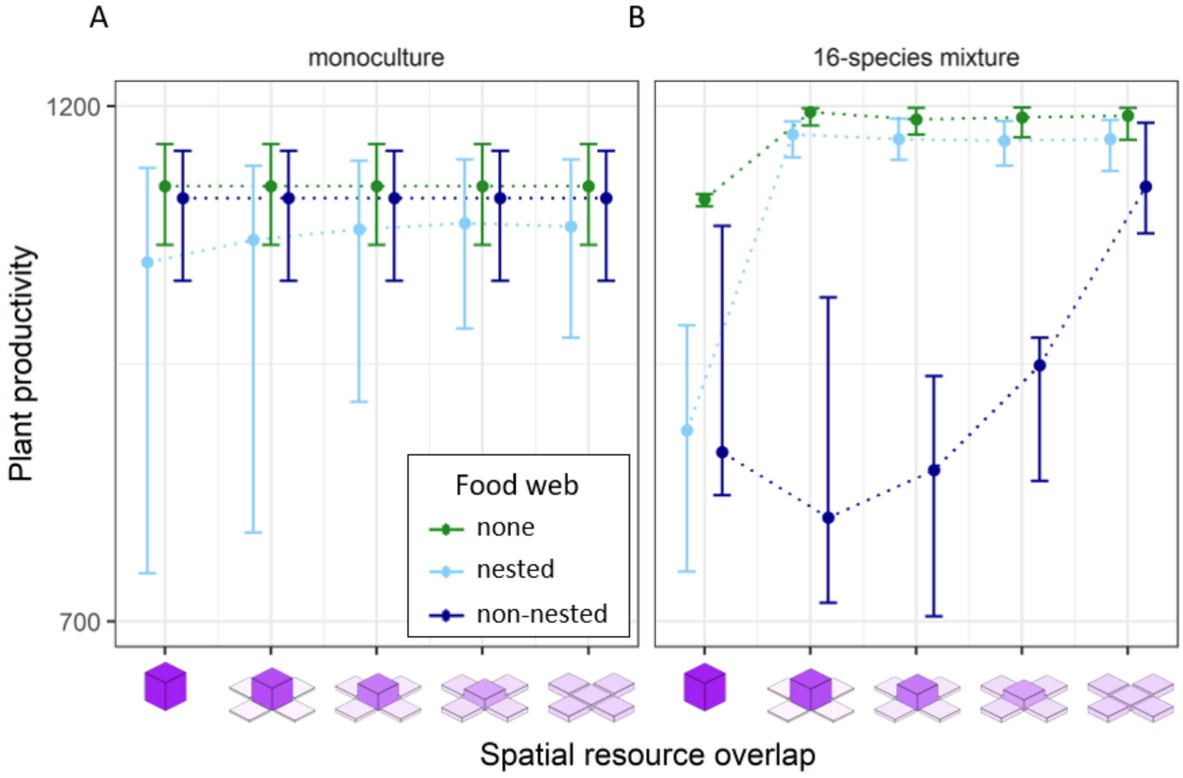


Fig. S1: Effects of increasing the spatial overlap in plant resource access ('spatial resource overlap') on plant productivity for the three food web scenarios considered, i.e. without food web ('none'), with spatially nested food web ('nested'), and with spatially non-nested food web ('non-nested'). Plant productivity is measured for the entire community. (A) Effects in plant species monocultures and (B) 16-species mixtures. Points show 50th percentile (i.e., median); Error bars show 25th and 75th percentile. Unviable monocultures not included.

