Synthesis of spatial and trophic networks and their response to global change

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Summary

Nature comprises of an incredible amount of biodiversity that is inspiring people and research all over the world. Biodiversity is critical for maintaining healthy ecosystems and human wellbeing. However, increasing food production, resource exploitation and expansion of human settlements lead to eutrophication, dissection and loss of habitat that is increasingly threatening biodiversity. Species in ecosystems that make up this biodiversity are organized into complex food webs and interact with each other. Furthermore, all organisms move through the landscape. Most animals move actively, and for most plants their propagules are moved passively (e.g. by wind or by animals). Environmental change such as fragmentation, habitat loss, and eutrophication may influence both movement of species and their trophic interactions. Traditionally, these two major processes in ecosystems have been looked at mostly separately. Food-web research has focused on complex trophic interactions but has mostly ignored species movement in complex landscapes. Metapopulation theory has mainly focused on metapopulation dynamics with dispersal of spatially separated populations of the same species disregarding interactions among species. Subsequently, metacommunity theory acknowledges both, spatial and biotic interactions, but remained predominantly limited to species competition for the latter. In either realm, many examples show how spatial or trophic structures and processes shape biodiversity. For example, the reintroduction of wolves in the Yellow Stone National Park resulted in trophic cascades, changes in prey behaviour, community composition and even in the structure of rivers. As an example of spatial structures and processes, one of the most fundamental theories in ecology, the theory of island biogeography predicts that small and more isolated islands harbour less species than large and well-connected islands. In both, spatial and trophic processes, body mass is an important trait affecting species metabolism, trophic interactions and movement. In addition, trophic interactions and dispersal are based on energy or biomass fluxes either between populations of a different species in the same location or from one population of the same species to another in a different location. Recent advances that incorporate trophic interactions into metacommunities were conceptualized as trophic metacommunities. To this date, the vast majority of trophic metacommunity research was, however, limited to simple food-web motives or food chains. However, the mechanisms by which complex trophic and spatial processes and structures interactively shape biodiversity remains largely unclear.

In this thesis I am to make a step towards the integration of ecosystem complexity in the interaction of spatial and trophic processes. To do so, I present a bioenergetic meta-food-web model integrating complex food webs and spatial networks that employs body mass as a single unifying trait. Using this model, I simulate the response of trophically and spatially connected communities to changes in their abiotic context. I show that several mechanisms driving species coexistence and community structure only arise as a consequence of this integration. I subsequently investigate interacting global change drivers and how they affect biodiversity in meta-food-webs. Model simulations are a powerful tool that can provide insight into the mechanisms and the complex and high-dimensional dynamics of meta-food-webs, which is very challenging in empirical research. These computer simulations reveal that the interactive effects of eutrophication, habitat fragmentation and isolation and habitat patch size are highly context dependent and interact with food-web structures, the trophic position of species and landscape configurations. Furthermore, the results show that global change drivers can add to, amplify or buffer each other. Therefore, this thesis suggests that mitigation strategies to prevent or buffer biodiversity losses need to take into account the trophic structures of communities as well as metaecosystem-scale landscape configuration.

In **Chapter 1**, I present a bioenergetic meta-food-web model integrating spatial and trophic processes and structures that employs body mass as a single unifying trait. This model is subsequently used to investigate interactive effects of habitat isolation and the number of habitat patches in fragmented landscapes. Large predators occupying high trophic levels suffer most from habitat isolation, despite of their dispersal advantages, due to a bottom-up accumulation of biomass loss caused by dispersal losses resulting from isolation. Increasing isolation causes local diversity to decrease, while an increase in the spatial turnover of species at intermediate to high isolation buffers the decrease of landscape biodiversity loss. Variation in the number of habitat patches did not produce a detectable effect on biodiversity.

In **Chapter 2**, I conceptualize fundamental mechanisms that arise from synthesizing trophic and spatial dynamics and investigate interactive effects of eutrophication, isolation and homogenisation. In **Chapter 1**, I have shown that isolation can be detrimental for large top-predators and undermines biodiversity. In addition, eutrophication poses a threat to the stability of food webs as increased energy fluxes can result in unstable population oscillations with subsequent extinctions. However, **Chapter 2** reveals that while isolation is detrimental for nutrient poor habitat patches, it can buffer eutrophic patches by removing excess energy through what we introduce as the “drainage effect”. The complex context dependency of isolation and eutrophication reveals the non-linearity of biodiversity response to these major global change drivers. Furthermore, the asymmetry of dispersal that gives rise to the newly introduced drainage effect and the well-known rescue effect provides a mechanistic explanation of how habitat heterogeneity promotes biodiversity in meta-food-webs.

In **Chapter 3**, I extend the theory of island biogeography to complex meta-food-webs and show that interactions between landscape configurations and food-web structures drive species-area relationships. While uncovering classical positive species-area relationships in landscapes that have relatively small dispersal fluxes, other more random landscape configurations that promote dispersal reveal negative species-area relationships. Particularly small patches that are well-connected to larger patches uniquely harbour species occupying high trophic levels that are supported by disproportionately high immigration of lower trophic levels.

Overall in this thesis, I (1) present a meta-food-web model capable of simulating complex metacommunities with interacting spatial and trophic processes and structures, (2) highlight the importance of the synthesis of typically mostly independent research areas, (3) uncover general mechanisms that only arise from the integration of spatial and trophic processes and structures into meta-food-webs and (4) use these mechanisms to reveal how biodiversity responses to interactive global change drivers such as habitat fragmentation and eutrophication.

Zusammenfassung

Die Natur verfügt über eine unglaubliche Artenvielfalt, die Menschen und Forschung auf der ganzen Welt gleichermassen inspiriert. Diese Biodiversität bildet die Existenzgrundlage für den Menschen und für einen Grossteil allen anderen Lebens. Steigende Nahrungsmittelproduktion, Ressourcenausbeutung und die Ausdehnung menschlicher Siedlungen führen zu Eutrophierung, Zerschneidung und zum Verlust von Lebensraum, was die biologische Vielfalt zunehmend bedroht. Alle Arten in Ökosystemen, die diese Biodiversität ausmachen, sind in komplexen Nahrungsnetzen organisiert und interagieren miteinander. Darüber hinaus bewegen sich alle Organismen auf die eine oder andere Weise durch die Landschaft. Klassischerweise wurden diese beiden Hauptprozesse in Ökosystemen meist getrennt voneinander betrachtet. Die Nahrungsnetz-Forschung konzentriert sich auf komplexe trophische Interaktionen, ignoriert dabei aber meist die Bewegung der Arten in komplexen Landschaften. Die Meta-Populationstheorie hingegen konzentriert sich hauptsächlich auf die Meta-Populationsdynamik mit der Ausbreitung von Arten, die räumlich getrennte Populationen derselben Art oder trophischen Gilde miteinander verbindet, ignoriert dabei jedoch die komplexen trophischen Interaktionen zwischen den Arten. In beiden Bereichen zeigen viele Beispiele, wie räumliche oder trophische Strukturen und Prozesse die Biodiversität beeinflussen. Als Beispiel für trophische Interaktionen, führte die Wiederansiedlung von Wölfen im Yellowstone-Nationalpark zu trophischen Kaskaden, zu Veränderungen im Verhalten der Beutetiere, in der Zusammensetzung der Artengemeinschaft und sogar in dem Lauf von Flüssen. Eine der grundlegendsten Theorien in der Ökologie, die Theorie der Insel-Biogeographie, sagt als Beispiel für räumliche Prozesse und Strukturen voraus, dass kleine und isoliertere Inseln weniger Arten beherbergen als grosse und gut miteinander verbundene Inseln. Sowohl räumlichen als auch trophischen Prozessen ist gemein, dass sie in der Regel von den Körpermassen der Akteure beeinflusst werden. Dies ist zum Beispiel beim Stoffwechsel, trophischen Interaktionen und der Bewegung der Arten der Fall. Darüber hinaus bestehen trophische Interaktionen wie auch bei der Ausbreitung grundsätzlich aus Energie- oder Biomassenflüssen, die entweder von einer Population zu einer anderen Population einer anderen Art am gleichen Ort fliessen oder von zwischen zwei Populationen derselben Art an verschiedenen Orten fliessen. Wie komplexe trophische und räumliche Prozesse und Strukturen die Biodiversität interaktiv beeinflussen, ist jedoch noch weitgehend unklar. Darüber hinaus bleiben die Erkenntnisse über die Auswirkungen interaktiver globaler Veränderungen auf trophische Meta-Gemeinschaften praktisch unerforscht, da es aufgrund ihrer hochdimensionalen Natur nahezu unmöglich ist, solche interaktiven Effekte auf komplexe Meta-Nahrungsnetz-Dynamiken empirisch zu untersuchen.

Modellsimulationen sind ein mächtiges Werkzeug, das Einblicke in Mechanismen und die komplexe und hochdimensionale Dynamik von Meta-Nahrungsnetzen ermöglicht, die die empirische Forschung nahezu nicht erfassen kann. In dieser Arbeit stelle ich ein bioenergetisches Meta-Nahrungsnetz-Modell vor, das trophische und räumliche Prozesse und Strukturen integriert und die Körpermasse als ein einheitliches Merkmal verwendet. Des Weiteren decke ich Meta-Nahrungsnetz-Mechanismen auf, die erst als Folge dieser Integration zum Vorschein treten, und untersuche anschliessend die interagierenden Triebkräfte des globalen Wandels und ihre Auswirkungen auf die biologische Vielfalt. Meine Computersimulationen zeigen, dass die interaktiven Auswirkungen von Eutrophierung, Habitatfragmentierung und -isolation sowie die Grösse der Habitatflächen stark kontextabhängig sind und mit den Strukturen der Nahrungsnetze, der trophischen Position der Arten und den Landschaftskonfigurationen interagieren. Hierbei können sich die Triebkräfte des globalen Wandels gegenseitig ergänzen, verstärken oder abpuffern. Meine Arbeit legt somit nahe, dass Minderungsstrategien zur Verhinderung oder Pufferung von Biodiversitätsverlusten die trophischen Strukturen von Gemeinschaften und Landschaftskonfigurationen im Meta-Ökosystem-Massstab berücksichtigen sollten.

Meine Arbeit ist in drei geschlossene Kapitel gegliedert. In **Kapitel 1** stelle ich ein bioenergetisches Meta-Nahrungsnetz-Modell vor, das räumliche und trophische Prozesse und Strukturen integriert und Körpermassen als ein einheitliches Merkmal einsetzt. Dieses Modell wird anschliessend zur Untersuchung interaktiver Effekte der Habitat-Isolation und der Anzahl von Habitat-Flächen in fragmentierten Landschaften verwendet. Die Modellierungen zeigen, dass grosse Prädatoren, die hohe trophische Ebenen besetzen, trotz ihrer Verbreitungsvorteile am meisten unter der Habitat-Isolation leiden. Der Grund hierfür sind sich von unten akkumulierenden Biomasseverlusten, die durch die Sterblichkeit während der Verbreitung aufgrund der Isolation verursacht werden. Zunehmende Isolation führt zu einer Abnahme der lokalen Biodiversität, während eine Zunahme des räumlichen Artenumsatzes bei mittlerer bis hoher Isolation den Rückgang des Verlusts an landschaftlicher Biodiversität puffert. Die Anzahl der Lebensraumflächen hatte keinen nachweisbaren Effekt auf die Biodiversität.

In **Kapitel 2** konzeptualisiere ich grundlegende Mechanismen, die erst durch die Synthese von trophischer und räumlicher Dynamik entstehen, und untersuche interaktive Effekte von Eutrophierung, Isolation und Homogenisierung. In Kapitel 1 zeige ich, dass Isolation für grosse Prädatoren schädlich sein und die Biodiversität untergraben kann. Ausserdem stellt

die Eutrophierung eine Bedrohung für die Stabilität der Nahrungsnetze dar, da erhöhte Energieflüsse zu instabilen Populationsschwankungen mit anschliessendem Aussterben führen können. Kapitel 2 zeigt jedoch, dass die Isolation zwar für nährstoffarme Lebensräume schädlich ist, dass sie aber eutrophierte Lebensräume puffern kann, indem sie für den Verlust von überschüssiger Energie, den sogenannten "Drainage-Effekt", verantwortlich ist. Die komplexe Kontextabhängigkeit von Isolation und Eutrophierung offenbart die Nichtlinearität der Reaktion der biologischen Vielfalt auf diese wichtigen Triebkräfte des globalen Wandels. Darüber hinaus liefert die Asymmetrie der Ausbreitung, die den neu eingeführten Drainage-Effekt und den bekannten Rescue-Effekt hervorruft, eine mechanistische Erklärung dafür, wie die Heterogenität der Lebensräume die Biodiversität in Meta-Nahrungsnetzen fördert.

In **Kapitel 3** erweitere ich die Theorie der Insel-Biogeographie auf komplexe Meta-Nahrungsnetze und zeige, dass Wechselwirkungen zwischen Landschafts-konfigurationen und Nahrungsnetzstrukturen die Artenzahl-Flächen-Beziehungen beeinflussen. Während klassische positive Artenzahl-Flächen-Beziehungen in Landschaften, die wie echte Festland-Insel-Landschaften strukturiert sind, auftauchen, zeigen andere, eher zufällige Landschaftskonfigurationen negative Artenzahl-Flächen-Beziehungen. Besonders kleine Habitatflächen, die gut mit grösseren Habitatflächen verbunden sind, beherbergen als Einzige Arten, die hohe trophische Ebenen besetzen, die durch eine unverhältnismässig hohe Einwanderung von niedrigeren trophischen Ebenen unterstützt werden.

Insgesamt stelle ich in dieser Arbeit und basierend auf meinen Forschungskapiteln (1) ein Meta-Nahrungsnetz-Modell vor, das in der Lage ist, komplexe Meta-Gemeinschaften mit interagierenden räumlichen und trophischen Prozessen und Strukturen zu simulieren, (2) betone ich die Bedeutung der Synthese klassischer, weitgehend unabhängiger Forschungsgebiete, (3) decke ich allgemeine Mechanismen auf, die nur durch die Integration räumlicher und trophischer Prozesse und Strukturen in Meta-Nahrungsnetzen entstehen, die im Wesentlichen in allen drei Kapiteln auftauchen, und (4) zeige ich Nichtlinearitäten der Reaktionen der Biodiversität auf interaktive globale Veränderungen auf.

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General introduction

Biodiversity

Biodiversity, that is the diversity of genes, species, populations and ecosystems (i.e. the variety of life (Gaston and Spicer, 2013)), has been cause for amazement and curiosity since the infancy of the research field of biology. Already Aristotle got fascinated by the biota on the island of Lesbos and was the first, that we have records of, to collect data on animal's food, reproduction and movement among others. He also developed theories based on the data to explain general patterns such as body mass scaling of gestation time and reproduction (Leroi, 2014). Over the years, as the field of biology developed and grew, biodiversity became a core feature of nature that inspired questions in ecology and evolution. Questions such as how biodiversity is shaped and maintained or what consequences the loss of biodiversity has for ecosystems is still fuelling research today.

Many species are threatened or driven to extinction by human impacts. Current extinction rates are comparable to previous mass extinctions and our time (termed the Anthropocene) is sometimes considered to be the age of the sixth mass extinction caused by humans (Ceballos et al., 2017; Payne et al., 2016). Various drivers have been identified as contributing to this disaster. Most prominent is global change, that has become an umbrella term that encompasses for example global warming, land-use change and pollution, and has been shown to drive species loss, alter community compositions and species interactions (Tylianakis et al., 2018). Increasing human demands for food production, resources for goods and energy, and space for roads and settlements, and resulting pollution of the biosphere are massively driving global change and threatening biodiversity. Increasing eutrophication through fertilizer use and pollution are changing natural species communities. For instance, eutrophication can lead to a decrease in plant diversity through increased light competition (Hautier et al., 2009). Also, intensification of agricultural systems typically undermines biodiversity (Foley et al., 2005; Tilman et al., 2001; Tylianakis et al., 2007). Furthermore, the dissection of natural habitats by roads or agricultural fields results in an ongoing habitat loss, isolation and fragmentation in ecosystems and is threatening biodiversity (Tilman et al., 1994). The loss of habitat can challenge organisms in finding enough food and drive populations to extinctions when their minimum habitat requirement is not available anymore. Furthermore, increasing isolation of remaining habitat patches poses an additional challenge when organisms become unable to reach other habitat patches or face increased dispersal mortality because of larger distances or higher landscape hostility (Fahrig, 2003; Prugh et al., 2008). For example, when due to the expanse of intensive pastures the habitat patch of a weasel becomes too small, it may not find enough mice to prey upon to survive. In addition, when it crosses a freshly mown meadow in search for food or a mate, it may have to travel further exhausting itself more or face an increased mortality risk. For example, the weasel could get run over by a car when crossing a road or being preyed upon by a hawk because it has less opportunities to hide in a shrub. The message from this example is, that the survival of the weasel and its population depends on its trophic interactions and how it can move through the landscape and that these aspects are affected by global change drivers. However, it remains unclear how interacting effects of isolation, habitat loss and fragmentation affect biodiversity (Fahrig et al., 2019). Moreover, nature is more complex and consists of many more species than mice, weasels and hawks.

In the last few decades, a lot of research has investigated the biodiversity-ecosystem functioning relationships and put forward arguments to conserve biodiversity to preserve ecosystem functions and services for humans and the ecosphere (Tilman et al., 2014). For instance, biodiversity has been recognized to buffer the loss of ecosystem functions and services through complementarity in interacting communities (Eisenhauer, 2012) and food webs (Poisot et al., 2013). Thus, to protect biodiversity and the natural world, and human wellbeing, we urgently need a mechanistic understanding of how biodiversity is shaped and how it responds to drivers of global change.

Food webs

Since I was a child I have been fascinated by the many ways spiders hunt and catch their prey and how could one not be amazed by an orb-web spiders architectural master piece and how it can quickly immobilize and envelope a trapped fly or by a jumping spider's incredible athletic abilities in leaping accurately several times its body length onto an unaware grasshopper. One thing these examples have in common is, that they both are about species interacting with each other, and more specifically, trophic interactions. All organisms need energy to live, thus trophic interactions are one of the most fundamental process in nature. Ecologists have recognized long ago, that all living organisms are interwoven into complex food webs (Egerton, 2007; Elton, 1927) and started to represent these in graphs where species are represented by the nodes and species' interactions by edges (Figure 1). When looking at such an interaction network, it becomes apparent that species cannot only have direct but also indirect effects on each other. For example, species A consumes species B, which consumes species C. Thus, by affecting the population size of species B, species A indirectly affects species C. One prominent example of such a cascade of effects is the reintroduction of wolves into Yellow Stone National Park (Ripple and Beschta, 2012). When wolves were reintroduced after decades of absence, they changed how elks behaved by hunting them. Because of that predation pressure, elks started to avoid open spaces at riverbanks or lakes and spent more time in dense woods. And because elks avoided feeding on riverbanks, more trees could grow as the saplings were eaten less. With more trees on the riverbanks, beavers thrived and could build more dams and thus changed the flow regime of rivers creating more shallow and slow flowing segments. This created habitat for many bird and insect species. Essentially, the predation pressure by the newly introduced wolves changed the whole community and even changed the landscape. This strongly emphasizes that food webs are more than the sum of species.

Trophic interactions are almost omnipresent in nature, and food-web research aims to explain and understand how these interactions and interaction networks shape biodiversity. May (1972) showed that complex random food webs tend to be unstable, implying that real, complex food webs must be non-random. This essentially urged ecologist to find organisational properties that allow complex food webs to exist and sparked a complexity-stability debate (Elton, 1958; Paine, 1969; Pimm, 1984) that continues today (Jacquet et al., 2016; Landi et al., 2018; Qian and Akçay, 2020). Since then, many advances in food-web research have been made. We know that structural properties of food webs influence their stability. For instance, food webs with a high connectance, that is the proportion of feeding links per species, are less likely to be stable when links are strong or randomly distributed (May, 1972). In contrast, simulations of empirical food webs have shown that robustness against secondary extinctions increases with connectance (Dunne et al., 2002). Furthermore, complex food webs prevent competitive exclusion of basal species (Brose, 2008). Then, high modularity, that is a metric that describes compartmentalisation (i.e. species within one compartment interact more among each other than with species from outside of this compartment), tends to be stabilizing by limiting the transmission of perturbations (Krause et al., 2003; Thébault and Fontaine, 2010; Stouffer and Bascompte, 2011).