Tab. S1: Parameters for simulations with their explanation and used values

Parameter	Explanation	Value
b_0	scaling constant of capture coefficient	carnivore: 50, omnivore: 100, herbivore: 400

β_i
β_j
	allometric scaling exponents of capture coefficient for consumer species i and resource species j respectively	carnivore: N(0.42, 0.05);
		omnivore: N(0.19, 0.04);
		herbivore: N(0.19, 0.04);
		plant: N(0, 0)

c_i	time lost due to consumer interference	N(0.8, 0.2)
D	turnover rate of resources	0.25
e_j	biomass conversion efficiency for resource species j	animals: 0.906, plants: 0.545
η_i	allometric scaling exponents of handling time for consumer species i and resource species j respectively	consumer: N(-0.48, 0.03); resource: N(-0.66, 0.02)
γ	constant that scales width of probability curve given by L_{xz}	2
h_0	scaling constant of handling time	0.4
K_{il}	half-saturation density of resource j at which resource uptake rate of primary producer species i is half of its maximum	U(0.1, 0.2)
m_i	body mass of animal species i	10^U(0, 8)
q_{max}	maximum value of Hill-exponent	1

q_0	half saturation value for Hill-exponent	100
R_{opt}	optimal consumer-resource body mass ratio	100
$n_{(ik)(k')}$	relative effort plant species i in patch k puts in taking resources from patch k'; defines spatial resource overlap gradient	$n_{(ik)(k)} = 1.0$, $n_{(ik)(k')} = 0.0$; $n_{(ik)(k)} = 0.8$, $n_{(ik)(k')} = 0.05$; $n_{(ik)(k)} = 0.6$, $n_{(ik)(k')} = 0.1$; $n_{(ik)(k)} = 0.4$, $n_{(ik)(k')} = 0.15$; $n_{(ik)(k)} = 0.2$, $n_{(ik)(k')} = 0.2$
S_l	maximum concentration of resource l	$S_1 = 50$; $S_2 = 25$
v_{li}	relative content of resource l in plant i	$v_{1i} = N(2/3, 0.05)$; $v_{2i} = 1 - v_{1i}$
x_i	per unit biomass metabolic demands	animals: $0.141 * m_i^{-0.305}$ plants: $0.138 * B_{ik}^{-0.25}$
y_i	scaling parameter for maximum feeding rate of herbivore species i	N(6, 1)

Appendix C: Supplementary – Chapter 3

S1: Different random effect structures

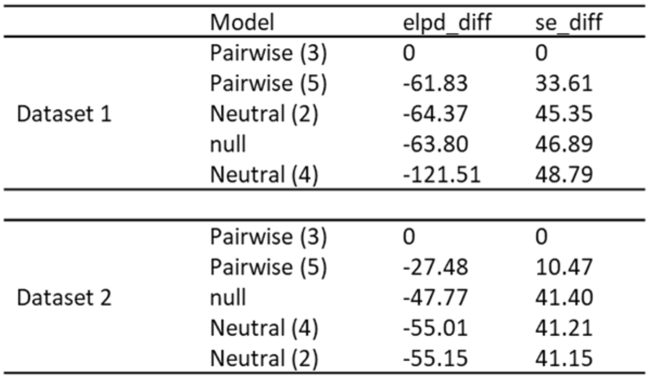
In addition to allowing the plot effects and annual environmental changes only affect the intrinsic growth, we also tested those environmental factors affecting intrinsic growth and interactions simultaneously, which were expressed by:

$$B_{t+1,i} - B_{t,i} = \left(\beta_{s(i)}\, B_{t,i}^{\theta} + \sum_{j \in n_j}^{nj \le 8} \alpha_{ave} B_{t,j}^{b}\right) * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) \qquad (4)$$

$$B_{t+1,i} - B_{t,i} = \left(\beta_{s(i)}\, B_{t,i}^{\theta} + \sum_{j \in n_j}^{nj \le 8} \alpha_{s(i),s(j)} B_{t,j}^{b}\right) * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) \qquad (5)$$

The model comparison results from both datasets showed the random effect structure that only affects the intrinsic growth performed better in the pairwise models, suggesting the temporal and environmental conditions mainly influence the intrinsic growth in BEF-China (Tab. S1).

Tab. S1: Model comparison results for all the models considered



	Model	elpd_diff	se_diff
Dataset 1	Pairwise (3)	0	0
	Pairwise (5)	-61.83	33.61
	Neutral (2)	-64.37	45.35
	null	-63.80	46.89
	Neutral (4)	-121.51	48.79
Dataset 2	Pairwise (3)	0	0
	Pairwise (5)	-27.48	10.47
	null	-47.77	41.40
	Neutral (4)	-55.01	41.21
	Neutral (2)	-55.15	41.15

S2: Testing the identifiability of our model

Given the complexity of *the pairwise interaction model*, we tested the feasibility to accurately retrieve all parameters in the model. We fitted the pairwise interaction model to simulated data with known parameters that mimic the structure of the empirical data (see methods in main). Specifically, we simulated datasets that span the full species richness gradient up to 8 species, with the considered species compositions following the broken stick design (i.e. all species in monoculture and 8 species mixture, as well as the species combinations {1, 2}, {3, 4}, {5, 6}, {7, 8}, {1, 2, 3, 4}, {5, 6, 7, 8}). We limited our simulation to the core area of the plots considered in the empirical data, simulating the growth of 6x6 trees for monocultures and 2 species mixtures, and 12x12 trees for 4 and 8 species mixtures. The identity of each tree was assigned randomly. To account for edge effects, we used periodic boundary conditions. As for the empirical data, we only considered edge trees as neighbours but not as focal. Each composition was replicated 3 times, leading to a total of 45 plots. Tree growth was simulated over 7 time steps, representing the 7 years of recorded empirical data.

Prior to simulation, we defined and recorded the parameters for our statistical model to estimate (Tab. S2). The 64 species-specific interaction coefficients $\alpha_{s(i),s(j)}$ were sampled from a normal distribution. We did not assume a reciprocity between the effects of species 1 on 2 and the effects of species 2 on 1. The species-specific scaling coefficient of the intrinsic growth term $\beta_{s(i)}$ was sampled from a normal distribution and constrained to positive values. In addition to the estimated parameters, we had to define additional parameters to simulate the testing data set. Most importantly, we had to assign starting biomasses $B_{t,i}$ to initiate tree growth (i.e. for t = 1). We randomly sampled biomass values from a lognormal distribution as it approximates the real distribution of our starting biomasses sufficiently well. We introduced mortality to account for the trees that died in the empirical datasets. Finally, we included process and measurement errors in our simulation framework. While the former captures growth processes which are not described in our model but propagate over time, the latter mimics errors done during measurement, hence has no effect on growth. Both errors were applied by sampling biomasses $B_{t,i}$ from a lognormal distribution. While the so retrieved biomasses replaced the old values during simulation to apply the processes error, the measurement error was applied to all biomasses after simulation. We assumed that starting biomasses, mortality rates, as well as measurement and process errors were independent of species identity.

Following the simulation process described above, we generated 10 sets of data. Subsequently, we fitted those ten datasets with the pairwise interaction model excluding the random effect (see equation 3). We compared the estimated parameters with the values used to generate the data (Fig. S1). The results showed that no estimated parameter values drastically deviated from the true values. In particular, the interaction coefficients $\alpha_{s(i),s(j)}$ can be accurately retrieved (Fig. S1(b)), proving the interaction coefficients can be effectively identified with our model and empirical data.

Tab. S2: Parameter components and distributions used in simulations.

Parameter and initial values		Distribution/value	Unique to
$\beta_{s(i)}$	Metabolic growth coefficient	Gaussian(mean 4, sd 1)	species
θ	Metabolic exponent	0.8	universal
b	Scaling exponent of the biomass of the neighbouring tree	0.2	universal
$\alpha_{s(i),s(j)}$	Interaction coefficients	Gaussian(mean 0, sd 1)	species pair
ε_p	Process error	0.05	universal
ε_m	Measurement error	0.05	universal
$B_{1,i}$	The biomass of the first year	Lognormal(mean 4, sd 1.1)	universal
$B_{t+1,i}$	The biomass of the next year	Lognormal(mean $B_{t+1,i}$, sd 0.05)	universal
M	Mortality rate	0.1	universal