Trophic interactions consist of energy or biomass fluxes from one species to another. Organisms spend energy to maintain their metabolism, to grow and reproduce and to acquire more energy. They acquire energy by feeding or by nutrient uptake. Through the food web, the amount of energy decreases with every trophic level because energy is lost through the metabolism of lower trophic levels and also through incomplete conversion of food to energy (Lang et al., 2017). Essentially, energy flows through a food web as a river flows through the landscape and the amount of energy that flows through which branch or link, and the total that flows through the system influences how stable the system is and which species occur in what abundance. If there is not enough energy available species starve and go extinct. Interestingly, large energy fluxes can produce top-heavy biomass-pyramids and oscillating population densities with subsequent extinctions. This phenomenon has become known as the paradox of enrichment (Rosenzweig, 1971). For instance, when a hare population is growing rapidly because of plenty of food or energy available, a cooccurring lynx population can profit from the abundance of prey and thus the lynx population also grows. At some point, however, the lynx population becomes so large and is preying on so many hares that the hare population starts to shrink. Then, because the hare population becomes smaller again, the lynxes have less food available and also start to shrink in population size. This then releases the hare population again from some of the predation pressure and it can grow again, and so on. Such oscillating predator-prey systems have been observed in nature (Elton and Nicholson, 1942) and in mesocosm experiments (Blasius et al., 2020). With further increase in energy, such oscillations increase in amplitude and can cause crashes and therefore extinctions of populations. For instance, when the previously mentioned lynx population becomes so large that they completely eradicate the hare population or when the hare population becomes so small, that the lynx population starves to extinction. In theory, if there is neither too little nor too much energy available, populations can persist in a stable equilibrium, neither growing nor shrinking. This happens, when energy expenditure und gain equal each other out and no exterior perturbations change population size (Rip and McCann, 2011). Therefore, the food-web structure (i.e. the pathways energy flows through) and the amount of energy in the system (e.g. nutrient availability) drive food-web dynamics.

Interestingly, body masses of organisms drive many aspects of food-web dynamics. For instance, metabolic rates scale with body size allometrically resulting in larger organisms being more efficient in their metabolic energy household per unit of biomass (Brown 2004). Based on the trade-off between attack rates, handling time, capture success and therefore prey preferences, body masses and their distribution across trophic levels drive structures, interaction strength and energy fluxes in food webs (Brose, 2010). Consequently, body masses of organisms set feasibility limits to with whom species can interact. Body mass limits the amount of energy gained in relation to the time spent searching and handling a prey in the lower prey size spectrum or by the success of catching and subduing a prey on the upper prey size spectrum (Brose, 2010; Brose et al., 2008; Petchey et al., 2008; Portalier et al., 2019). Movement speed of organisms scales with body mass with larger organisms being faster and thus influencing encounter rates of organisms within a habitat (Dell et al., 2014; Hirt et al., 2017b; Pawar et al., 2012).

In a nutshell, food-web research investigates the mechanisms of how species traits such as body masses, trophic interactions, food-web structures and energy conditions drive with whom species can coexist and thus biodiversity. Furthermore, ecosystem functions (e.g. primary production or pest control) depend on population sizes and energy fluxes.

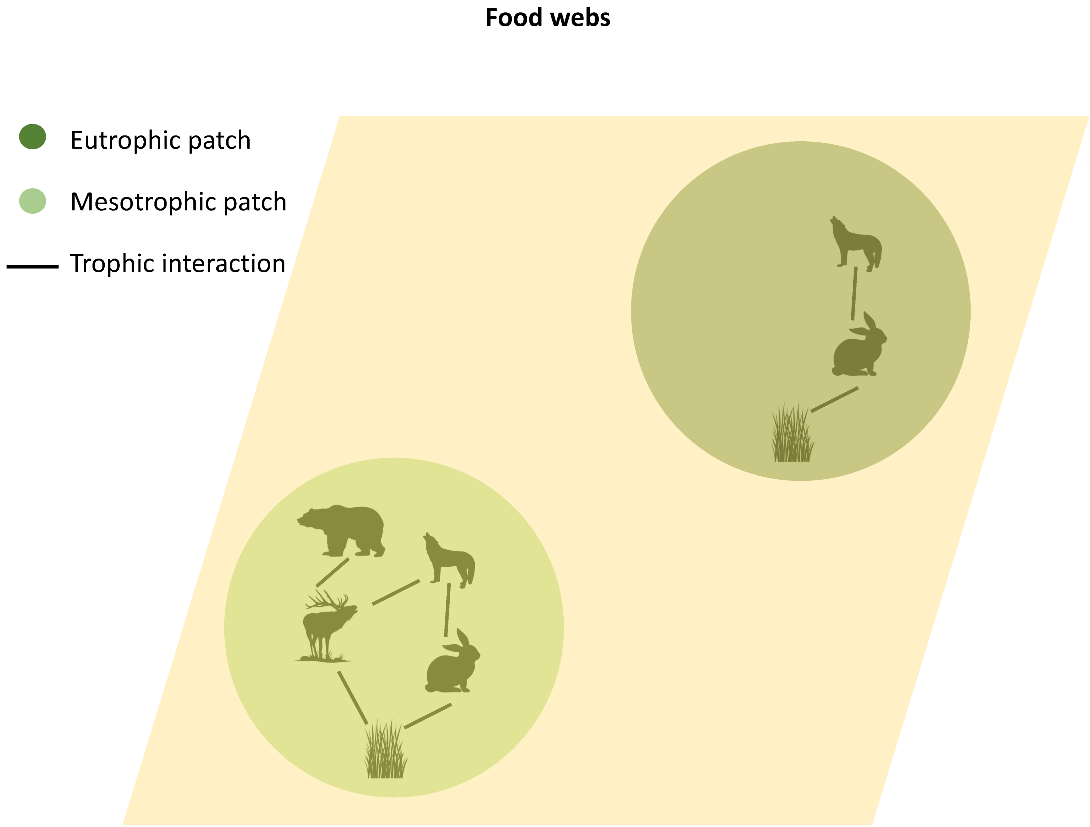

Figure 1: Conceptualisation of food webs. Food-web research shows how food-web structures, energy fluxes and local conditions (e.g. nutrient conditions) shape biodiversity.

Landscapes and metapopulations

Landscapes on earth are diverse and have sparked at least as much inspiration and curiosity for how they form as biodiversity has. Growing up in Switzerland, I have been intrigued by the majestic mountains in the alps, the crystal-clear alpine lakes left from retreating glaciers and the turquoise rivers that spread like a network through the valleys and the Swiss plateau forming and harbouring many different types of habitats. Some habitat patches in the mountains are small and only consist of a few plants clinging to the rock with almost nothing to live off, whereas others are vast and rich from millennia old depositions of organic matter. Humans have also changed the landscape by establishing settlements and gardens, deforestation, expanding agricultural fields and redirecting rivers.

One cornerstone in ecology is the theory of island biogeography (MacArthur and Wilson, 1967) that first conceptualized how spatial structures, such as the size of an island and its distance from the mainland (i.e. dispersal limitations) shape biodiversity. The theory predicts that smaller and more isolated islands hold fewer species because reduced immigration rates lead to lower colonisation success and smaller populations are more at risk of stochastic extinctions. This fundamental theory in ecology goes hand in hand with the concept of metapopulations, as species dispersal is at the core of both (Hanski, 1998; Hanski and Ovaskainen, 2000; Hansson, 1991; Rybicki and Hanski, 2013). Metapopulations describe populations of the same species in different geographical locations that are connected by dispersal of organisms (Figure 2). All organisms move in one way or the other. Sometimes it is just the propagules that are passively moved by wind, water or that hitchhike on other animals, but most animals actively disperse through the landscape. There are many motivations to disperse (Baguette et al., 2012; Fronhofer et al., 2018), for example to find a mate to reproduce, to find food when prey is scarce or to avoid competitors and predators. For instance, a bear might be better off dispersing to a different valley, when the local deer population is very small or a pack of wolves is constantly competing for prey costing the bear energy and time, but also if there are many other bears competing for the same food.

This movement of individuals from one population to another can create so-called source-sink dynamics (Pulliam, 1988) when there are differences in size among the populations in a metapopulation. Source-sink dynamics describe the asymmetrical exchange among populations. For instance, a large bear population in one valley that constantly produces many offspring can provide a dispersal flux to another small population in a different valley that is larger than the dispersal flux coming back from the small bear population. Thus, the large population is a source as the emigration is larger than the immigration and the small population, where for example food is limited and only supports a few individuals, is a sink population as there are more bears immigrating than emigrating. Such a dynamic exchange of individuals or bear biomass then gives rise to a rescue effect (Brown and Kodric-Brown, 1977). The rescue effect essentially describes that the small bear population can be maintained and thus rescued through the immigration of bears from the source population when it otherwise would have negative growth rates or be recolonised after extinctions.

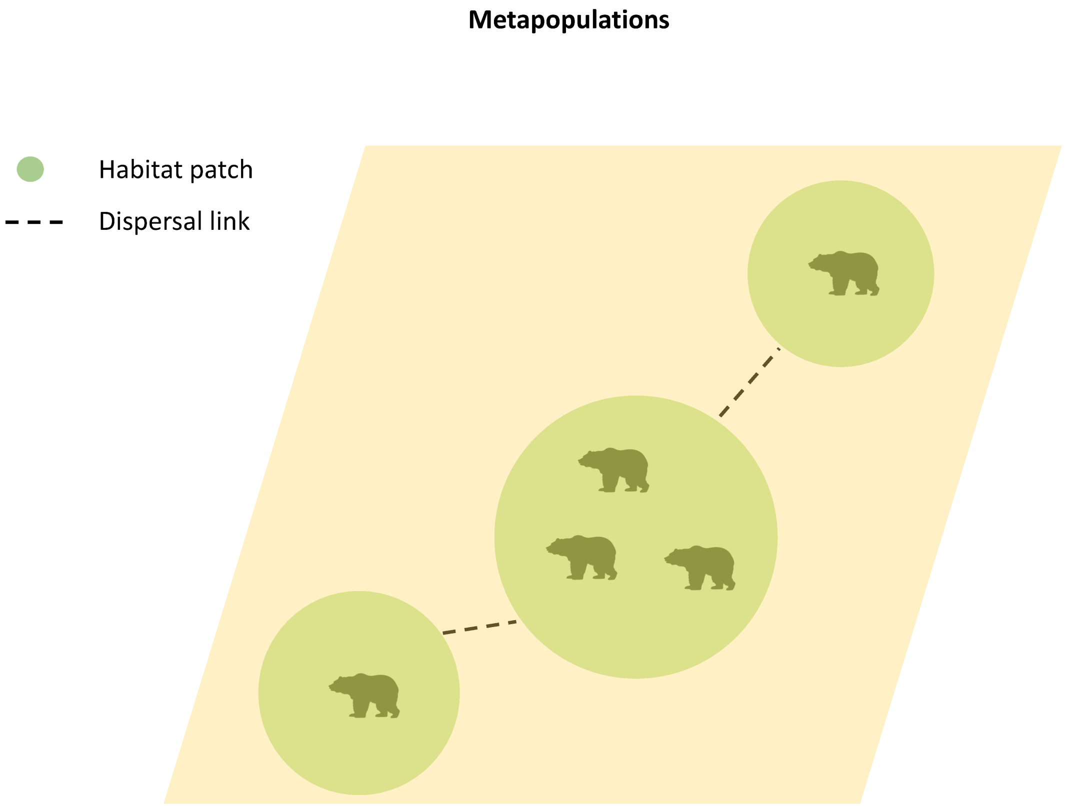

Figure 2: Conceptualisation of a metapopulations. Metapopulation theory conceptualises how larger population on a larger patch and smaller populations on smaller patches are connected by dispersal.

Movement of organisms strongly depends on their traits such as the movement mode, i.e. flying, swimming or walking. Among those traits, the body size of organism is one very important trait. For instance, how fast and how far animals move scales with their body size (Hirt et al., 2017b, 2017a; Teitelbaum et al., 2015). Larger animals tend to be able to move further, thus having larger dispersal ranges and home ranges (Hirt et al., 2018). Furthermore, organisms of different size likely experience a landscape on a different scale and experience different barriers. For example, a large bear may only take a few steps from one meadow to another, but for a small beetle it could be a once in a life-time journey. Therefore, body masses of organisms essentially create species-specific spatial networks.

Spatial networks are a useful abstraction of a landscape and can, similar to food webs, be represented in a graph where nodes constitute habitat patches and links constitute dispersal connections (Minor and Urban, 2008). All these diverse landscapes can be simplified to spatial networks. Some may be more clustered such as coral reefs (Kininmonth et al., 2010), and others have a dendritic structure such as rivers or look like islands in the ocean. For instance, deforestation results in a spatially autocorrelated distribution of patch sizes across the landscape during the process of increasing fragmentation and human alteration (García et al., 2005; Taubert et al., 2018). All these aspects in spatial networks have the potential to affect dispersal links, either by their strength or their number. Furthermore, this allows for the attribution of landscape structures and ecological processes to different scales (e.g. local or regional). Complex spatial network configurations can influence population sizes and densities by modifying dispersal fluxes through the network (Altermatt, 2013; Harvey et al., 2020) and allow biodiversity to be quantified at different scales (e.g. α-, β- and γ-diversity).

In a nutshell, spatial structures such as patch size, isolation, spatial networks and landscape configuration shape population sizes and community composition and therefore drive biodiversity and ecosystem functioning.

From food webs and metapopulations to meta-food-webs

In nature, organisms move through complex landscapes and organisms interact with each other. Food-web research has identified mechanisms in trophic interactions shaping biodiversity and metapopulation research has provided mechanisms in spatial processes that shape biodiversity. The two fields have historically been mostly separate. Here, I am to make a step towards the integration of complex food webs into complex landscapes to which I refer to as "meta-food-web" (see Figure 3 and Box 1 "What is a meta-food-web" for clarification of terms).

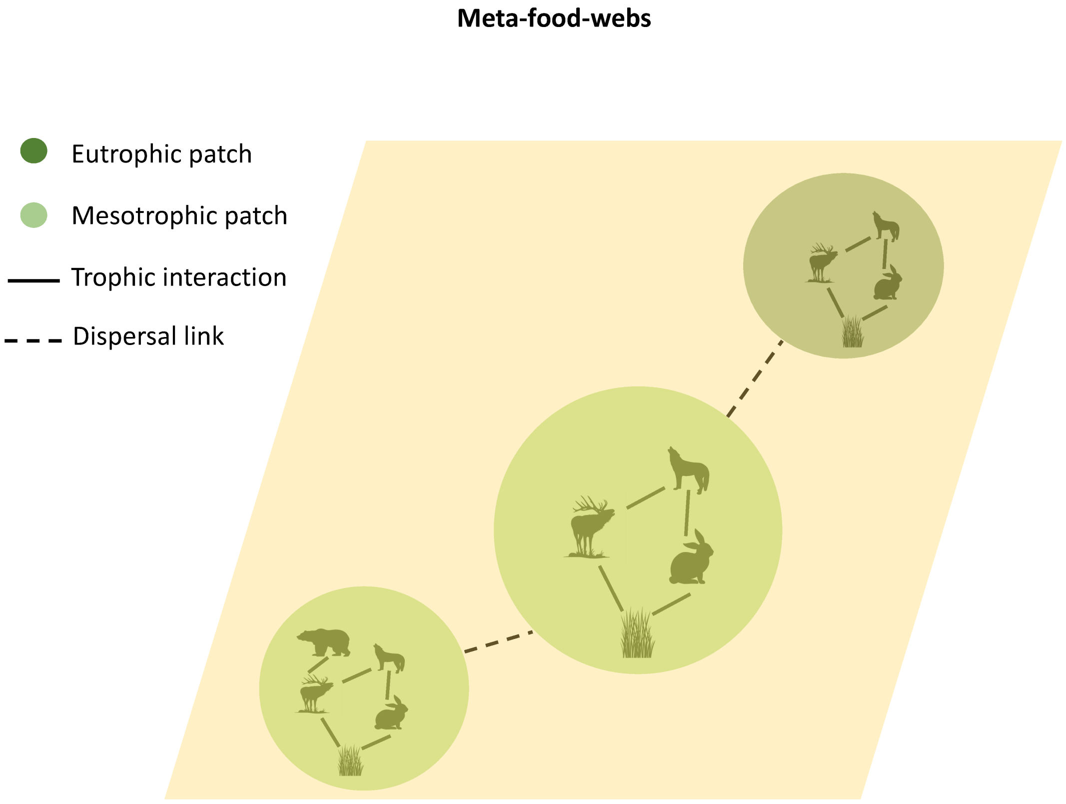
Meta-food-webs

Figure 3: Conceptualisation of a meta-food-web. Meta-food-webs integrate spatial and trophic networks connected by trophic interactions and dispersal.

Box 1: *What is a meta-food-web?*

Here, I use the term "*meta-food-web*" in the sense of a multiplex network that connects populations of different species in the same local habitat by trophic interactions and at the same time populations of the same species across different local habitats by dispersal. Thus, two patches are not connected through one dispersal link that applies to all species, but instead through one dispersal link per species. Including the allometric scaling of dispersal ranges with body size, two patches may only be connected by dispersal for larger species, depending on the distance between the patches.

Furthermore, I differentiate two types of meta-food-webs. First, the "potential" meta-food-web comprises all species of the metacommunity and all of their possible trophic links, irrespective of whether they are realised anywhere in the local food webs. Here, a trophic link can be possible based on morphological and physiological constraints (i.e. the prey species falls into the size spectrum that would be feasible for the consumer species), but it does not need to be realised anywhere in the meta-community if the consumer and the resource do not co-occur. These potential meta-food-webs were used to initiate the simulations in my research chapters. Second, the "realised" meta-food-web describes all species that persist in the simulations of the metacommunity and all trophic interactions that occur in any of the local communities.

In contrast, and due to a historical lack of trophic interactions in metacommunity research, I use the term *metacommunity* to describe a set of local communities with species linked by dispersal and competition only. Some recent studies included trophic interactions in metacommunities and employed the term "*trophic metacommunities*" (Guzman et al., 2018). Here, I differentiate between meta-food-webs and trophic metacommunities similarly as I would separate trophic interactions from food webs in local communities. In this sense, trophic metacommunity is an umbrella term that includes complex meta-food-webs as well as simple trophic structures such as food chains or food-web motives that are distributed across the local habitats of a metacommunity. In contrast, the term meta-food-web (or similar terms) is deeply rooted in food-web ecology to describe the complex topology of trophic interaction networks at a spatial scale beyond local habitats (Brose et al., 2004).

Moreover, I use the term "*metaecosystem*" as a metacommunity where non-living entities such as nutrients can move or be moved from one location to another.

Biotic interactions have been included in the concept of metacommunities. Metacommunity theory identifies four core processes (i.e. ecological drift through demographic stochasticity, abiotic environmental filtering of species, dispersal across landscapes and biotic interactions) that shape occurrence and abundance of species (Chase et al., 2020). Thus, metacommunity research often acknowledges the importance of both dispersal and biotic interactions but the latter has mostly been focused on species competition (Chesson, 2000; Leibold et al., 2004). Subsequent inclusion of trophic interactions into metacommunities has been termed trophic metacommunities (Guzman et al., 2018). Most studies that integrate spatial and trophic interactions have, however, been limited to small species motifs such as food chains and do not consider complex networks and landscape configuration (Holt, 2002; Koelle and Vandermeer, 2005; Liao et al., 2017). There is evidence that they have important impacts on each other and should therefore been looked at interactively. For example, in a synthesis of island biogeography and trophic interactions it has been shown that species-area relationships change with trophic levels (Holt et al., 1999). Also, spatial patterns of species distributions drive food-web structures (Brose et al., 2004). The trophic theory of island biogeography further integrated spatial and trophic processes and predicts species-area relationships based on food-web structures (Gravel et al., 2011). Furthermore, a trait-based theory of island biogeography predicted the distribution of traits depending on island area and isolation (Jacquet et al., 2017). Moreover, it has been shown that dispersal can synchronize population dynamics which can pose a threat do biodiversity by simultaneous local extinctions (Blasius et al., 1999; Gouhier et al., 2010). Dispersal can also dampen oscillations depending on the trophic level that is dispersing (Gounand et al., 2014) and induce compensatory population dynamics (McCann et al., 2005) and thus, prevent extinctions. Furthermore, it can reduce strong interspecific interactions and increase resilience (Gravel et al., 2016; Massol et al., 2011). Moreover, the structure of the food web influences whether the effect of dispersal on persistence is positive or negative (Koelle and Vandermeer, 2005). However, none of them consider interacting effects of complex food-web structures and landscape configuration. Recent advances are, however, rapidly filling this gap (Gravel et al., 2016). However, a mechanistic framework that integrates both into complex multilayer networks is largely lacking (Guzman et al., 2018).

Excitingly, both, food webs and landscapes of habitat patches, can be represented by networks that follow similar rules. In food webs, links describe energy or biomass fluxes from one population to another population of a different species in the same location. In spatial networks, links describe energy or biomass fluxes from one population to another of the same species in a different location. Thus, food webs and dispersal networks share the same currency. On top of that, they also have an important and common driver that is body size. As spatial and trophic processes influence population sizes of species, and food web and spatial network structure shape biodiversity, those both aspects of natural communities are bound to interact.

Furthermore, and as outlined before, global change drivers have the potential to affect core processes of meta-food-webs. While some of these stressors such as habitat fragmentation and isolation more directly affect spatial structures and dispersal, others such as eutrophication more directly affect local trophic dynamics. Recent calls for biodiversity conservation to take metacommunity perspectives into account have highlighted potential benefits of such a integrative and scale-inclusive view (Chase et al., 2020). Thus, investigating the effects of global change on meta-food-webs is of great interest. Moreover, interacting effects of habitat loss, fragmentation, isolation and eutrophication could create non-linearity in biodiversity responses rather than being additive. In summary, this calls for research that takes not only interactions among the different processes and structures (i.e. dispersal, landscape configurations and food webs) into account, but also interactions with and among global change drivers.

In this thesis and the chapters within, I contribute to filling these gaps by addressing interacting global change drivers while considering interacting spatial and trophic processes and structures in meta-food-webs (Figure 4).

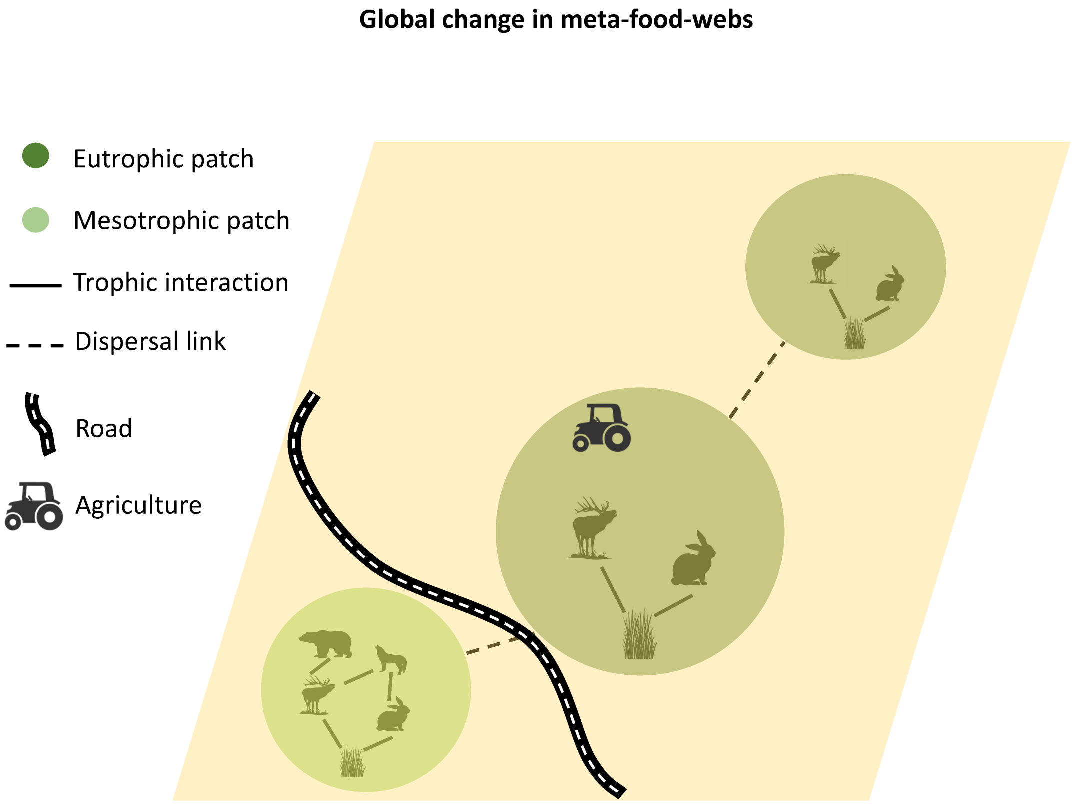

Figure 4: Global change in meta-food-webs. This figure conceptualises global change drivers (e.g. eutrophication through agriculture or landscape dissection by roads) affecting spatial and trophic processes in meta-food-webs.

Modelling

In **Chapter 1**, I present a meta-food-web model that is then further developed in **Chapter 2 & 3**. The model fills the gap of unifying spatial and trophic processes and structures by integrating complex landscapes and food webs through a trait-based approach and numerically solves ordinary differential equations that formulate the dynamics. Body mass, that is sometimes called a super trait as it is strong in predicting many other traits and processes of organisms in ecology, is the unifying trait that integrates spatial and trophic structures and processes in the model. The model employs body masses to construct food-web topologies by creating trophic niches for each animal species based on predator-prey body-mass ratios and subsequently defines interaction strengths (Schneider et al., 2016). Also, body mass allometries parameterize metabolic rates, encounter rate, handling time and dispersal ranges. Dispersal ranges then creates based on spatially explicit habitat patch locations species-specific spatial networks and determines dispersal losses. Dispersal losses are defined by a linear relationship of the dispersal range of an organism and the actual distance between two given patches. Thus, the further the journey of an organism is, the more biomass is lost. In this sense, the model includes movement of organisms on two different scales (i.e. (1) within habitat patch movement that influences encounter rates and therefore attack rates, and (2) between habitat patch dispersal).Moreover, the model deploys a nutrient model as the energetic basis of the food web (Brose, 2008; Schneider et al., 2016).

The dispersal model closely links the trophic and spatial realm not only through modifications in biomass densities of populations but also by employing local net growth rates to define emigration rates. This summarizes biological meaningful dispersal triggers such as resource availability, competition and predation pressure (Fronhofer et al., 2018). In **Chapter 3**, the model further employs explicit patch areas that modify extinction thresholds and dispersing biomasses. Detailed equations are presented within the chapters and the corresponding Supplements.

Model simulations are a powerful tool to dissect mechanisms in complex systems. For instance, these in silico experiments allow to investigate consequences of isolation independent of the number of habitat fragments and vice-versa as it is possible to simply increase distances but keep the number of habitats and their configuration constant. On the one hand, distilling out mechanisms provides a good a priory basis for expectations for drivers that affect the same processes, and can be a guideline for empirical research by suggesting what to measure in the real world. On the other hand, such modelling exercises allow to "experimentally" test fully cross-replicated interacting effects, for instance, eutrophication and fragmentation, that are almost impossible to achieve in empirical research. Also, with the use of a fast computer language the model is written in (i.e. C++), it is possible to trace the dynamics of thousands of populations of different species in hundreds of locations in different landscapes at virtually every time step. While these models rather provide answers in a manner of "if x then y", the model presented in here, remains despite of its complexity relatively parsimonious as it predominantly relays on a single, easy to measure trait, that is body mass, to parameterize the functions. In addition, body mass dependent parameters are informed by empirically derived allometries and ratios, i.e. metabolic rates, handling time and encounter rates.

Study Outline

Already before starting this thesis, I was interested in what mechanisms underly biological patterns and processes that are observed in nature. Also, I have always been intrigued by complex systems. When I built an air-tight biosphere with plants and isopods to measure CO_2 cycles for my matura thesis (general qualification for university entrance in Switzerland), which disastrously failed and everything died, I realised how complex the interplay of organisms is and how fragile that balance can be. In my bachelors and master thesis, while working on plant-pollinator interactions and light pollution, I became fascinated by networks and how anthropogenic stressors can change them. From that point on, I wanted to work on networks, preferably on food webs, and in this thesis, I got to work not only on food webs, but on meta-food-webs, thus satisfying my curiosity for networks and complexity.

As outlined before, given the relevance of food webs and spatial structures and processes for biodiversity, this thesis consists of the development of a spatially explicit meta-food-web model that predominantly employs body mass as a single unifying trait that is capable of simulating complex food webs in complex landscapes. Furthermore, I use this model to uncover basic mechanisms driving community composition and species diversity and address interactive effects of global change drivers on meta-food-webs.

In **Chapter 1**, I present the meta-food-web model and concept and show that habitat isolation deconstructs complex food webs from top to bottom and that while local diversity (alpha) decreases across a gradient of habitat isolation, landscape diversity (gamma) shows a u-shaped relationship. This is because an increase in species spatial turnover (beta) compensates for the loss of local diversity at high isolation. The deconstruction of food webs from top to bottom with isolation is driven by the loss of large top-predators that are driven to extinction through a bottom-up energy limitation. This energy limitation increases with isolation and resulting dispersal losses despite of their dispersal advantage over smaller species. The number of habitat fragments, which could be kept independent of habitat isolation given the liberty of modelling, did not show any detectable effect on species diversity. Hence, the study identifies mechanisms how habitat fragmentation, specifically isolation threatens large top-predators. As top-predators are known to have stabilizing effects in food webs, it also highlights the importance of habitat isolation for biodiversity conservation.

In **Chapter 2**, I conceptualize the mechanisms of spatial biomass loss in meta-food-webs as the "drainage effect". This drainage effect is, from the perspective of a source population, the counterpart to the rescue effect. Subsequently, this concept is applied to interactive effects of habitat fragmentation, eutrophication and landscape heterogeneity. Computer simulations with the meta-food-web model uncover non-additive effects of habitat fragmentation and eutrophication and provides a mechanistic explanation of how habitat heterogeneity promotes biodiversity. The drainage effect can stabilise large populations on eutrophic patches by removing biomass or energy from top-heavy biomass pyramids and thus reduce oscillations in population densities counteracting the paradox of enrichment. The magnitude of the drainage effect depends on how much biomass is lost during dispersal, i.e. due to isolation or landscape hostility, and on how much biomass is absorbed or returned from neighbouring patches. Thus, an oligotrophic neighbouring patch can absorb excess energy from a eutrophic patch resulting in a rescue effect on the oligotrophic patch as well as a drainage effect on the eutrophic patch and thereby reduce extinctions on both. This also highlights biodiversity threats under three important global change drivers that are habitat fragmentation, eutrophication and habitat homogenization and suggests a basis for potential mitigation strategies.

In **Chapter 3**, I adapt the meta-food-web model to employ specific patch areas and different landscape configurations with differently structured potential meta-food-webs. I recover positive species-area relationships according to the theory of island biogeography in a typical mainland-island landscape configuration when dispersal fluxes are small but uncover flat or negative species-area relationships in landscapes configurations that create large dispersal fluxes. I generate six distinct landscape configurations containing three different spatial network structures and two distinct rules of how patch sizes are distributed in the landscape. Especially small patches at low levels of isolation and in landscapes where patch sizes are distributed randomly, as opposed to spatially autocorrelated, contain communities where the relative influence of dispersal on trophic dynamics is higher. Through trophic bottom-up cascades these small patches sustain higher trophic levels which results in negative species-area relationships. Furthermore, I show that the structures of the potential meta-food-webs change species-area-isolation relationships interactively with landscape configurations. This chapter uncovers basic mechanisms of how spatial and trophic network properties interactively shape biodiversity. As anthropogenic land-use change shapes landscapes non-randomly, i.e. the expansion of agricultural fields, deforestation or the construction of settlements, understanding the effect of landscape configuration on biodiversity is of great importance to conservation.

Overall, this thesis presents a dynamical and spatially explicit meta-food-web model integrating trophic dynamics in complex food webs into complex landscapes and metacommunities. It uncovers basic mechanisms that emerge from this integration of spatial and trophic structures and processes that shape biodiversity. Moreover, computer simulations show how interactive global change drivers threaten biodiversity and thereby provide a basis for biodiversity conservation.

Research chapters

Chapter 1

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Research

The biggest losers: habitat isolation deconstructs complex food webs from top to bottom

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Habitat fragmentation threatens global biodiversity. To date, there is only limited understanding of how the different aspects of habitat fragmentation (habitat loss, number of fragments and isolation) affect species diversity within complex ecological networks such as food webs. Here, we present a dynamic and spatially explicit food web model which integrates complex food web dynamics at the local scale and species-specific dispersal dynamics at the landscape scale, allowing us to study the interplay of local and spatial processes in metacommunities. We here explore how the number of habitat patches, i.e. the number of fragments, and an increase of habitat isolation affect the species diversity patterns of complex food webs (α-, β-, γ-diversities). We specifically test whether there is a trophic dependency in the effect of these two factors on species diversity. In our model, habitat isolation is the main driver causing species loss and diversity decline. Our results emphasize that large-bodied consumer species at high trophic positions go extinct faster than smaller species at lower trophic levels, despite being superior dispersers that connect fragmented landscapes better. We attribute the loss of top species to a combined effect of higher biomass loss during dispersal with increasing habitat isolation in general, and the associated energy limitation in highly fragmented landscapes, preventing higher trophic levels to persist. To maintain trophic-complex and species-rich communities calls for effective conservation planning which considers the interdependence of trophic and spatial dynamics as well as the spatial context of a landscape and its energy availability.

1. Introduction

Understanding the impact of habitat fragmentation (habitat loss, number of fragments and isolation) on biodiversity is crucial for ecology and conservation biology [1–3]. A general observation and prediction is that large-bodied predators at high trophic levels which depend on sufficient food supplied by lower trophic levels are most sensitive to fragmentation, and thus, might respond more strongly than species at lower trophic levels [4,5]. However, most conclusions regarding the effect of fragmentation are based on single species or competitively interacting species (see references within [6–8], but see for example [9–11] for food chains and simple food web motifs). There is thus limited understanding how species embedded in complex food webs with multiple trophic levels respond to habitat fragmentation [4,12–15], even though these networks are a central organizing theme in nature [16,17].

The stability of complex food webs is, among others, determined by the number and strength of trophic interactions [18]. While it is broadly recognized that habitat fragmentation can have substantial impacts on such feeding relationships [19,20],

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[†]These authors contributed equally to this study.

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we lack a comprehensive and mechanistic understanding of how the disruption or loss of these interactions will affect species persistence and food web stability [15,19,21,22]. Assuming that a loss of habitat, a decreasing number of fragments, and increasing isolation of the remaining fragments disrupt or weaken trophic interactions [7], thereby causing species extinctions [15,20], population and community dynamics might change in unexpected and unpredictable ways. This change in community dynamics might lead to secondary extinctions which potentially cascade through the food web [23,24].

Habitat loss, i.e. the decrease of total habitable area in the landscape or a reduction in patch size, can limit population sizes and biomass production, which might drive energy-limited species extinct [25,26] and subsequently entail cascading extinctions [23]. Successful dispersal among habitat patches might prevent local extinctions (spatial rescue effects), and thus, ensure species persistence at the landscape scale [27,28]. Whether dispersal is successful or not depends, among other factors, on the distance an organism has to travel to reach the next habitat patch and on the quality of the matrix the habitat patches are embedded in (in short: the habitat matrix) [29]. With progressing habitat fragmentation, suitable habitat becomes scarce and the remaining habitat fragments increasingly isolated [3,30], affecting the dispersal network of a species. As a consequence, organisms have to disperse over longer distances to connect habitat patches, which in turn might increase dispersal mortality and thus promote species extinctions [2]. Also, habitat fragmentation often increases the hostility of the habitat matrix, e.g. owing to human land use and landscape degeneration [3,31,32]. The increased matrix hostility might further reduce the likelihood of successful dispersal between habitat patches as the movement through a hostile habitat matrix is energy intensive, and thus, population biomass is lost [29,31]. This loss depends on the distance an organism has to travel and its dispersal ability, i.e. its dispersal range and the energy it can invest into movement. Finally, the detrimental effects of habitat loss and increasing isolation are likely to interact, as dispersal mortality can be expected to have a larger *per capita* effect when a population is already declining owing to decreasing habitat.

In this context, superior dispersers might have an advantage over species with restricted dispersal abilities if the distances between habitat patches expand to a point where dispersal-limited species can no longer connect habitat patches. If this is the case, increasing habitat isolation impedes the ability of organisms to move across a fragmented landscape and prevents spatial rescue effects buffering against local extinctions. Increasing habitat isolation might result in increased extinction rates and ultimately lead to the loss of dispersal-limited species from the regional species pool. As large animal species are, at least up to a certain threshold, faster than smaller ones [33,34], they should also be able to disperse over longer distances [4,35,36]. In fragmented landscapes, this body mass-dependent scaling of dispersal range might favour large-bodied consumers such as top predators, and thus, increase top-down pressure resulting in top-down regulated communities.

Empirical evidence and results from previous modelling approaches, however, suggest that species at higher trophic positions are most sensitive to isolation [9,15,37–39]. Modelling tritrophic food chains in a patch-dynamic framework, Liao *et al.* [9,10], for example, show that increasing habitat fragmentation leads to faster extinctions of species at higher trophic levels, which they ascribe to reduced availability of prey [9]. In the fragmentation experiment by Davies *et al.* [39], on the other hand, the observed loss of top species is attributed to the unstable population dynamics of top species under environmental change.

Despite its relevance, a realistic picture and comprehensive understanding of how natural food webs might respond to different aspects of fragmentation such as habitat loss or increasing isolation, and any alteration to the spatial configuration of habitat in general, are lacking. To understand how fragmentation affects the diversity of communities organized in complex food webs requires knowledge of the interplay between their local (trophic) and spatial (dispersal) dynamics. The latter are determined by the number of fragments in the landscape and the distance between them, which can potentially affect the local trophic dynamics. We address this issue using a novel modelling approach which integrates local population dynamics of complex food webs and species-specific dispersal dynamics at the landscape scale (which we hereafter refer to as the meta-food-web model, see figure 1 for a conceptual illustration). Our spatially explicit dynamic meta-food-web model allows us to explore how direct and indirect interactions between species in complex food webs together with spatial processes that connect sub-populations in different habitat patches interact to produce diversity patterns across increasingly fragmented landscapes. Specifically, we ask how the number of fragments and increasing habitat isolation impact the diversity patterns in complex food webs. We further ask which species or trophic groups shape these patterns.

Following general observations and predictions, we expect species diversity within complex food webs to decrease along a gradient of isolation. Based on the substantial variation in both dispersal abilities and energy requirements among species and across trophic levels [4,25,39], we expect species at different trophic levels to strongly vary in their response to isolation. Specifically, we expect certain trophic groups such as consumer species at lower trophic ranks with limited dispersal abilities or top predators with strong resource constraints to be particularly sensitive to isolation. Additionally, with a larger number of fragments we expect more potential for rescue effects, thus fostering survival. This might especially apply to species with large dispersal ranges, which allow them to connect many habitat patches. We test our expectations using Whittaker's classical approach of α-, β- and γ-diversity [40], where α- and γ-diversity describe species richness at the local (patch) and regional (metacommunity) scale, respectively, and β-diversity accounts for compositional differences between local communities.