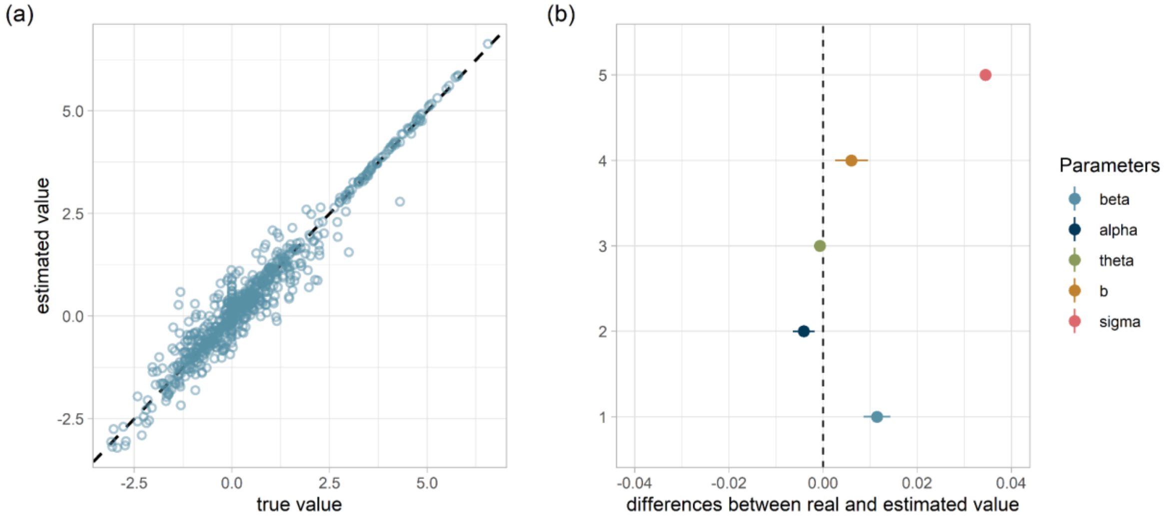
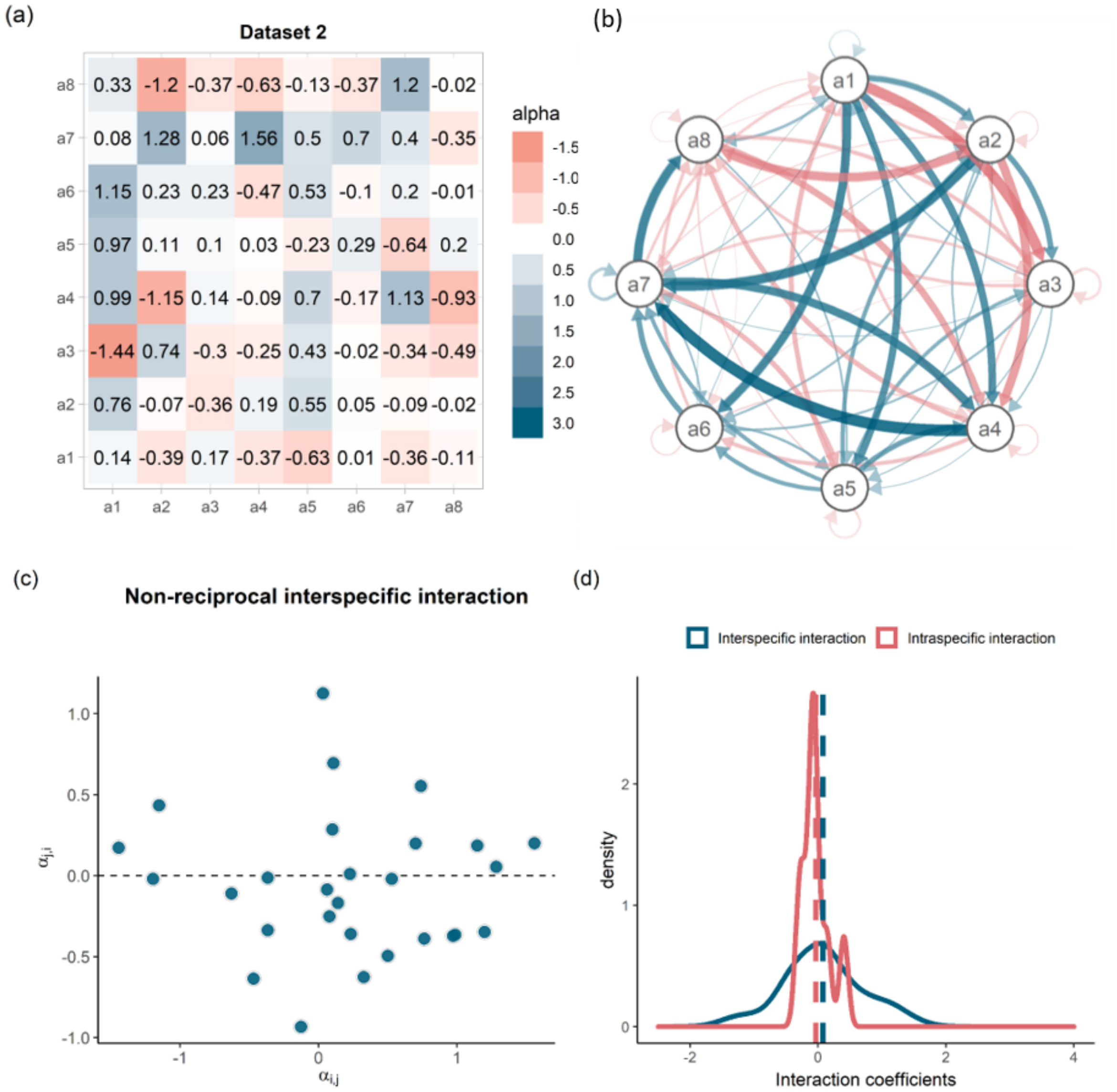