2. Methods

In the following, we outline a methods summary, for detailed information on equations and parameters see the methods section in the electronic supplementary material. We consider a multitrophic metacommunity consisting of 40 species on a varying number of randomly positioned habitat patches (the meta-food-web, figure 1*b*). All patches have the same abiotic conditions and each patch can potentially harbour the full food web, consisting of 10 basal plant and 30 animal consumer species. The potential feeding links (i.e. who eats whom) are constant over all patches (figure 1*a*,*b*) and are as well as the feeding dynamics determined by the allometric food web model by Schneider *et al.* [41]. We use a dynamic bioenergetic model formulated in terms of ordinary differential equations that describe the feeding and dispersal dynamics. The rate of change in biomass density of a species depends on its biomass gain by feeding and immigration and its biomass loss by

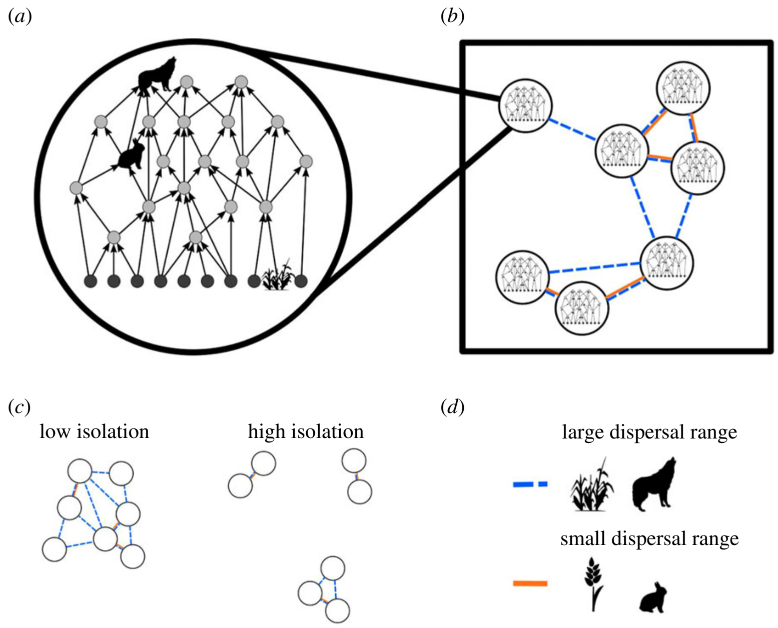

Figure 1. Conceptual illustration of our modelling framework. In our meta-food-web model (*b*), we link local food web dynamics at the patch level (*a*) through dynamic and species-specific dispersal at the landscape scale (*d*). We consider landscapes with identical but randomly distributed habitat patches, i.e. all patches have the same abiotic conditions, and each patch can potentially harbour the full food web. We model fragmented landscapes which differ in the number of habitat patches and the mean distance between patches (*c*).

metabolism, being preyed upon and emigration. We integrate dispersal as species-specific biomass flow between habitat patches (figure 1*b*,*d*). Based on empirical observations (e.g. [35]) and previous theoretical frameworks (e.g. [4,12,34,42]), we assume that the maximum dispersal distance of animal species increases with their body mass. As plants are passive dispersers, we model their maximum dispersal distance as random and body mass independent. We model emigration rates as a function of each species' *per capita* net growth rate, which is summarizing local conditions such as resource availability, predation pressure, and inter- and intraspecific competition [43]. During dispersal, distance-dependent mortality occurs, i.e. the further two patches are apart, the more biomass is lost to the hostile matrix separating them. We constructed 30 model food webs and simulated each food web on 72 different landscapes. For each simulation, we generated landscapes on two independent gradients covering two aspects of fragmentation, namely number of patches and habitat isolation (figure 1*c*). We achieved a full range for the gradient of habitat isolation (landscape connectance ranging from 0 to 1, figure 3*c*). Additionally, we performed dedicated simulation runs to reference the two extreme cases, i.e. (i) landscapes in which all patches are direct neighbours without a hostile matrix, and thus, no dispersal mortality and (ii) fully isolated landscapes, in which no species can bridge between patches, and thus, a dispersal mortality of 100%. Additionally, we tested a null model in which all species have the same maximum dispersal distance. To visualize the impact of number of patches and habitat isolation on species diversity, we used generalized additive mixed models from the mgcv package in R [44,45]. See the electronic supplementary material for detailed information on the maximum dispersal distance, the additional simulations and the statistical analysis.

3. Results

(a) Species diversity patterns

Our simulation results identify habitat isolation (defined as the mean distance between habitat patches, $\overline{\tau}$, figure 2, x-axis) as the key factor driving species diversity loss. As expected, we find fewer species on patches (the averaged local diversity, $\overline{\alpha}$) in landscapes in which habitats are highly isolated (figure 2*a*). In contrast to the decrease in $\overline{\alpha}$-diversity, β-diversity (figure 2*b*), which describes differences in the community composition between patches, increases with habitat isolation. This increase starts around the inflection point of the landscape connectance at a mean patch distance of $\log_{10}\overline{\tau} \approx$ of -0.5, at which 50% of all possible patch to patch connections are lost (figure 3*c* and the electronic supplementary material, figure S4). γ-diversity, the species diversity in the landscape, shows a more complicated pattern. First it decreases owing to the loss of $\overline{\alpha}$-diversity with habitat isolation. This decrease is then reversed by the increase of β-diversity and the γ-diversity increases again with habitat isolation (figure 2*c*). The number of habitat patches in a landscape, Z (figure 2, y-axis), only marginally affects the diversity patterns. The additional simulations of the two extreme cases (i.e. joint scenario with no dispersal loss and fully isolated scenario with 100% dispersal mortality) support these patterns (see the electronic supplementary material, section S7 for the corresponding results). We further show that the isolation-induced species loss also translates into a loss of trophic complexity, i.e. isolated landscapes are characterized by reduced food webs with fewer species and fewer trophic levels (see the electronic supplementary material, figure S2).

(b) Differences among trophic levels

As the number of patches only marginally affects the species diversity patterns, we hereafter focus on the effects of habitat isolation on trophic-dependent differences among species (figure 3). In figure 3, biomass densities, B_i, and landscape connectances, ρ_i, represent the average of each species i over all food webs. Species are ranked according to their body

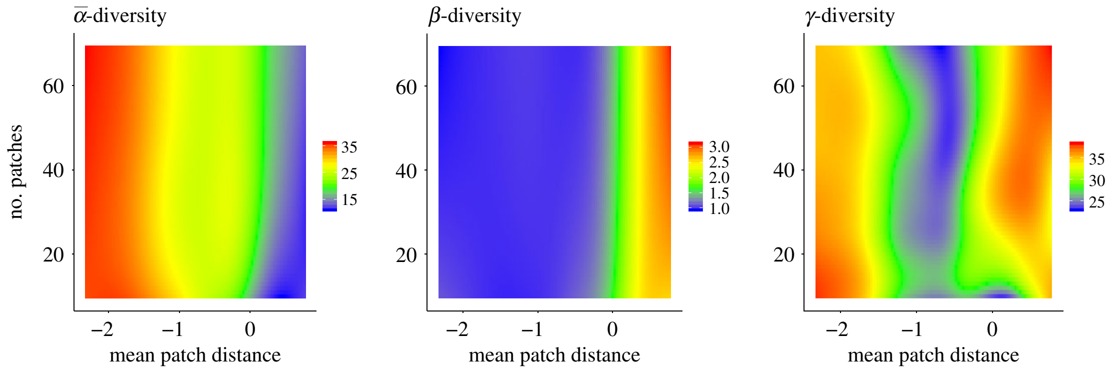

Figure 2. Heatmaps visualizing $\overline{\alpha}$-, β- and γ-diversity (colour-coded; z-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis) and the number of habitat patches (Z; y-axis), respectively. We generated the heatmaps based on the statistical model predictions (see the electronic supplementary material).

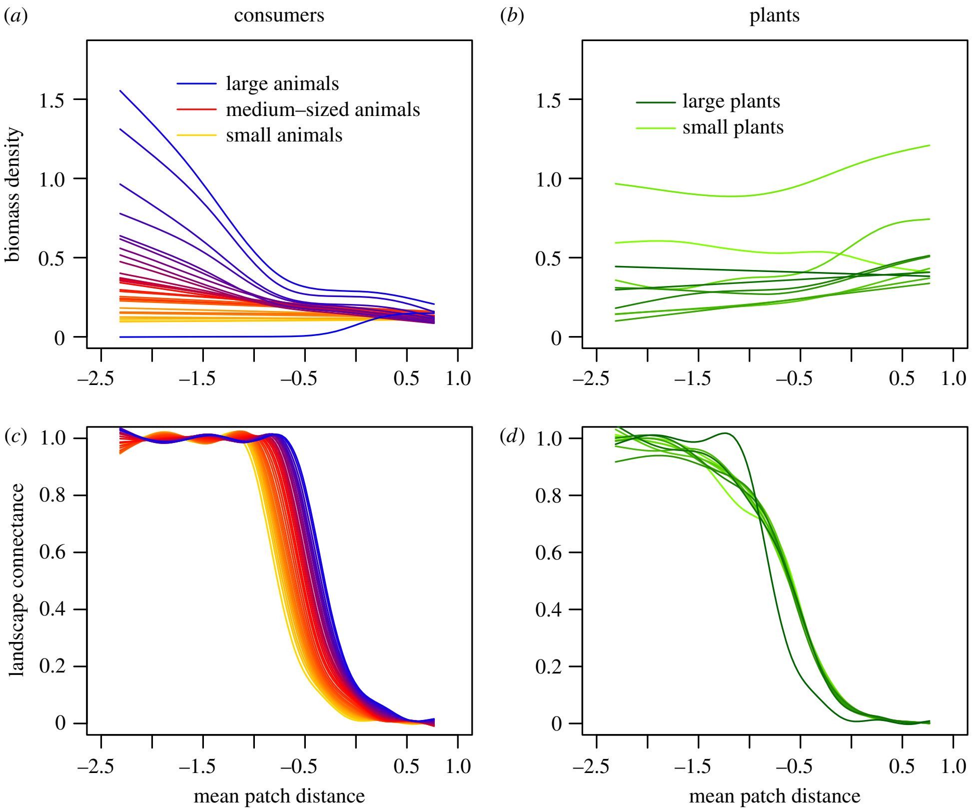

Figure 3. Top row: Mean biomass densities [$\log_{10}$(biomass density + 1)] of animal consumer species (*a*) and basal plant species (*b*) over all food webs (B_i, $\log_{10}$-transformed; y-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Each colour depicts the biomass density of species i averaged over all food webs: (*a*) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (*b*) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; y-axis) for consumer (*c*) and plant species (*d*) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). See the electronic supplementary material, figure S9 for standard errors in biomass densities for four exemplary species.

mass. Thus, although species body masses differ between food webs, species 1 is always the smallest, species 2 the second smallest and so forth. The same applies to ρ_i, where the landscape connectance of consumer species is body mass dependent, but the connectance of plant species is body mass independent (see the methods section). In well-connected landscapes (i.e. landscapes with small mean patch distances, $\overline{\tau}$), large and medium-sized consumer species (except the very largest) have higher population biomass densities than smaller consumers (figure 3*a*,*c*). With expanding distances between habitat patches, large-bodied consumers at high trophic positions (figure 3*a*, red to blue lines) show a particularly strong decrease in population biomass densities. Small consumer species (figure 3*a*, orange lines) are generally less affected by increasing habitat isolation. Plant species show a less consistent response to increased isolation, with most species slightly increasing their biomass density (figure 3*b*). Based on our assumption that the maximum dispersal distance of animals scales with body mass, the ability to connect a landscape follows the same allometric scaling (figure 3*c*). Despite this dispersal advantage, intermediate-sized and large animal species (figure 3*a*, red to blue lines) lose biomass in landscapes in which they still have the potential to fully connect (almost) all habitat patches (figure 3*c*). The differences in plant species biomass densities cannot be attributed to body mass dependent species-specific dispersal distances as for plants maximum dispersal distances were randomly assigned, and thus, there is no connection between body mass and landscape connectance (ρ_i, figure 3*d*). Additional simulations, in which we assumed a constant maximum dispersal distance for all species of $\delta_i = \delta_{\max} = 0.5$, support the negligibility of species-specific differences in dispersal ability for the emerging diversity patterns (see the electronic supplementary material, figure S3).

4. Discussion

Habitat fragmentation is a major driver of global biodiversity decline. To date, a comprehensive understanding of how the different aspects of habitat fragmentation, i.e. habitat loss [6], number of fragments and isolation, affect the diversity patterns of species embedded in complex ecological networks such as food webs is lacking (see e.g. meta-analysis by Martinson & Fagan [15], and references therein). Our simulation experiment allows us to independently explore the effects of number of fragments (i.e. number of habitat patches in the landscape), and of habitat isolation (i.e. distance between patches) on persistence and biomass densities of species in complex communities. We identified habitat isolation to be responsible for species diversity decline both at the local and regional scale.

The rate at which a species loses biomass density strongly depends on its trophic position. Large-bodied consumer species at the top of the food web are most sensitive to isolation although they are dispersing most effectively (i.e. for them, increasing distances between habitat patches do not necessarily result in the loss of dispersal pathways or a substantial increase of dispersal mortality). Surprisingly, we find top species to lose biomass density and sometimes even go extinct in landscapes they can still fully connect, whereas the biomass densities of small consumer species at lower trophic levels and plant species are only marginally affected by increasing habitat isolation. We attribute the accelerated loss of top species to the energy limitation propagated through the food web: with increasing habitat isolation an increasing fraction of the biomass production of the lower trophic levels is lost owing to mortality during dispersal and is thus no longer available to support the higher trophic levels. Additionally, the reduced top-down pressure on smaller consumers seems to compensate for their increased dispersal loss. Our model adds a complementary perspective to previous research pointing towards a trophic-dependent extinction risk owing to constraints in resource availability with increasing habitat fragmentation [9,38].

(a) Habitat isolation drives species loss

The increasing isolation of habitat fragments poses a severe threat to species persistence (but see [46,47]). We demonstrate in our simulation experiment that the generally observed pattern of species loss with increasing habitat isolation (e.g. [3]) also holds for species embedded in large food webs. The loss of species occurs both at the local ($\overline{\alpha}$-diversity) and regional (γ-diversity) scale. For the latter, however, an increase in β-diversity compensates the loss in local diversity ($\overline{\alpha}$) when landscapes become very isolated and γ-diversity increases again (see section below: Habitat isolation promotes β-diversity).

We modelled dispersal between habitat patches by assuming an energy loss for the dispersing organisms—a biologically realistic assumption as landscape degeneration, which often occurs concurrently with habitat fragmentation, increases the hostility of the habitat matrix [3]. Consequently, the dispersal mortality, and thus, biomass loss of populations to the habitat matrix increases substantially when dispersal distances between habitat patches expand. To account for the variation in dispersal ability among trophic groups, we incorporated species-specific maximum dispersal distances. For animal species, this maximum dispersal distance increases like a power law with body mass, therefore weakening the direct effect of habitat isolation the larger a species is. Despite this, top predators and other large consumer species respond strongly to isolation. These species exhibit a dramatic loss in biomass density or even go extinct in landscapes they still perceive as almost fully connected (landscape connectance, ρ_i, close to one), which indicates that their response to habitat isolation is mediated by indirect effects originating from the local food web dynamics.

(b) Local food web dynamics and energy limitation drive top predator loss

In local food webs, energy is transported rather inefficiently from the basal to the top species, with transfer efficiency in natural systems often only around 10% [48]. This energy limitation effectively controls the food chain length [26] and renders large species at high trophic levels vulnerable to extinction owing to resource shortage [49]. In our model, energy availability decreases if habitat isolation is high as this increases biomass loss during dispersal. This affects particularly small species at lower trophic levels because they generally have the highest metabolic costs per unit biomass and therefore the highest biomass losses per distance travelled [33,41]. The biomass loss during dispersal consequently reduces the net biomass production at the bottom of the food web and severely threatens species at higher trophic positions that already operate on a very limited resource supply.

Moreover, owing to the feedback mechanisms regulating the community dynamics within complex food webs, a loss of top consumer species can have severe consequences for the functioning and stability of the network [21,22]. A loss of top-down regulation can, for instance, lead to secondary extinctions resulting in simpler food webs [21,50]—an additional mechanism that can foster the loss of biodiversity as observed in our simulations. However, we also see a much more direct effect of the changing community composition: the biomass densities of small species that suffer most from increased dispersal mortality do not, as one might expect, decline much as isolation progresses. We attribute this to a release from top-down control as their consumers lose biomass or even go extinct, which counters the negative direct effect of habitat isolation. These arguments suggest that differential dispersal capabilities are less important than energetic limitations in explaining the strong negative response of large consumers to habitat isolation. This claim is supported by the additional simulations where all species experienced the same level of dispersal mortality, which yielded similar results (see the electronic supplementary material, figure S3).

We did not find an effect of the number of patches on $\overline{\alpha}$-, β- and γ-diversity. As we model biomass densities on patches without defined area (see section below: Model specifications), fewer patches do not reflect habitat loss, but rather the loss of fragments, i.e. stepping stones in the dispersal network. Thus, the energy limitation in our simulated landscapes derives from direct dispersal loss and cascading effects of dispersal losses of resources. For plant and small animal species, this can be understood easily, as these species are less energy limited and thus are able to persist on a single habitat patch. For larger animal species the situation is more subtle: while they can integrate over multiple patches, feeding interactions still always occur on one patch at a time. If the biomass densities of their resources (and thus also the realized feeding rate) is too low on a particular patch to cover their metabolic requirements, they gain no advantage from the addition of more patches with equally low resource abundance.

(c) Habitat isolation promotes β-diversity

Contrary to the decline in $\overline{\alpha}$-diversity with increasing habitat isolation, we find an increase in β-diversity starting from around $\log_{10}$ mean patch distance $\overline{\tau} \approx -0.5$. We assumed identical abiotic conditions on all habitat patches, i.e. there are no differences in nutrient availability or background mortality rates. Therefore, any differences in conditions experienced by the species on different patches can only originate from the initial community composition and the structure of the dispersal network. One way for such different conditions to emerge is the disintegration of the dispersal network into several smaller clusters. Up to a $\log_{10}$ mean patch distance $\overline{\tau} \approx -0.5$, the species with the largest maximum dispersal distance (which could be both large animals that have not already gone extinct and plants with a randomly selected large dispersal distance) have a landscape connectance (ρ_i) of at least 0.5. This dispersal advantage easily allows them to connect all patches to a single network component, thereby providing homogenization for the meta-food-web. However, as the mean patch distance increases further, even these species cannot bridge all gaps in the habitat matrix any more and clusters of patches emerge that are for all species disconnected from the other patches. As these clusters vary in the number of patches and mean patch distance within the cluster, the level of dispersal mortality experienced by the species on the different clusters can also vary considerably. Any further increase in mean patch distance causes the landscape connectance to drop to nearly zero for all species and all patches within the landscape approach complete isolation. With no immigration into isolated patches, non-resident species cannot colonize them and initial community compositions drive dissimilarities among patches. However, the initial β-diversity is not sufficient in explaining the high β-diversity in strongly isolated landscapes (electronic supplementary material, figure S4). This suggests that different food web positions of initial species lead to different cascading effects in local food web dynamics with more or less secondary extinctions on isolated patches further increasing differences in local community compositions. The increase in β-diversity is even stronger than the loss of local diversity resulting in an increase in γ-diversity in highly isolated landscapes. However, species contributing to this high γ-diversity tend to occur on fewer patches and thus are more prone to go extinct in the whole landscape owing to stochastic extinction events.

(d) Model specifications

The framework we propose here for modelling meta-food-webs is very general and allows for a straightforward implementation of future empirical insight where we so far had to rely on plausible assumptions. The trophic network model for the local food webs is based on a tested and realistic allometric framework [41] with a fixed number of 40 species—a typical value in dynamic food web modelling (e.g. [51,52]). We based all model parameters on allometric principles [33,53] allowing for a simple adaptation of our modelling approach to other trophic networks such as empirically sampled food webs [54] or other food web models such as the niche model [55]. Moreover, empirical patch networks (e.g. the coordinates of meadows in a forest landscape) or other dispersal mechanisms [6,56] may be incorporated in the future. In our simulations, biomass loss during dispersal is predominantly responsible for the decline in species diversity. We linked the maximum dispersal distance of animals and thereby also their mortality during dispersal to body mass, which is plausible because larger animal species can move faster [34], and thus, have to spend less time in the hostile habitat matrix. Interestingly, however, we did not find any empirical study relating body mass directly to mortality or biomass loss during migration. If such information becomes available in the future, it can be easily incorporated into our modelling framework. Further, we deliberately assumed all habitat patches to share the same abiotic conditions [57] as we wanted to focus on the general effects of the interaction of complex food web and dispersal dynamics. Adding habitat heterogeneity among patches, e.g. by modifying nutrient availability or mean temperature, however, is straightforward and can be expected to yield additional insight into the mechanisms for the maintenance of species diversity in meta-food-webs. Finally, by using a dynamical model formulated in terms of biomass densities instead of absolute biomasses (or population sizes), we make the implicit assumption that patches do not have an absolute size. Thus, the number of patches in a landscape cannot be directly linked to the total amount of habitat but rather reflects the number of fragments, i.e. stepping stones in the dispersal network of a species. A decreasing number of patches thus does not necessarily imply habitat loss. In order to also address effects of habitat loss (in terms of area), the model could be adapted to include, for example, area-specific extinction thresholds and absolute biomasses in dispersal dynamics, but this was beyond the scope of this study.