Fig. S1: True parameters and fitted model parameter estimates.

S3: Results from dataset 2



	a1	a2	a3	a4	a5	a6	a7	a8
a8	0.33	-1.2	-0.37	-0.63	-0.13	-0.37	1.2	-0.02
a7	0.08	1.28	0.06	1.56	0.5	0.7	0.4	-0.35
a6	1.15	0.23	0.23	-0.47	0.53	-0.1	0.2	-0.01
a5	0.97	0.11	0.1	0.03	-0.23	0.29	-0.64	0.2
a4	0.99	-1.15	0.14	-0.09	0.7	-0.17	1.13	-0.93
a3	-1.44	0.74	-0.3	-0.25	0.43	-0.02	-0.34	-0.49
a2	0.76	-0.07	-0.36	0.19	0.55	0.05	-0.09	-0.02
a1	0.14	-0.39	0.17	-0.37	-0.63	0.01	-0.36	-0.11

Fig. S2: Overview of estimated interaction coefficients. (a) shows interaction coefficients matrices for dataset 1, i.e. row a1 and column a4 denote interaction coefficient $\alpha_{1,4}$, representing the effect that species 4 has on species 1. (b) depicts the interaction networks for dataset 1 with blue and red colour denote positive and negative interaction coefficients respectively. The thickness and colour saturation correspond to the magnitude of interaction coefficients. The arrows point to the species which is affected by the connecting species. (c) demonstrates that there is no pattern between the two interaction coefficients of a specific tree pair. (d) depicts the density distribution of intra- (red) and interspecific (blue) interaction coefficients for dataset 1 with dashed lines representing the means.

S4: Description of alpha matrix reshuffling approach

To test the internal structure of the empirical interaction matrix, we use a reshuffling approach. The setup follows in large parts the one for testing the identifiability of our model (see S2), but uses fitted values and reshuffled alpha matrices as an input. Additionally, we assumed that all trees were initially equal in der biomasses. We further removed random effects, mortality, as well as process and measurement errors. We considered two reshuffling scenarios. First, to test the non-randomness of the interaction matrix, we reshuffled values without any constraints. Second, we constrained the reshuffling to intra- and interspecific interactions to test for the effect of their average difference. As in the identifiability framework (S2), we simulated growth over seven years and recorded net interactions, biomasses and the manipulated interaction matrix in addition to the meta-data (i.e. species richness, year, plot ID).

Appendix D: Contribution to figures

Manuscript No. (sequence number in the dissertation): 1

Short reference [e.g.: Müller et al (2020), J. Biol. Chem.]: Albert et al. (2022) Ecol.Lett.

Contribution of the doctoral candidate:

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) 2-4; S1-S13	■	100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
	☐	0% (the data presented in this figure are based exclusively on the work of other co-authors)
	☐	Approximate contribution of the doctoral candidate to the figure: ____% Brief description of the contribution: *(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)*

Manuscript No. (sequence number in the dissertation): 2

Short reference [e.g.: Müller et al (2020), J. Biol. Chem.]: Albert et al. (in prep.)

Contribution of the doctoral candidate:

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) 2-3; S1	■	100% (the data presented in this figure come entirely from experimental work carried out by the candidate)
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	☐	Approximate contribution of the doctoral candidate to the figure: ____% Brief description of the contribution: *(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)*

Manuscript No. (sequence number in the dissertation): 3

Short reference [e.g.: Müller et al (2020), J. Biol. Chem.]: Yu et al. (in prep.)

Contribution of the doctoral candidate:

Contribution of the doctoral candidate to figures reflecting experimental data (only for original articles):

Figure(s) 2	☐ 100% (the data presented in this figure come entirely from experimental work carried out by the candidate) ■ 0% (the data presented in this figure are based exclusively on the work of other co-authors) ☐ Approximate contribution of the doctoral candidate to the figure: _____% Brief description of the contribution: *(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)*

Figure(s) 3, S2	☐ 100% (the data presented in this figure come entirely from experimental work carried out by the candidate) ☐ 0% (the data presented in this figure are based exclusively on the work of other co-authors) ■ Approximate contribution of the doctoral candidate to the figure: 20 % Brief description of the contribution: *(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)* Figure based on simulation experiment using estimates from field data

Figure(s) S1	■ 100% (the data presented in this figure come entirely from experimental work carried out by the candidate) ☐ 0% (the data presented in this figure are based exclusively on the work of other co-authors) ☐ Approximate contribution of the doctoral candidate to the figure: 20 % Brief description of the contribution: *(e.g. "Figure parts a, d and f" or "Evaluation of the data" etc.)*

Appendix E: Ehrenwörtliche Erklärung

Ehrenwörtliche Erklärung

Ich versichere, dass mir die geltende Promotionsordnung bekannt ist (Promotionsordnung der Fakultät für Biowissenschaften der Friedrich-Schiller-Universität Jena vom 23.09.2019), ich die Dissertation selbstständig und ohne unerlaubte Hilfe Dritter angefertigt habe, keine Textabschnitte Dritter oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe und alle benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen in der Arbeit angegeben habe. Alle Stellen, die inhaltlich oder wörtlich aus Veröffentlichungen stammen sind kenntlich gemacht. Ich habe keine Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Folgende Personen haben mich bei der Auswahl und Auswertung des Materials sowie bei der Herstellung der einzelnen Manuskripte unterstützt: Ulrich Brose, Helge Bruelheide, John Connolly, Benoit Gauzens, Werner Härdtle, Michel Loreau, Goddert von Oheimb, Benjamin Rosenbaum, Nadja Rüger, Remo Ryser, Florian Schnabel, Elisa Thébault, Stefan Trogisch, Shaopeng Wang, Wentao Yu. Nähere Angaben sind den *Author Contributions* und Forschungskapiteln zu entnehmen.

Diese Dissertation lag noch nicht als staatliche oder andere wissenschaftliche Prüfungsarbeit einer Prüfungsbehörde vor und wurde bisher noch nicht veröffentlicht. Ich habe die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei keiner anderen Hochschule oder anderen Fakultät als Dissertation eingereicht.

Leipzig, den ……………………………….

Georg Albert