(e) Synthesis and outlook

Our simulation experiment demonstrates that habitat isolation reduces species diversity in complex food webs in general, with differences in the effect across trophic levels. In increasingly isolated landscapes, energy becomes limited, which decreases the biomass density of large consumers or even drives them extinct. These primary extinctions may result in a cascade of secondary extinctions, given the importance of top predators for food web stability [24,58]. The increased risk of network downsizing, i.e. simple food webs with fewer and smaller species [14,59], stresses the importance to consider both direct and indirect trophic interactions as well as dispersal when assessing the extinction risk of species embedded in complex food webs and other ecological networks.

To date, most conservation research focuses on single species and does not consider the complex networks of interactions in natural communities [7,14]. However, the patterns we presented here clearly support previous studies highlighting the importance of trophic interactions (e.g. [9,37,38]). We show that the fragmentation-induced extinction risk of species strongly depends on their trophic position, with top species being particularly vulnerable. Given that top-down regulation can stabilize food webs [24,58], the loss of top predators might entail unpredictable consequences for adjacent trophic levels, destabilize food webs, reduce species diversity and trophic complexity and ultimately compromise ecosystem functioning [23,24]. In addition to the trophic position of a species, the trophic structure of the food web has also been shown to be an important aspect [11]. Our results suggest that bottom-up energy limitation caused by dispersal mortality owing to habitat isolation can be a critical factor driving species loss and the reduction of trophic complexity. The extent of this loss strongly depends on the spatial context (see also [6]). Thus, to maintain species-rich and trophic-complex natural communities under future environmental change, effective conservation planning must consider this interdependence of spatial and trophic dynamics. Notably, conservation planning should also consider habitat isolation and matrix hostility (and consequently dispersal mortality) to ensure sufficient biomass exchange between local populations, capable of inducing spatial rescue effects and to alleviate bottom-up energy limitation of large consumers. Energy limitations can also result from habitat loss (which we did not model here), decreasing energy availability at the bottom of the food web affecting local dynamics intrinsically independent of dispersal. Thus, avoiding habitat loss remains a crucial aspect [2,47]. We highlight the need to explore food webs and other complex ecological networks in a spatial context to achieve a more holistic understanding of biodiversity and ecosystem processes.

Data accessibility. We enable full reproducibility of our study by providing the original C- and R-code on the Dryad Digital Repository at: https://doi.org/10.5061/dryad.c624907 [60].

Authors' contributions. All authors conceived and designed the modelling framework; J.H. and R.R. ran the simulations on the high-performance-cluster; R.R. analysed the data with support from all other authors; all authors contributed to interpreting the results; J.H. wrote the first draft of the manuscript with support from R.R. and M.S.; and J.H. and R.R. led the editing. All authors contributed critically to the drafts and gave final approval for publication.

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Chapter 2

Landscape heterogeneity buffers biodiversity of meta-food-webs under global change through rescue and drainage effects

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The impacts of habitat fragmentation and eutrophication on biodiversity have been studied in different scientific realms. Metacommunity research[1–5] has shown that reduction in landscape connectivity may cause biodiversity loss in fragmentated landscapes. Food-web research addressed how eutrophication increases biomass accumulations at high trophic levels causing the breakdown of local biodiversity[6–9]. However, there is very limited understanding of their cumulative impacts as they could amplify or cancel each other. Here, we show with simulations of meta-food-webs that landscape heterogeneity provides a buffering capacity against increasing nutrient eutrophication. An interaction between eutrophication and landscape

homogenization precipitates the decline of biodiversity. We attribute our results to two complementary mechanisms related to source and sink dynamics. First, the "rescue effect" maintains local biodiversity by rapid recolonization after a local crash in population densities. Second, the "drainage effect" allows a more uniform spreading of biomass across the landscape, reducing overall interaction strengths and therefore stabilizing dynamics. In complex food webs on large spatial networks of habitat patches, these effects yield systematically higher biodiversity in heterogeneous than in homogeneous landscapes. Our meta-food-web approach reveals a strong interaction between habitat fragmentation and eutrophication and provides a mechanistic explanation of how landscape heterogeneity promotes biodiversity.

Increasing human demands for production of goods in natural landscapes have caused habitat fragmentation and homogenisation, eutrophication and increasing land-use intensity. This resulted in an erosion of biodiversity and associated ecosystem services at global scales. Habitat fragmentation describes how production areas dissect continuous natural landscapes into habitat patches embedded in a landscape matrix whose hostility for the species increases with land-use intensity. Increasing nutrient inputs from agricultural practices yield biomass accumulations at higher trophic levels, eroding biodiversity by increased species' interaction strengths[6,9]. Despite growing evidence on the importance of these global change factors, we still do not understand how their interaction drives biodiversity changes. While fragmentation and eutrophication are often studied in isolation, complex feedback loops in multi-trophic food webs can generate non-linearities in the response of biodiversity, which is rendering our knowledge of the interactive effects of these stressors in natural landscapes fraught with uncertainty. The high-dimensional interplay between spatial and trophic processes prevents experimental studies on such complex interactions. Simulations of spatial food web dynamics are therefore needed to reveal the mechanisms underlying how these global change stressors interact.

One key challenge is the integration of spatial processes connecting local populations across habitat patches into metapopulations and interaction processes connecting local species into complex food webs (Fig. 1). Traditionally, independent and mostly separated research areas have addressed these two types of ecological networks. First, metacommunity theory describes how dispersing individuals connect local populations across complex spatial networks of habitat patches[10]. Depending on their size and quality, patches can comprise large source populations that yield a net dispersal flux of individuals to small sink populations[1,4] (Fig. 1a). These source-sink dynamics[11] can facilitate persistence of small populations by rescue effects[12], which is undermined by increasing fragmentation or land-use intensity that prevent successful dispersal. Second, food-web theory addresses how biomass fluxes (i.e. energy and matter) between species drive population dynamics (Fig. 1b). Weak biomass fluxes can cause consumer extinction due to energy limitations while strong biomass fluxes can result in top-heavy consumer-resource biomass pyramids with unstable dynamics[6,9]. Eutrophication in particular increases all biomass fluxes and thus undermines biodiversity of local food webs[7]. Although both research areas documented strongly negative effects of either fragmentation or eutrophication on biodiversity, the interplay of these stressors in complex natural communities has remained virtually untapped.

So far, studies synthesizing spatial and trophic processes have been limited to small species motifs such as food chains[13,14]. They showed that dispersal can synchronize population dynamics, which reduces biodiversity by correlated local extinctions[15,16]. However, consumer dispersal can also induce compensatory dynamics[17] and dampen oscillations[18], which prevents extinctions. Moreover, dispersal may increase resilience of complex food webs by reducing strong interspecific interactions[19] depending on the trophic level that is dispersing[18]. The relative strength of these potentially counteracting positive and negative effects of dispersal on population persistence depends on the trophic interaction structure[14]. While these studies have demonstrated interactions between spatial and trophic processes in small modules, the study of impacts on biodiversity in large spatial networks with many species has remained in its infancy.

Traits of organisms play an important role in both spatial and trophic processes. In metacommunities, body mass and movement mode determine which patches compose species-specific spatial networks[20]. Similarly, the propagation of energy fluxes through food webs is driven by species' interaction strengths that depend strongly on body masses[8]. Although metapopulation and food-web theories have been developed mostly independently, they have identified the same important drivers (i.e. body mass), and the same currencies (i.e. biomass fluxes). To date, a trophic metacommunity framework incorporating spatial use properties is still lacking[21]. Also, as spatial and trophic processes in real landscapes are coupled (Fig. 1c), a mechanistic understanding of global change effects on ecosystems will benefit from an integrated approach. We address this challenge by synthesizing metapopulation and food-web models that use allometric scaling relationships of spatial and trophic processes as a unifying principle into a meta-food-web model. We identify key mechanisms complementary to the rescue effect in landscapes under eutrophication and isolation (Fig. 1).

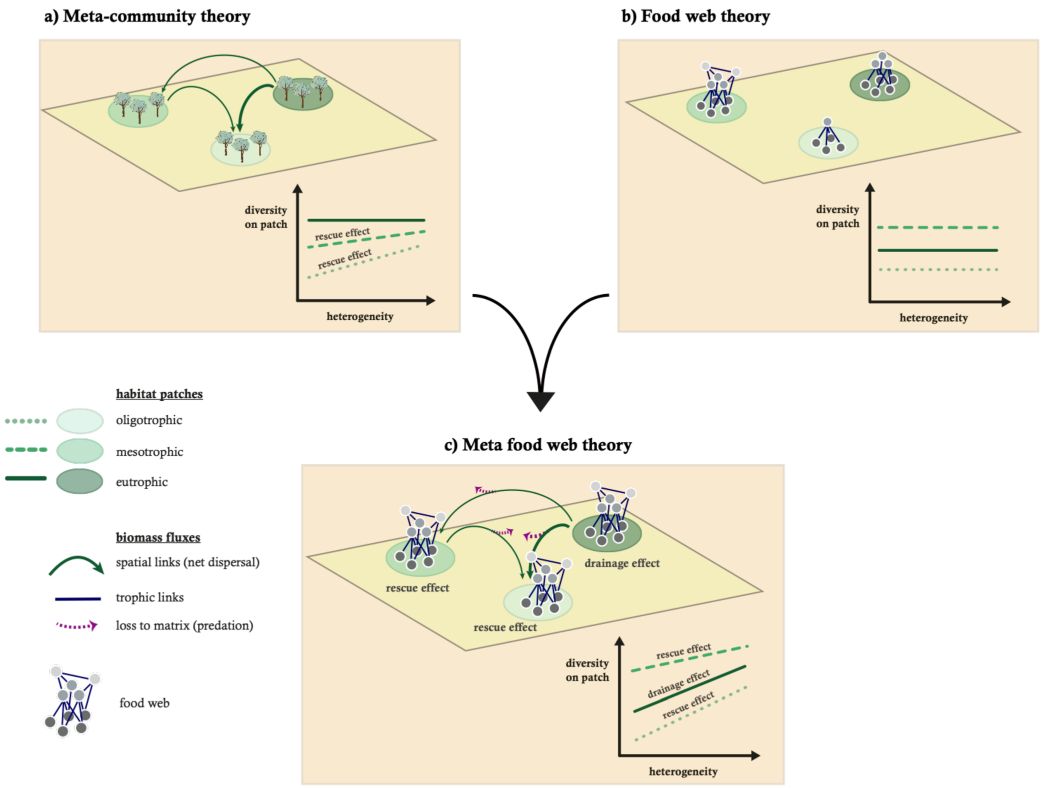

Fig. 1. Conceptual figure illustrating the synthesis of metacommunity theory and food-web theory into meta-food-web theory. Panel a) illustrates metacommunity dynamics with net dispersal from larger (nutrient richer patches) to smaller populations (nutrient poorer patches) and the associated rescue effect on local diversity. Panel b) illustrates local food-web dynamics on patches with different nutrient richness and the effect of the paradox of enrichment on local diversity. Panel c) illustrates the synthesis of metacommunity and food web dynamics and the interaction of respective key effects and their consequence for biodiversity.

We use a bioenergetic model to analyse population dynamics across a gradient of complexity from simple (tri-trophic food chain on a single patch) to complex systems (40-species food web on 50 habitat patches). This model employs body masses as the unifying trait that determines not only trophic links and interaction strengths of the food webs but also the dispersal ranges. Dispersal rates depend on local net growth rates, summarizing resource availability, competition and predator pressure arising from local trophic dynamics[22].

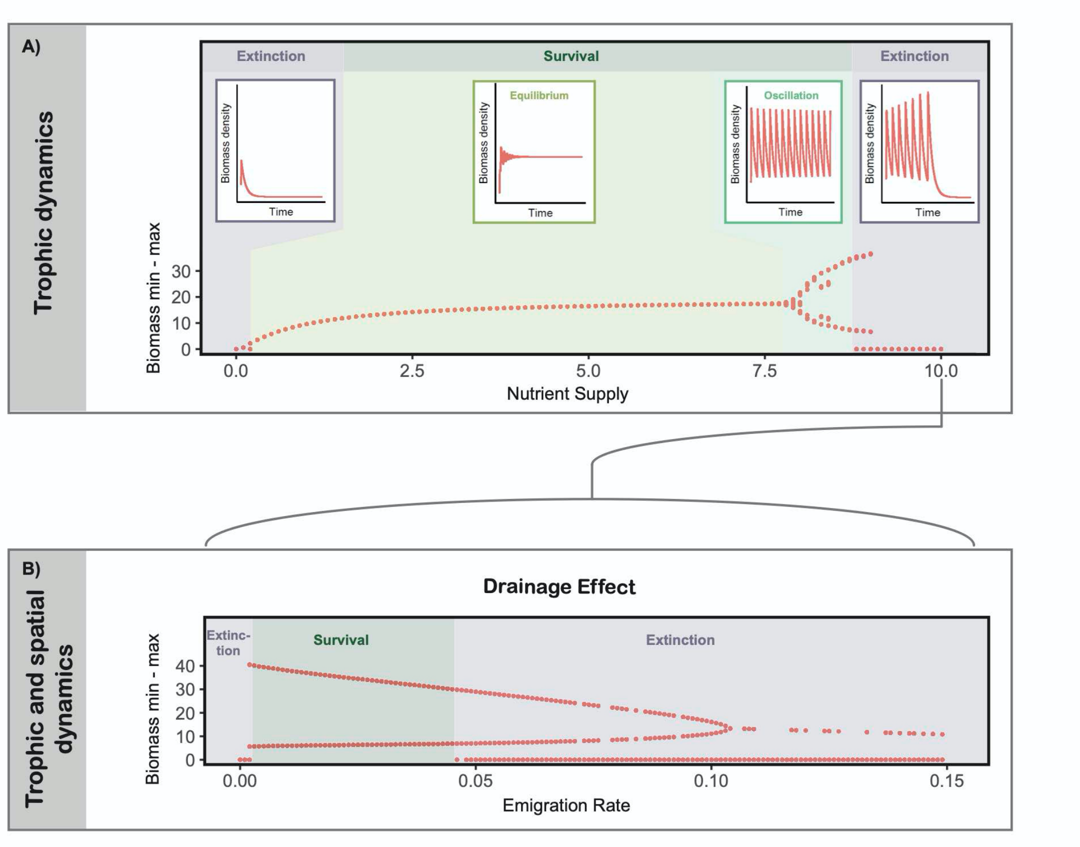

Fig. 2: Top predator dynamics of a tri-tropic food chain on a single patch. A) Exemplary time series of biomass densities of the predator at different nutrient supply concentrations (boxes; from left to right: 0.1 (oligotrophic); 3 (mesotrophic); 8.5 and 10 (eutrophic)) corresponding to points in the bifurcation diagram showing maximum and minimum biomass density (y-axis) across a gradient of nutrient supply concentrations (x-axis). B) Bifurcation diagram showing maximum and minimum biomass density (y-axis) when enabling emigration across a gradient of emigration rates (x-axis) with a nutrient supply concentration of 10, which corresponds to the last point in panel A).

Firstly, on a single patch, low nutrient supply for a tri-trophic food chain causes predator starvation (Fig. 2a, extinction, left side). Increasing nutrient supply first promotes predator equilibrium biomass densities (Fig. 2a, survival, equilibrium) and therefore top-heavy biomass pyramids causing biomass oscillations (Fig. 2a, survival, oscillation), which paradoxically eventually yield predator extinction (Fig. 2a, extinction, right side). Such extinctions due to unstable oscillations under eutrophication have first been described as the "paradox of enrichment"[6]. Subsequently, they were generalized to systems with an increased energy flux to the predator relative to its loss rate[9,23]. Turning around this "principle of energy flux", however, also suggests that an additional drainage effect arises from energy transfer from large populations (sources) to small populations (sinks), preventing unstable dynamics in top-heavy systems. Consistent with this hypothesis, we find that increasing emigration rates that drain biomass out of a eutrophic location can prevent predator extinction by reducing oscillations (Fig. 2b). Spatial fluxes tend to increase with dispersal rates and the underlying variability in the landscape. This demonstrates the drainage effect as a mechanism by which spatial processes can stabilize trophic population dynamics in heterogeneous landscapes.

Subsequently, we studied this drainage effect in systems of two connected habitats across gradients of landscape hostility and habitat heterogeneity (represented by the difference in nutrient supply concentration of the two locations). Landscape hostility summarizes all factors that drive the loss of biomass during dispersal including higher metabolic costs and increased mortality rates by predation pressure in the unsuitable landscape matrix. Dispersal synchronizes unstable dynamics, causing predator extinction (Fig. 3, lower left corner), in simulations without heterogeneity and without hostility. Increasing landscape hostility yields drainage of biomass during dispersal, facilitates predator persistence and then also reduces oscillations (Fig. 3, along the hostility axis). At very high levels of landscape hostility, however, extreme death rates during dispersal cause predator extinction. Similarly, increasing patch heterogeneity also enables predator persistence and decreases oscillations (Fig. 3, along the heterogeneity axis). The drainage effect offers general mechanistic explanations for these emergent patterns despite of some slightly more complex patterns in population oscillations (e.g. some combinations of landscape hostility and patch heterogeneity yield weak spatial links between patches and desynchronization of biomass oscillation frequencies, see Supplement Fig. S2 for details). For eutrophic patches, increased dispersal losses by landscape hostility or the coupling with an oligotrophic patch (patch heterogeneity) both increase the biomass drainage through increased net migration. For oligotrophic patches, however, there are differences between effects of landscape hostility and patch heterogeneity. Drainage by landscape hostility supresses small populations even more, whereas patch heterogeneity causes a gain in biomass via dispersal that supports predator populations via rescue effects (see Supplement Fig. S1). Patch heterogeneity thus creates dispersal fluxes in biomass that are responsible for not only the well-known rescue effects[12] supporting small populations on oligotrophic sink patches by net-immigration but also the drainage effects sustaining large populations on eutrophic patches.

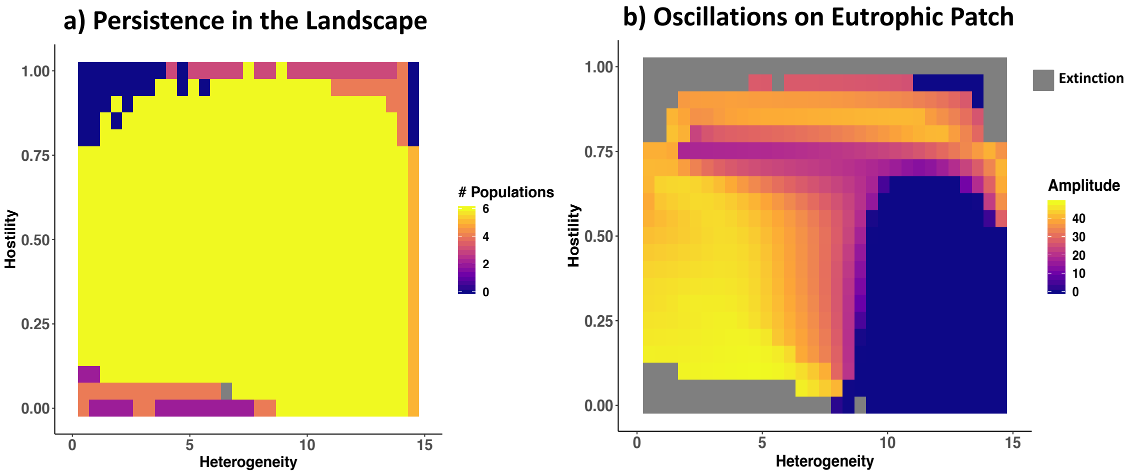

Fig. 3: Top predator dynamics of a tri-tropic food chain on two coupled patches. a) Heat map showing the number of persisting populations (colour coded; plant, herbivore and predator on 2 patches; maximum of 6) in the landscape across gradients of landscape heterogeneity (x-axis; difference in nutrient supply concentration across the two patches; on the left: two eutrophic patches, on the right: an eutrophic and an oligotrophic patch) and matrix hostility (y-axis). b) Heat map showing the amplitude of biomass density oscillations of the predator (z-axis; colour coded) in the (always) eutrophic patch across gradients of landscape heterogeneity (x-axis; difference in nutrient supply concentration between the two patches) and matrix hostility (y-axis). Amplitudes of 0 (blue) stand for an equilibrium state of the predator. Grey areas are where the predator went extinct.

To generalize the mechanistic understanding of drainage effects from food chains, we simulated the dynamics of a complex food web consisting of 10 plants and 30 animals on different complex landscapes containing 50 habitat patches (Fig. 4). We simulated homogeneous landscapes, where all patches have the same nutrient supply concentration. These simulations were replicated across a gradient of nutrient supply concentrations ranging from $10^{-0.8}$ (oligotrophic) to 10^{2} (eutrophic). We also simulated three types of heterogeneous landscapes with landscape averages being oligotrophic, mesotrophic or eutrophic (Fig. 4). Nutrient supply concentration for each patch of heterogenous landscapes is assigned randomly from the same gradient as in the homogeneous scenario, but with a higher sampling density in the lower or higher nutrient supply values for oligotrophic and eutrophic heterogeneous landscapes, respectively, and uniform sampling for the mesotrophic heterogeneous landscapes. In line with our results from the food chain simulations, we found that local species richness in homogeneous landscapes is lowest on oligotrophic patches due to energy limitation. Higher nutrient supply first increases species richness on mesotrophic patches before decreasing it again on eutrophic patches (Fig. 4, purple). Species richness is highest in mesotrophic heterogeneous landscapes because oligotrophic patches profit from the rescue effect and eutrophic patches profit from the drainage effect (Fig. 4, orange). If there are only a few oligotrophic patches in a eutrophic heterogeneous landscape, rescue and drainage effects still increase local diversity, although the recue effect is weaker (Fig. 4, blue). Similarly, a few eutrophic patches in an oligotrophic landscape foster local diversity through rescue and drainage effects (Fig. 4, green). Thus, rescue effects and drainage effects also apply to complex food webs in complex landscapes. This shows that the interaction of strong and weak spatial and trophic biomass fluxes increases stability and species richness in metacommunities.

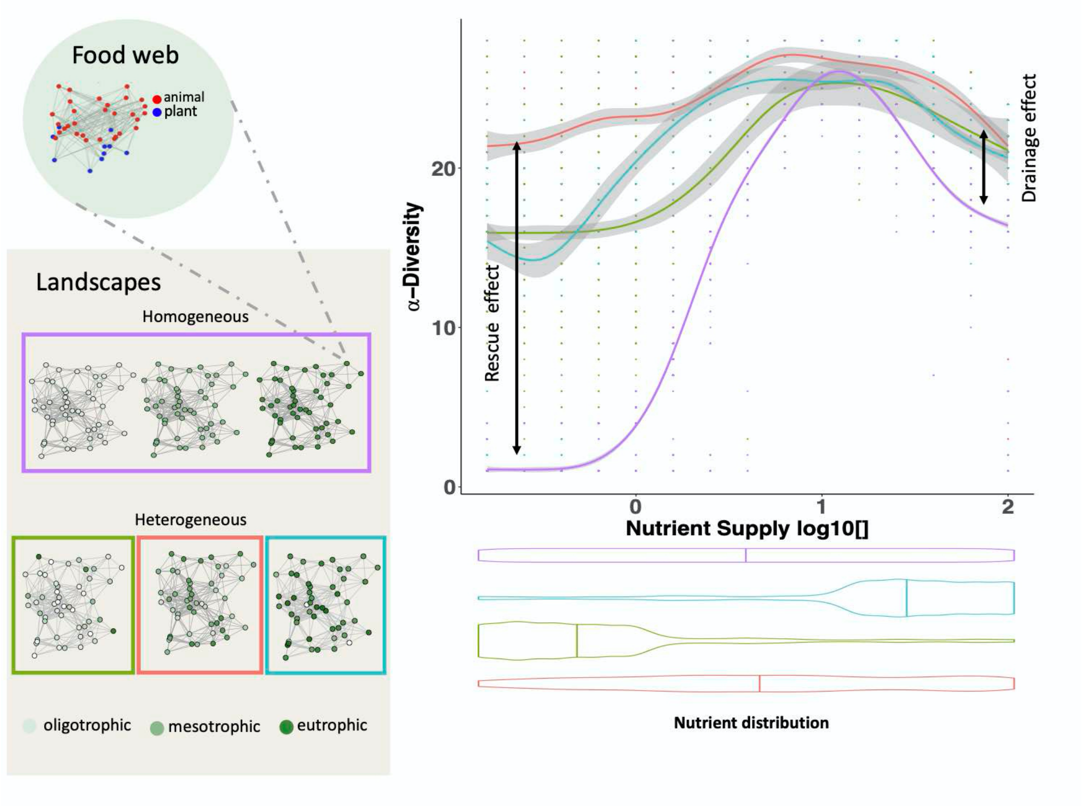

Fig. 4 Landscape heterogeneity drives biodiversity in complex meta-food-webs. Local diversity (y-axis) across a gradient of patch nutrient supply concentration in homogeneous (purple) and heterogeneous (green, orange, blue) landscapes. Violin plots below the x-axis show nutrient distributions within the landscape for each scenario. The meta-food-web consists of a complex food web of 10 plants and 30 animals and large homogeneous and heterogeneous landscapes with 50 habitat patches with different patch nutrient supply concentrations (nutrient supply concentrations on habitat patches are colour coded). Edges indicate dispersal links for an exemplary species with a dispersal range of 0.3. Lines are a smooth fit from a GAM model with 95% confidence intervals in ggplot2 and points represent the data.

Spatial processes in heterogenous landscapes stabilise local food-web dynamics and translate into higher diversity. This stresses the importance of addressing global change drivers in a meta-food-web framework. Various mechanisms are involved, all related to source-sink dynamics where energy moves from high biomass locations to low biomass locations. We have found that the well-known rescue effect allows persistence on oligotrophic patches, while the novel drainage effect buffers eutrophic patches. Complex interactions among these phenomena may further promote diversity. For instance, nutrient spillover from a eutrophic to a neighbouring oligotrophic location may promote local productivity and increase food-chain length[24]. Such spatial nutrient diffusion can destabilize simple food chains and decrease spatial heterogeneity in a meta-ecosystem model[18] and thus cross-ecosystem nutrient fluxes can change community composition[25]. These meta-ecosystem approaches have synthesized nutrient fluxes with simple trophic modules, and our meta-food-web approach provides a flexible tool to scale-up these findings to the levels of landscape and food-web complexity that characterize natural ecosystems.

In real landscapes, which suffer more and more from fragmentation, land-use intensification and eutrophication due to human activities, managing connectivity and heterogeneity is an important aspect of biodiversity conservation and restoration. Traditionally, increasing landscape hostility due to higher dispersal mortality or increased distances between habitat fragments have been perceived as threats to the biodiversity of habitat patches as they reduce rescue effects[12]. Hence, wildlife bridges across highways and other corridors to increase connectivity between habitat patches have been propagated as important tools to remedy the consequences of land-use intensification as the reduced hostility may benefit small sink populations by rescue effects and thus lower extinction risks[26]. Our results, however, indicate that the consequences of increasing habitat connectivity are highly context-dependent. We found that higher connectivity between large populations can undermine biodiversity by decreasing the drainage effect, whereas connecting large and small populations is generally beneficial for both. Thus, in managing landscape connectivity, connections between eutrophic and oligotrophic habitats or among oligotrophic habitats should be enhanced to reduce the hostility effect. However, connections among eutrophic habitats should only be established with caution, as a reduced hostility effect results in less drainage effect and thus has the potential do destabilize both populations.

Broader implications for ecosystem services can arise as two habitat patches that suffer from eutrophication may lose predatory pest control agents if they are well connected to each other but may maintain pest control when coupled with less intensive or natural habitats. Thus, the management of connectivity and heterogeneity in landscapes suffering from fragmentation and eutrophication may benefit from fostering rescue and drainage effects to maintain biodiversity and ecosystem services. Our meta-food-web approach has revealed interactions between spatial and trophic dynamics beyond the rescue effect that provide a mechanistic explanation of how landscape heterogeneity enhances biodiversity, which facilitates new strategies for active landscape management to foster natural biodiversity and ecosystem services.

Author contributions

R.R., U.B. and M.R.H. developed the idea, R.R. built the model, did the analyses and wrote the first draft of the manuscript. M.R.H. designed the figures. All authors contributed to the interpretation and the final version of this manuscript.

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Competing interests

None declared.

Materials and Correspondence

Requests should be addressed to U.B.

Methods summary

Model

We model a tritrophic food chain of one plant, one herbivore and one predator population on one or two habitat patches and complex meta-food-webs consisting of 10 plants and 30 animals in different landscapes containing 50 patches. The feeding dynamics are constant over all patches and are determined by the allometric food-web model by Schneider et al. 2016[27]. We integrate dispersal as species-specific biomass flux between habitat patches according to Ryser et al. 2019[28]. With the use of a dynamic bioenergetic model we formulate feeding and dispersal dynamics in terms of ordinary differential equations. The rate of change in biomass densities of a species are the sum of its biomass loss by metabolism, being preyed upon and emigration and its biomass gain by feeding and immigration. For detailed equations see Ryser et al. 2019[28] and for model parameters see the supplement (TS1).

Local food-web dynamics

Following the allometric food-web model by Schneider et al. 2016[27] each species is fully characterised by its average adult body mass. For the complex food web $\log_{10}$ body masses were randomly drawn from a uniform distribution from 0 to 3 for plants and from 2 to 6 for animals. For the food chain the plant body mass was set to 10^2, the herbivore body mass to 10^4 and the predator body mass to 10^6. We set mass ratios of the herbivore to the plant and the predator to the herbivore to the optimum of 100, thus the respective resource being a one-hundredth of its consumer's body mass. Trophic dynamical parameters, such as metabolic rates and feeding rates, scale with body masses of model species. Also, we assume a type II functional response. Capture rates were reduced to 5% to achieve viable food chains and food webs with no interference competition.

Nutrient model

We have an underlying nutrient model with one nutrient that is driving the nutrient uptake and therefore the growth rate of the plant population[8,27]. The nutrient model consists of one nutrient, a nutrient turnover rate of 0.25 and a nutrient supply concentration. The nutrient supply concentration was varied to get eutrophic and oligotrophic patches (see Setup).

Spatial dynamics

We model dispersal between local communities as a dynamic process of emigration and immigration, assuming dispersal to occur at the same timescale as the local population dynamics[29]. Thus, biomass flows change dynamically between local populations and the dispersal dynamics directly influence local population dynamics and vice versa[22].

Dispersal rates of animals are modelled with an adaptive emigration rate depending on the net growth rate on the given patch. Dispersal ranges depend on the body masses of our model species with larger species having a higher dispersal range. We model a hostile matrix between habitat patches that does not allow feeding interactions to occur during dispersal. Depending on the scenario, we define a landscape with one or two patches. In cases with two patches, their locations are spatially explicit and were chosen in a way that the distances between reflect the dispersal loss of the predator across the matrix hostility gradient.

Emigration and immigration

Based on empirical observations[30] and previous theoretical frameworks[13,20,31], we assume that the maximum dispersal distance of animal species increases with their body mass. For simplicity, we do not let the plants disperse, as they don't move themselves and the dispersal of plant propagules strongly depends on their dispersal strategy. We model emigration rates as a function of each species' per capita net growth rate, which is summarising local conditions such as resource availability, predation pressure, and inter- and intraspecific competition[22]. Dispersal losses scale linearly with the distance between two patches and are 100% in scenarios with only one patch or when the distance between the two patches surpasses the dispersal range of an animal. Even though we model dispersal losses according to dispersal distances, this loss term could also represent any other sort of dispersal loss. For numerical reasons, we did not allow dispersal flows smaller than 10^{-10}.

Numerical simulations

We initialised each local population with a biomass density randomly sampled from a uniform probability density within the interval (0,10). Starting from these random initial conditions, we numerically simulated food web and dispersal dynamics over 100,000 time steps by integrating the system of differential equations implemented in C++ using procedures of the SUNDIALS CVODE solver version 2.7.0 (backward differentiation formula with absolute and relative error tolerances of 10^{-10}) and the time series of biomass densities were saved for last 10,000 time steps. For numerical reasons, a local population was considered extinct and was set to 0 once its biomass density dropped below 10^{-20}.

Equations and parameters

For detailed equations and parameters, see Ryser et al. 2019[28] and the Supplementary Material.

Setup

To answer our questions, we model the following scenarios:

Nutrient enrichment: Simulations across a gradient of nutrient supply concentrations (0, 10) on one patch without emigration and therefore also no dispersal loss.

Drainage effect: Simulations across a gradient of maximal emigration rates (0, 0.15) on one eutrophic patch with a nutrient supply concentration of 10.

Hostility effect with two patches: Simulations across a gradient of dispersal losses (0, 1) on two eutrophic patches with a nutrient supply concentration of 15 on each and a maximal dispersal rate of 0.05.

Heterogeneity effect with two patches: Simulations across a gradient of nutrient supply concentrations (0, 15) on one of two patches with the other patch being a eutrophic patch with a nutrient supply concentration of 15, a maximal emigration rate of 0.05 and no dispersal loss.

Interaction of hostility effect and heterogeneity effect: For each level of heterogeneity (difference in nutrient supply between the two patches) we simulated the whole gradient of the hostility effect (dispersal loss of the predator from 0 to 1).

Heterogeneity effect on complex food webs in complex landscapes: For a complex meta-food-web, we generated 5 random geometric graphs consisting of 50 patches. Each patch was initialised with a complex food web consisting of 10 plant and 30 animal species. For all random geometric graphs, we simulated 15 homogeneous landscapes, where all patches have the same nutrient supply concentration with simulations across a gradient of nutrient supply concentrations ranging from $10^{-0.8}$ (oligotrophic) to 10^{2} (eutrophic) in steps of 0.2 in the exponent, and 5 heterogeneous landscapes, where the nutrient supply concentration for each patch is assigned randomly from the same gradient as in the homogeneous scenario.

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Chapter 3

Landscape configurations and trophic network structures interactively drive species-area relationships in meta-food-webs

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Jonathan M. Chase, Ulrich Brose

Abstract

Spatial and trophic processes simultaneously shape biodiversity in nature, but they are addressed by mostly independent ecological theories. The theory of island biogeography, as well as related theories, predict higher species richness with increasing area across islands or habitat patches, whereas food web theory explores effects of traits and network structure on coexistence within local communities. Hence, how landscape configurations interact with food-web dynamics in regulating metacommunities has remained unclear. Here, we explore these interacting effects in a meta-food-web model and show that when habitat patches are interconnected by dispersal, more species can persist on smaller islands than predicted by the classical island biogeography model. When patch sizes are distributed in an autocorrelated way in the landscape, this effect flattens the slope of the species area relationship. Surprisingly, however, when landscapes have random patch-size distributions, the slope of the species-area relationships can even become negative, indicating that small patches harbour higher diversity than larger ones. These relationships are further affected by the structure of trophic networks. This highlights the importance of simultaneously considering landscape configuration and trophic network structure to understand drivers of species-area relationships in metacommunities.

Introduction

Ecological theories on the maintenance of biodiversity have tended to bifurcate into those that focus on regional-scale spatial processes such as habitat heterogeneity and dispersal (Hanski, 1998; Leibold et al., 2004; Leibold and Chase, 2017; MacArthur and Wilson, 1967) and those that focus on local-scale interspecific interactions, coexistence, and ecological networks (Brose et al., 2017; Chesson, 2000; May, 1972; Montoya et al., 2006; Otto et al., 2007; Paine, 1969; Stouffer and Bascompte, 2010). More recently, it is becoming increasingly recognized as a key challenge to understand how these processes interact in shaping biodiversity patterns (e.g., (Gravel et al., 2016, 2011; Guzman et al., 2018; Thompson et al., 2020). Combining these processes will be crucial to understand fundamental limits to biodiversity, as well as to understand how biodiversity patterns will change in the face of anthropogenic drivers that influence spatial processes, such as habitat fragmentation, as well as alterations to the structure of local food webs.

One of the earliest conceptualizations of the importance of spatial processes was the theory of island biogeography, which envisioned the number of species co-occurring on islands as a balance between species colonization rates and extinction rates (MacArthur and Wilson, 1967). These rates are, in turn, influenced by island size (larger islands have lower extinction rates and higher colonization rates) and island isolation (more distant islands have higher extinction rates). The theory of island biogeography, and related theories, predicts a generally positive relationship between island size and the number of species on that island—the island species area relationship (ISAR)—and this is frequently observed in natural systems (Connor and McCoy, 1979; Triantis et al., 2019). We hereafter use ISAR for both island and island-like habitat patches to differentiate this species area relationships from other types (e.g., nested species area relationships) that are sometimes inappropriately used synonymously (Scheiner, 2003; Scheiner et al., 2011).

The ISAR is typically positive (more species on larger islands) in mainland-island island biogeography models and observations (Connor and McCoy, 1979; Triantis et al., 2019). However, the spatial distribution of patches in a landscape can influence the shape of the ISAR. For example, dispersal-mediated processes such as rescue effects (Brown and Kodric-Brown, 1977) and source-sink dynamics (Hanski and Ovaskainen, 2000) can often lead to flatter ISAR relationships because more species are able to persist on smaller islands than would have been possible without such metacommunity-level process.

Species interactions, particularly trophic interactions in food webs, can also strongly influence community biodiversity and how it scales with area in manifold ways (Brose et al., 2017, 2004; Montoya et al., 2006). Body mass, for example, strongly influences interaction strengths and their distribution across food-web links that drive community biodiversity (Heckmann et al., 2012; Otto et al., 2007), and also influences spatial processes, such as how far animals can disperse (Hirt et al., 2018). Moreover, larger animals that tend to occupy higher trophic levels need large habitats to meet their energetic demands (Jetz, 2004; Kelt and Van Vuren, 2001; Tucker et al., 2014), and tend to suffer most from isolation (Ryser et al., 2019). As a result, the shape of the ISAR can be strongly influenced by trophic interactions and the manifold interactions between traits and dispersal (e.g. (Holt et al., 1999; Jacquet et al., 2017; Pillai et al., 2011)).

The trophic theory of island biogeography (Gravel et al., 2011) integrates spatial and trophic processes by using food-web properties to predict ISARs and other patterns on islands of different size. In this model, ISARs are generally shallower, and depend on patch isolation and interisland dispersal rates. This rests on the idea that species are more likely to persist on large islands, but also need their prey species present, favouring generalist species and highly connected food webs. Based on the general patterns that species traits, such as body mass, impose strong constraints on possible dispersal distances (Hirt et al., 2018) and trophic linkage patterns (Brose et al., 2019; Digel et al., 2011), a trait-based theory of island biogeography predicted the distribution of traits also depended on island area and isolation (Jacquet et al., 2017).

The trophic island biogeography theory, while clearly more realistic than classical island biogeography which ignores species interactions, still represents a highly simplified perspective for how landscape configurations and food-web topologies interactively affect biodiversity patterns. Here, we further integrate the theory of island biogeography with meta-food-web theory and show that the strength of species-area relationships depends on an interaction between landscape configurations and food-web structures. For example, patches within metacommunities can vary considerably in their spatial configuration in several ways (see Figure 1 for examples that we examined here). For example, patches can have a mainland-island structure, such as that envisioned in island biogeography theories; they can have a 'random graph' structure, in which all patches tend to have the same number of dispersal connections (e.g. habitat networks of song birds, (Minor and Urban, 2008)); or they can have as most naturally forming networks a 'small world' structure, which has many short connections within a cluster (e,g, larval dispersal network of the Great Barrier reef (Kininmonth et al., 2010)) that can promote the spread of disturbances within clusters but not among clusters (Minor and Urban, 2008). In addition, island patch sizes within those landscapes can be autocorrelated (larger islands near larger islands), or randomly distributed. For instance, in the case of forest fragments and wetlands, the distribution of patch sizes across the landscape can change systematically from random to autocorrelated distributions during the process of increasing fragmentation and human alteration of the landscape (García et al., 2005; Karlsson et al., 2014; Li et al., 2009; Meter and Basu, 2015; Taubert et al., 2018). All these aspects in spatial networks have the potential to affect dispersal links, either by their strength or their number.

Likewise, food web topology can also very considerably among metacommunities, for example, highly connected food webs are more resistant to secondary extinctions (Dunne et al., 2002), complex food webs with higher maximum trophic levels and more omnivory prevent competitive exclusion of basal species (Brose, 2008; Wang et al., 2019; Wang and Brose, 2018) and higher modularity can limit the propagation of disturbances (Krause et al., 2003; Stouffer and Bascompte, 2011). Thus, the potential food-web structure (i.e. the trophic interactions when all species are present) shapes what species can coexist and may therefore affect ISARs.

In this study, we use a simulation-based approach to meta-food-webs employing body-mass driven trophic and spatial processes to address how landscape configurations and food-web topology affect ISARs. Specifically, we show how landscape configurations (distributions of patches and patch sizes across the landscape as shown in Figure 1) drive (1) the slope and intercept of the ISARs and (2) local food-web structures (here: trophic levels and distribution of biomass densities). Subsequently, we analyse (3) how differences in the topology of the meta-food-web affect the slope and intercept of the ISARs. Together, these analyses tackle the question how spatial and trophic processes drive biodiversity in multilayer networks that are complex in trophic as well as spatial topologies.

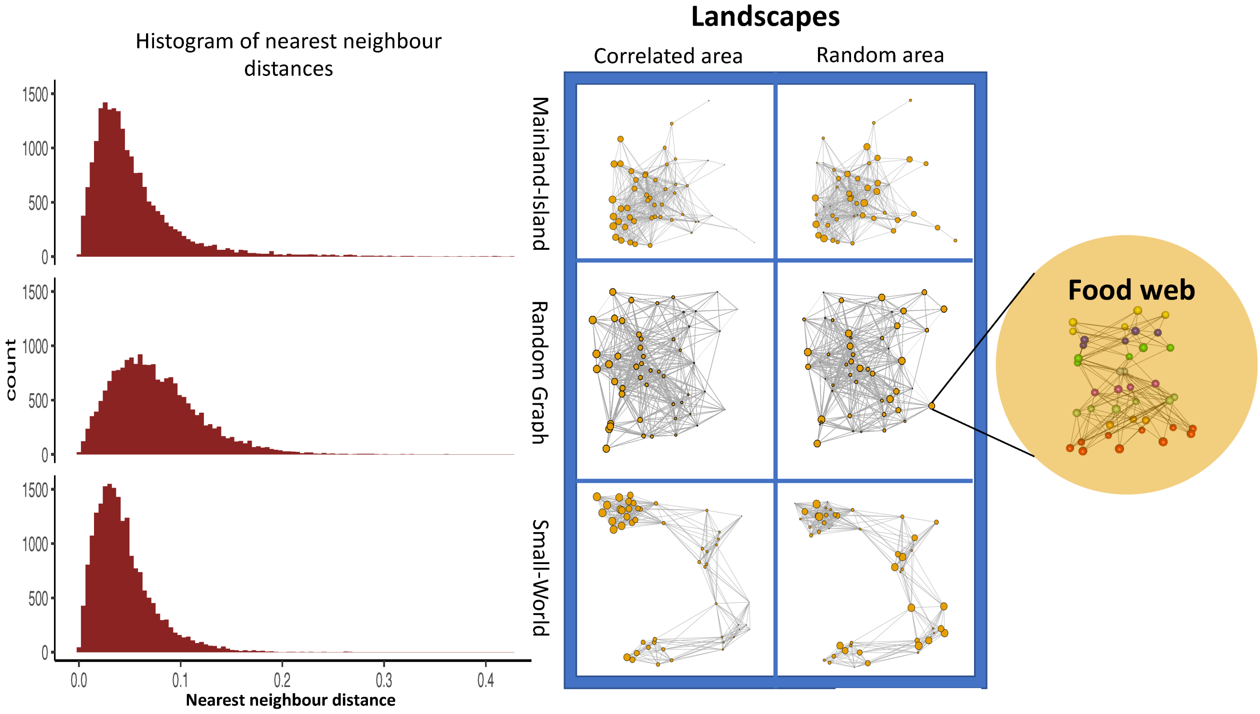

Figure 1: Conceptual figure of different landscape configurations. Illustrated here are six different landscape configurations. In rows three different landscape types named “Mainland-Island”, ”Random Graph” and “Small-World” that exhibit different distributions of patch locations and isolation (nearest neighbour distance; histogram on the left) and in columns, different patch size distributions (correlated or random). Each patch can harbour a food web.

Methods

Generating landscape networks

We created 20 landscape replicates for each combination of three different spatial network structures and two patch size distribution regimes resulting in 120 different landscapes. For the three different spatial network structures, namely mainland-island, random-graph and small-world (see Figure1) we defined following rules for generating the 50 patch locations in the landscapes. In the mainland-island landscapes, x and y coordinates were drawn from a skewed beta distribution with shape parameters α = 1 and β = 3 resulting in a high patch density in the bottom left corner of the landscape, that is representing the mainland, and a progressively lower patch density towards the top right corner of the landscape representing islands. In the random graph landscape, x and y coordinates were drawn from uniform distributions between 0 and 1. In small-world landscapes, x and y coordinates for centre patches of five patch clusters were randomly drawn from a uniform distribution between 0 and 1. Subsequently and for each patch aggregation, 9 additional neighbour patches were set with x and y coordinates drawn from gaussian distributions with means of the location of the centre patch and a standard deviation of 0.08. This resulted in five clusters of 10 patches each. For the two patch-size distributions (random or correlated; see Figure 1) patch areas were randomly drawn from a uniform distribution between 10^5 and 10^7 and either randomly distributed among all locations (random distribution) or ordered according to the x coordinate of the patch location with the largest patches on the left side and the smallest on the right side of the landscape (correlated distribution). The same patch areas were used for all 6 landscape types within each replicate.

Generating food webs

According to the allometric food web model by Schneider et al. 2016(Schneider et al., 2016) each species is fully characterised by its average adult body mass. For the complex food web $\log_{10}$ body masses were randomly drawn from a uniform distribution from 0 to 3 for plants and from 2 to 6 for animals. The structure of the food web is then based on a unimodal feeding niche on the body mass axis (see equation 5 below). To achieve differences in food web structures, we created food webs with different numbers of species (between 10 and 60), with different fractions of basal species (between 0.2 and 0.5) and used different width of species feeding niches (γ between 4 and 13; see below). Food-web structures (see the Supplement TS2 for parameter description) of the potential food webs were analysed by the *igraph* package in R. These food webs correspond to the potential trophic interactions if all species are present.

Model

We modelled 40 complex meta-food-webs with 10 to 60 species in 120 complex landscapes of different configuration containing 50 patches of different size. Each food web was simulated on each landscape resulting in a total of 4800 meta-food-web simulations. Feeding links (i.e. who eats whom) are constant over all patches and are as well as the feeding dynamics determined by the allometric food web model by Schneider et al. 2016 (Schneider et al., 2016). We integrate dispersal as species-specific biomass flow between habitat patches (Ryser et al., 2019). We use ordinary differential equations to describe the feeding and spatial dynamics, the rate of change in biomass density $B_{i,z}$ of species *i* on patch *z* is given by

$$\frac{dB_{i,z}}{dt} = B_{i,z} \sum_j e_j F_{ij,z} - \sum_j B_{j,z} F_{ji,z} - x_i B_{i,z} - E_{i,z} + I_{i,z} \qquad \text{(for animals)} \quad (1)$$

$$\frac{dB_{i,z}}{dt} = r_i G_i B_{i,z} - \sum_j B_{j,z} F_{ji,z} - x_i B_{i,z} - E_{i,z} + I_{i,z} \qquad \text{(for plants)} \quad (2)$$

with the first three terms describing local trophic dynamics and the last two terms describing emigration, $E_{i,z}$ (equation 9), and immigration, $I_{i,z}$ (equation 11). Trophic dynamics are driven by following three processes. First, predation or herbivory on species *j* with assimilation efficiency *e* ($e_j = 0.545$, if *j* is a plant, typical for herbivory; $e_j = 0.906$ if *j* is an animal, typical for carnivory(Lang et al., 2017)) and the functional response $F_{ij,z}$ (equation 3) for animals, and a nutrient dependent growth (equation 7) for plants. Second, losses due to predation or herbivory respectively. Third, losses by metabolic demands with $x_i = x_A m^{-0.305}$ with scaling constant $x_A = 0.141$ (tenfold laboratory metabolic rate (Ehnes et al., 2011) at a temperature of 20° Celsius to represent field metabolic rates) for animals and $x_i = x_P m^{-0.25}$ with $x_P = 0.138$ for plants. We used a dynamic nutrient model (equation 8) as the energetic basis of our food web. Each species *i* is fully characterized by its average adult body mass m_i. Body masses determine the interaction strengths of feeding links as well as the metabolic demands of species. From each m_i a unimodal attack kernel, called feeding efficiency L_{ij} is constructed which determines the probability of consumer species *i* to attack and capture an encountered resource species *j*. We model L_{ij} as an asymmetrical hump-shaped Ricker's function (equation 5) that is maximized for an energetically optimal resource body mass (optimal resource body mass (optimal consumer-resource body mass ratio $R_{opt} = 100$) and has a width of γ. The maximum of the feeding efficiency L_{ij} equals 1. Table TS1 is an overview of the standard parameter set for the equations.

Area effect on extinction

A species population was considered locally extinct when its biomass density translated to less than one individual and was immediately set to zero. The number of individuals [Ind.]per species on a patch was calculated by first obtaining the population density $[\frac{Biomass}{Area}]$ by dividing the biomass density with a species body mass resulting in individuals pre area $[\frac{Ind.}{Area}]$. Therefore, the same biomass densities translate into low and high abundances for small and large species. Subsequently, the population density $[\frac{Ind.}{Area}]$ was multiplied with the patch area to obtain the number of individuals.

Functional response

The functional response $F_{ij,z}$ describes the per unit biomass feeding rate of a consumer i over prey j in patch z. It is defined as:

$$F_{ij,z} = \frac{\omega_i b_{i,j} B_{j,z}^{1+q}}{1+cB_{i,z}+\omega_i \sum_k b_{ik} h_{ik} B_{k,z}^{1+q}} \cdot \frac{1}{m_i} \quad , \tag{3}$$

where $b_{i,j}$ is the resource specific capture coefficient (Eqation 4), $h$ij the resource-specific handling time (Equation 6) and c is sets the interference competition between consumers. $\omega_i = 1/$(number of resource species of *i*) defines relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.

Capture coefficient

$$b_{ij} = f a_k m_i^{\beta_i} m_j^{\beta_j} L_{ij} \tag{4}$$

Resource specific capture coefficient of consumer species *i* on resource species *j* scaling the feeding kernel Lij (Equation 5) by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed with β_i ,β_j =0.42 for carnivorous links and β_i = 0.19 (Hirt et al., 2017) and $m^{\beta j}$ was replaced with the constant value of 1 when the resource is a plant (as plants do not move). We divide here feeding links into the subgroup of carnivorous and herbivorous interactions each comprising a constant scaling factor for their capture coefficients a_k with $k \in 0, 1$ (a_0 = 15 for carnivorous links and a_1 = 3500 for herbivorous links).

Feeding efficiency

$$L_{i,j} = \left(\frac{m_i}{m_j R_{opt}} e^{1-\frac{m_i}{m_j R_{opt}}}\right)^{\gamma} \tag{5}$$

The probability of consumer *i* to attack and capture an encountered resource *j* (which can be either plant or animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width γ (between 4 and 13, see section *Generating foodwebs*) centered around an optimal consumer-resource body mass ratio R_{opt} = 100.

Handling time

$$h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j} \tag{6}$$

The time consumer *i* needs to kill, ingest and digest resource species *j*, with scaling constant h_0 = 0.4 and allometric exponents η_i = −0.48 and η_j = −0.66.

Growth factor for plants

$$G_i = min\left(\frac{N_1}{K_{i,1}+N_1}, \frac{N_2}{K_{i,2}+N_2}\right) \tag{7}$$

Species-specific growth factor of plants determined dynamically by the nutrient; with K_i, half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species *i* and (uniform distribution within (0.1, 0.2)). The term in the minimum operator approaches 1 for high nutrient concentrations.

Nutrient dynamics

$$\frac{dN_{l,z}}{dt} = D(S_l - N_l) - \sum_{i,z} r_i G_i P_{i,z} \tag{8}$$

Rate of change of nutrient concentration N of nutrient $l \in \{1, 2\}$ on patch z, with global turnover rate $D = 0.25$, determining the rate at which nutrients are refreshed and the nutrient supply concentration S_l, determining the maximum nutrient concentration of each nutrient drawn from a normal distribution with mean $\mu_S = 50$ and standard deviation $\sigma_S = 2$ and relative nutrient content in plant species biomass ν_l ($\nu_1 = 1$, $\nu_2 = 0.5$).

Spatial dynamics

No-dispersal model

To test the pure effect of habitat area on species-area relationships, we simulated a model without dispersal. This model was based on simulations of all food webs on single patches of different sizes (six levels covering the same range as in the main simulations). Hence, species could not emigrate from or immigrate to patches and the results represent the effects of varying extinction rates according to patch size (see section *Area effect on extinction* above) without being confounded by spatial between-patch dynamics caused by dispersal.

Emigration

Subsequently, we model dispersal between local communities as a dynamic process of emigration and immigration. Thus, biomass flows change dynamically between local populations and the spatial dynamics directly influence local population dynamics and vice versa (Fronhofer et al., 2018). During dispersal across the habitat matrix, feeding does not occur. The total rate of emigration of species i from patch z is

$$E_{i,z} = d_{i,z} B_{i,z} \tag{9}$$

with $d_{i,z}$ as the corresponding per capita dispersal rate. We model $d_{i,z}$ as

$$d_{i,z} \frac{a}{1+\mathrm{e}^{b(x_i - v_{i,z})}} \tag{10}$$

with $a = 0.1$, the maximum dispersal rate, $b = 10$ for animals and $b = 0$ for plants, a parameter determining the shape of the dispersal rate, x_i, the inflection point determined by the metabolic demands per unit biomass of species i, and $\upsilon_{i,z}$, the per capita net growth rate of species i on patch z. We model emigration rates $d_{i,z}$ as a function of each (animal) species' per capita net growth rate, which is summarising local conditions such as resource availability, predation pressure, and inter- and intraspecific competition (Fronhofer et al., 2018). Note that for plants with a shape parameter b = 0, $d_{i,z}$ simplifies to a constant dispersal rate of 0.05.

Immigration

The rate of immigration of biomass density of species *i* into patch *z* follows

$$I_{i,z} = \sum_{n \, \epsilon \, N_z} E_{i,n}\left(1 - \delta_{i,nz}\right) \frac{1 - \delta_{i,nz}}{\sum_{m \, \epsilon \, N_n} 1 - \delta_{i,nm}} * \frac{Area_n}{Area_z} \tag{11}$$

where N_z and N_n are the sets of all patches within the dispersal range of species *i* on patches *z* and *n*, respectively. In this equation, $E_{i,n}$ is the emigration rate of species *i* from patch n, $(1 - \delta_{i,nz})$ is the fraction of successfully dispersing biomass, i.e. the fraction of biomass not lost to the matrix, and $\delta_{i,nz}$ is the distance between patches n and z relative to species i's maximum dispersal distance δ_i (see below). The term $\frac{1 - \delta_{i,nz}}{\sum_{m \, \epsilon \, N_n} 1 - \delta_{i,nm}}$ determines the fraction of biomass of species *i* emigrating from source patch n towards target patch *z*. This fraction depends on the relative distance between the patches, $\delta_{i,nz}$, and the relative distances to all other potential target patches m of species *i* on the source patch *n*, $\delta_{i,nm}$. Thus, the flow of biomass is greatest between patches that are closer together. We assume that the maximum dispersal distance of animal species δ_i increases with their body mass based on empirical observations (Jenkins et al., 2007) and previous theoretical frameworks (Hirt et al., 2018; Holt, 2002; Jetz, 2004). Each species perceives its own dispersal network dependent on its species-specific maximum dispersal distance

$$\delta_i = \delta_0 m_i^{\epsilon} \tag{13}$$

with $\delta_0 = 0.1256$ and where the exponent $\varepsilon = 0.05$ determines the slope of the body mass scaling of δ_i. Dispersal losses scale linearly with the distance between two patches and are 100% when the distance between the two patches surpasses the dispersal range of an organism. Dispersing biomass densities are transformed into absolute biomasses by multiplication with the area of the donor patch and then back transformed to biomass densities by dividing the biomasses by the area of the recipient patch. Minimal immigration thresholds were set to 1 individual per species.

Numerical simulations

We initialised a sample of species from the species pool on each patch and each local population with a biomass density randomly sampled from a uniform probability density within the interval (0,10). From these random initial conditions, we numerically simulated food web and spatial dynamics over 50,000 time steps by integrating the system of differential equations implemented in C++ using procedures of the SUNDIALS CVODE solver version 2.7.0 (backward differentiation formula with absolute and relative error tolerances of 10^{-6}).

Analyses

Species-area relationships were obtained by fitting linear models (lm in R, version 3.6.2) of ln species richness (S) depending on ln patch area (A), thus expressing the linear relationship in log-space according to

$$\ln(S) = c + z * \ln(A). \tag{14}$$

Isolation categories were assigned after binning log-transformed nearest neighbor distances with an equal number of data points in each bin. This resulted in the three categories of isolation “low”, “medium” and “high”. Furthermore, we recorded the densities and trophic levels of all persistent populations at the end of the simulations to obtain an understanding which populations survive under which landscape configurations. To visualize the effect of the initial food-web structures on species-area relationships, effect sizes of food web parameters were obtained from three-way interaction between the respective food web parameter with patch area and isolation as explanatory variables and species richness as response variable in linear models (lm in R, version 3.6.2). Food-web structures were normalized prior to analyses with the scale function in R.

Results

Landscape configuration influence species-area relationships

In the model without dispersal, species richness is affected only by extinction risks that are high and low on small and large patches, respectively. Here, we found positive species-area relationships (Fig 2, dashed lines, exponent z = 0.116, 95% CI = (0.109,0.122)). Note that the exponents of species-area relationships presented here should only be interpreted in relation to each other as patch sizes and distances have artificial units. All subsequent models included several patches and thus exhibit responses in species richness that mix area effects with those of spatial dynamics between patches.

The different landscape configurations include three landscape types (Figure 2, rows) across patch size distributions that are either random (Figure 2, right column) or spatially correlated (Figure 2, left column, decreasing patch size from left to right). In mainland-island landscapes (with spatially correlated patch densities and thus most patches in the bottom left corner and fewer and fewer patches towards the top right corner; Figure 1, mainland-island) and spatially correlated patch sizes (Figure 1, correlated area) we also find positive species-area relationships and their slope is highest under high isolation (exponent = 0.070, 95% CI = (0.064,0.075) (Figure 2, mainland-island - correlated, (a)). The species-area relationship for highly isolated patches is similar to the area effect on species richness in the model without dispersal, which suggests that species richness is mainly driven by area effects on extinction risks. Under decreasing isolation, the species-area curve flattens (i.e. the slope, z, decreases; low isolation; exponent = 0.021, 95% CI = (0.016,0.026)) as small patches can harbour more species (i.e. the intercept, c, increases, Figure 2a). The other two landscape types with spatially correlated patch sizes (Figure 2c, random graph; Figure 2e, small-world) also show positive species-area relationships but less differences in slopes across different levels of isolation. The species-area relationships in small-world landscapes are shallower (see supplementary TS1 for all slopes).

Moreover, we found negative species-area relationships in landscapes with randomly distributed patch sizes for all three landscape types (increase in c, negative z, Figure 2b,d,f). The slopes for these negative species-area relationships are steepest for patches at low isolation. The large patches show a similar species richness ($\ln(S)\sim2.4$) in model without dispersal and all landscapes independent of the patch size distribution suggesting that the negative slopes z, arise from an increase in the intercept c. Small patches, however, support the fewest number of species in landscapes that have spatially correlated patch size distributions at a high level of isolation. Here, species richness is generally not much higher than in the model without dispersal. Furthermore, we found that in landscapes with random patch size distributions the highest number of species persisting occur on small patches with low isolation. Here, species richness exceeds not only the model without dispersal substantially but also that of the large patches, which is causing the negative species-area relationships.

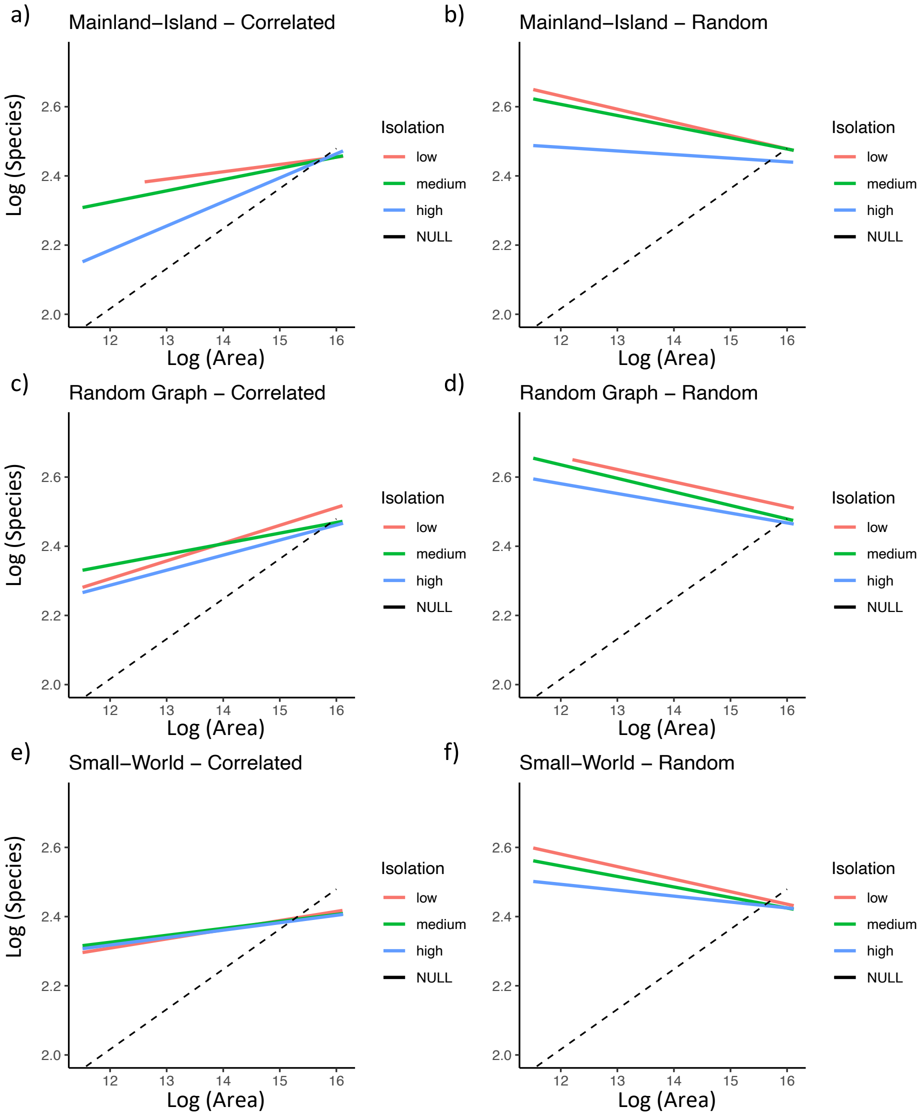

Figure 2: Interaction of landscape configuration with species-area relationships. Species-area relationships in the different landscapes (a-f) and different isolation. Dashed lines represent area effects obtained from the no-dispersal model.

Landscape configurations affect population densities and trophic levels

Our subsequent analysis aimed at a mechanistic understanding of why small patches in landscapes with random patch size distributions have a substantially higher species richness than those in landscapes with correlated patch size distributions. Most species that exclusively persisted in landscapes with random patch size distributions occur on small patches and occupy high trophic levels (Figure 3a). These small patches also harbour higher population densities across all trophic levels compared to small patches that are in landscapes with correlated patch sizes and larger patches in all landscapes (Figure 3b). Medium sized and large patches harbour similar biomass densities in landscapes with either random or correlated patch size distributions.

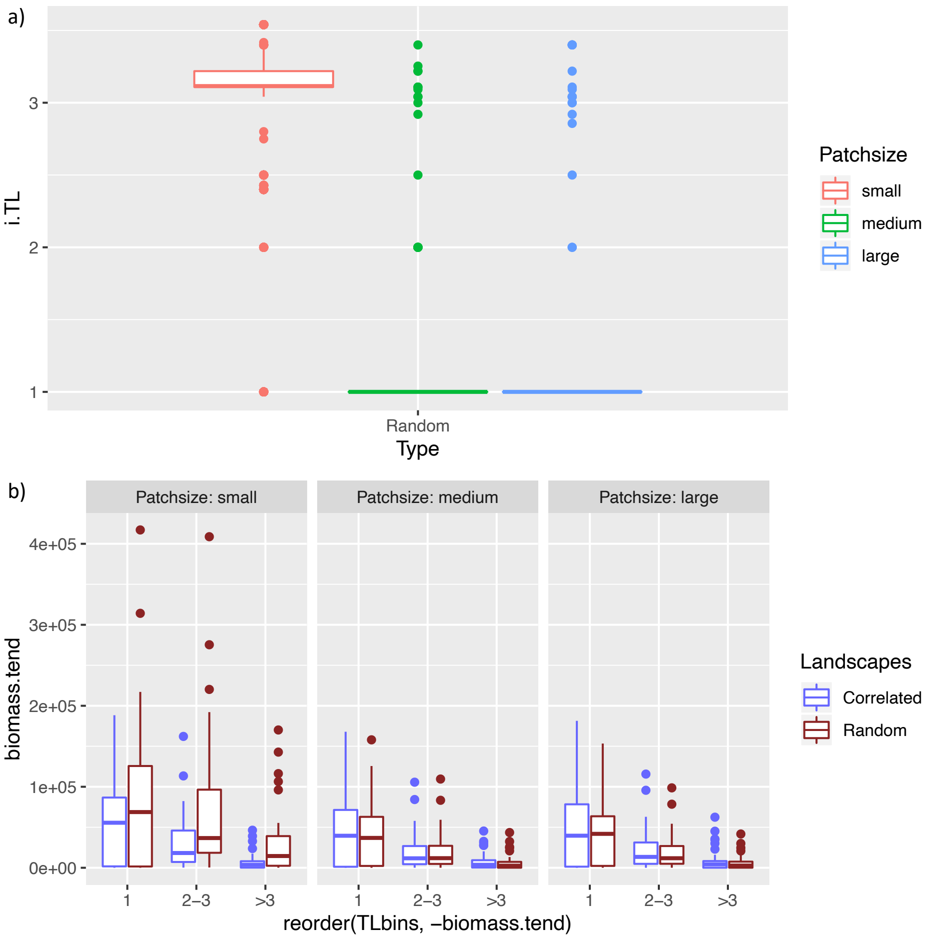

Figure 3: Species occupying higher trophic levels occurring on small and well-connected patches drive negative species-area relationships. a) Trophic level of species that only occur in landscapes with random patch size distributions on small (red), medium (green) and large (blue) patches. b) Total biomass of trophic levels on small, medium or large patches in either landscapes with correlated (red) or random (blue) patch size distributions.

Food-web structures and landscape configuration interactively drive ISAR

We also found that the topology of the meta-food-web can modify the slope of the ISARs, but the strength and sign of these effects differs not only across the three landscape types (Figure 4 panels a-c) but also between random and correlated distributions of patch sizes (Figure 4, blue and red). Despite this complex interplay between trophic and spatial networks, two general patterns emerged. First, the effects of food-web structures on the ISAR slope are strongest in mainland-island landscapes, intermediate in random landscape, and weakest in small-world landscapes. As an example, the absolute value of the effect size of the standard deviation of generality (Figure 4, i.sdG) on the ISAR slope is 50 times higher in mainland-island than in small-world landscapes. Second, in most cases (19 out 33) the food-web parameters change the slope of the ISAR in different directions (i.e. positive or negative effects) in landscapes with correlated patch sizes distributions (blue) compared to landscapes with random patch size distribution (red). For instance, in mainland-island landscapes the standard deviation of generality (Figure 4, i.sdG) has positive or negative effects on the ISAR slope under random and correlated patch size distributions, respectively. Finally, we addressed effects of some topological food-web parameters of particular importance. A lower maximum trophic level or a higher modularity reduce isolation effects and flatten ISAR slopes in random landscapes (i.e. z approaches zero). The intercept of the ISARs, c, is generally lower if the potential food web is highly modular (see the Supplement). Overall, however, our results indicate a complex interplay between landscape configurations and food-web topologies that drive the ISAR slope and intercept (Figure 4).

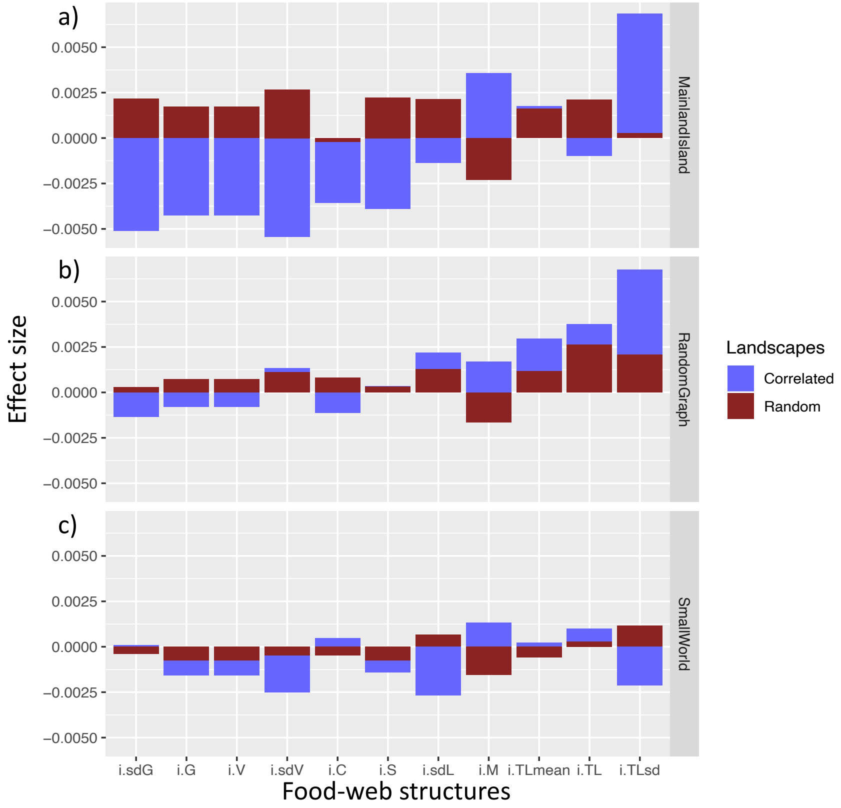

Figure 4: Food-web structures modify with species-area relationships. Effect sizes of different structural properties of the potential foodweb on the interaction effect of patch size and isolation on species persistence in the different landscapes. (x-axis from left to right: sd generality, generality, vulnerability, sd vulnerability, connectance, species-richness, sd linkedness, modularity, mean trophic level, maximum trophic level and sd trophic level.

Discussion

Here, we have extended the trophic theory of island biogeography (Gravel et al., 2011; Holt et al., 1999; Jacquet et al., 2017), to include meta-food-webs with interacting spatial and trophic dynamics. Overall, when there is no interpatch dispersal, our model recovers the expected strong and positive effect of patch size on species richness, with a relatively low intercept (low *c*, meaning few species on the smallest patches) that emerges from typical island biogeography theory (MacArthur and Wilson, 1967). However, when we allow there to be important interpatch dispersal, the shape of the ISAR shifts considerably. First, in all cases, many more species persist on smaller patches than when there is interpatch dispersal (higher *c* values). Second, we found that the typically increasing ISAR (positive *z* values) when patch sizes on the landscape were spatially autocorrelated, rather surprisingly switched to the unusual case of negative ISAR slopes (*z*) in landscapes with random distributions of patch sizes. Moreover, we found that food-web structures can modify species-area-isolation relationships.

In our study, differences in ISAR slope and intercept are mainly driven by differences in patch size distribution across the landscape and isolation. We found that large patches all have a similar species richness, independent of what landscape they are embedded in or whether or not dispersal process occurs. This suggests that the decrease in *z* with decreasing isolation as well as the switch to negative z values in landscapes with random patch size distribution arises from an increase in c that characterizes the species density within small areas. This increase in *c* is driven by large immigration fluxes from neighbouring patches. There are two main factors that increase immigration fluxes. First, lower isolation results in lower dispersal losses and therefore increases immigration. Second, the relative size of a patch compared to its neighbours drives the magnitude of immigration fluxes. In line of classical source-sink dynamics (Pulliam, 1988), a small patch receives a lot of immigrating biomass from a large patch, but a large patch receives relatively little biomass from a small patch. This explains the consistent increase in *c* with decreasing isolation and a further increase in *c* in landscapes with random patch size distributions, because only in these landscapes small patches can have large neighbours. Generally, these fluxes increase species richness on small patches, thus increasing *c*, by rescue effects that recover populations after local extinctions (Brown and Kodric-Brown, 1977). In addition, we found that the strong immigration fluxes from large to small patches can lead to an oversaturation in biomass on the small patches. This implies that the biomass densities are mainly driven by spatial fluxes and thus higher than those caused by trophic dynamics. These higher population densities across all trophic levels then have a bottom-up effect that allows for the persistence of high trophic level species that cannot survive on larger patches.

Many of the ISAR patterns that our meta-food-web simulations reveal are consistent with empirical findings including (1) the steep ISAR of isolated islands and (2) the decreases in ISAR slopes *z* and increases in intercepts *c* with lower island isolation (Wilson, 1961; Johnson et al., 1968; Johnson and Simberloff, 1974; Rosenzweig, 1995). The counterintuitive finding of negative *z* values in landscapes with random patch-size distributions has found an explanation in dispersal fluxes that increase *c* and override the typical high extinction rates on small patches expected from classical island biogeography theory. However, empirical examples of negative ISARs are scarce (Karatayev et al., 2005; Logue et al., 2012; Price et al., 2004), whereas there is evidence for negative density-area relationships (Wilder and Meikle, 2005). For instance, Bowers and Matter (1997) (Bowers and Matter, 1997) found that some mammal species tend to exhibit negative area-density relationship in landscapes with small and less isolated patches, which switches to positive area-density relationships in landscapes with larger and more isolated patches. Consistent with our simulations, a study in the Swiss Alps showed that wolves as large top-predators occupying high trophic levels occur where their prey density is high (Roder et al., 2020).

Despite this anecdotal empirical support, our results suggest that negative ISARs should be more common in nature. This discrepancy might find its explanation in processes that are not accounted for in our model. For instance, the matrix resistance to dispersal might be higher in natural ecosystems, which should diminish the effects of spatial dynamics found here. For instance, real islands are surrounded by water, which may increase the matrix resistance to dispersal considerably. Thus, dispersal processes among real islands are likely to be much smaller compared to for example terrestrial habitats, where the unsuitable habitat matrix mostly restricts trophic interactions. The negative z values observed here are driven by dispersal processes and thus may not apply to real island systems. However, our results suggest that dispersal can overwrite extinction effects that arise from patch size limitations. Therefore, positive species-area relationships may be driven by other mechanisms when dispersal fluxes are large. For instance, patches in natural landscapes may not only differ in size but also in within-patch heterogeneity of abiotic parameters such as nutrient supply and habitat structure. Especially real islands are very diverse in their abiotic conditions (Weigelt et al., 2013). As within patch heterogeneity is typically correlated with patch size, it can overwrite the negative ISARs predicted by our model simulations and yield increases in species richness with area that are almost exclusively driven by habitat heterogeneity (Brose, 2001; Haila et al., 1983; Hortal et al., 2015). This calls for an integration of different levels of matrix hostility and habitat heterogeneity into future extensions of our meta-food-web approach.

Moreover, our approach is also based on a simplified concept of between-patch dispersal that is only driven by body masses. Species of the same community can also differ strongly in their movement ability (e.g. running vs. flying; (Hirt et al., 2018, 2017)).

While we model species-specific spatial networks, patches are regarded as habitat for all species, despite of the possibility that some species perceive habitat patches on different scales. Including a species-specific nested structure of habitat patches in a metacommunity could further improve our understanding of interacting spatial and trophic processes. We anticipate that future extensions of our meta-food-web approach can greatly benefit from including empirical realism of habitat structures and species dispersal capacities, which could allow to dovetail the models with real communities.

We found that the shape of ISARs not only depend on landscape configurations but also on the food-web structure. Food webs that have a high modularity or did not include species occupying high tropic levels exhibit z values close to zero but also low c values. With a high modularity, species tend to interact more with species belonging to the same compartment, thus the dispersal of other species that do not belong to that compartment is less likely to affect them. Furthermore, a species depends more on their module (i.e. their limited set of prey) being present on a patch to persist, rendering their own dispersal less important. Hence, the resident community composition on the patches becomes more important than dispersal fluxes, which thus decreases the importance of the landscape configuration. Interestingly, many other food web properties modify the species-area relationship in a different direction depending on the landscape configuration. When neighbouring patches are of a similar size under correlated patch-size distributions, they have similar extinction rates (due to the similar patch area) and the net-dispersal is low as immigration and emigration are of similar magnitude. In this context, local dynamics are mainly driven by inherent food web dynamics. When neighbouring patches tend to be of a different size under random patch-size distributions, small patches receive a net-influx of biomass as the immigration of biomass from the surrounding large patches is higher than their biomass emigration. In this case, the effect of biomass immigration may become larger relative to the biomass fluxes that are driven by food web dynamics. Consequently, the biomass fluxes in the food web interact with the spatial fluxes of biomass and thus with the landscape configuration. In summary, the strength of the correlation between the sizes of neighbouring patches corresponds to a gradient from more food-web (landscapes with correlated distributions of patch area) to more landscape-driven communities (landscapes with random distributions of patch area). This provides an explanation of why many food web structures affect species-area relationships in a different direction in landscapes with random distributions of patch sizes compared to the ones with a correlated patch size distribution.

Our use of a meta-food-web model revealed that the interaction between spatial processes (dispersal) and trophic fluxes (bottom-up resource supply) can produce negative species-area relationships under some landscape configurations driven by dispersal processes. While ecologists have stressed the importance of either spatial processes or species interaction networks for biodiversity patterns for a long time, our meta-food-web approach has integrated both aspects of species dynamics. This has revealed that it depends on the landscape configuration whether biodiversity patterns on habitat patches mostly depend on dispersal, food-web dynamics or a combination of both. We anticipate that the different landscape configurations may characterize different natural ecosystems. However, our results demonstrate that the largest differences in species-area relationships occur between landscapes with random or correlated distributions of patch sizes across the landscape that in turn produce large immigration rates on small patches.

As biodiversity is becoming increasingly threatened by global change and habitat fragmentation, it has become a key challenge to understand basic mechanisms of how spatial processes and the structure of ecological networks interact in shaping biodiversity patterns (Gravel et al., 2016; Jacquet et al., 2017; Guzman et al., 2018). Here, our study has indicated that consideration of landscape configuration and food-web structures may be of crucial importance in conservation decisions to develop habitat protection strategies that particularly include small patches. It is these small patches in landscapes with uncorrelated patch sizes that harbour species that do not occur anywhere else. This surprising result can only be uncovered and understood as a consequence of the integration of spatial and trophic networks into meta-food-webs.

Author contributions

R.R. and U.B. developed the idea. R.R. built the model, analysed the data and wrote the first manuscript. All authors contributed to interpreting the results and to the final version of the manuscript.

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General discussion

Biodiversity is shaped by organisms that move and interact. On the one hand, the theory of island biogeography and metapopulation research has shown the importance of spatial structures and movement of organisms in shaping biodiversity patterns (Hanski and Ovaskainen, 2000; MacArthur and Wilson, 1967; Rybicki and Hanski, 2013). On the other hand, food-web research has shown the impact of trophic interactions on patterns of biodiversity (Brose, 2008; Curtsdotter et al., 2011; Kalinkat et al., 2013; Otto et al., 2007; Rall et al., 2008). Metacommunity theory incorporates both spatial and biotic interactions but has mainly considered species competition, and the integration of complex food webs remains in its infancy (Gravel et al., 2016). Therefore, the integration of food webs and spatial networks into meta-food-webs is crucial to understand mechanisms in trophic metacommunities and their response to environmental change. Recent advances in metacommunity research have considered competitive or simple trophic interactions (Gounand et al., 2014; Holt, 2002; Koelle and Vandermeer, 2005) but lack a unifying framework (Guzman et al., 2018) and a realistic complexity of either trophic communities or landscapes. Furthermore, there is a need to understand interactive effects of different global change drivers to identify the biggest threats and make predictions for future scenarios. As it is very challenging to empirically investigate interactive effects of environmental change on complex meta-food-web interactions and dynamics, modelling studies such as those presented in this thesis can contribute to filling this gap. In **Chapter 1**, I presented a model that fulfils the integration of complex food webs and landscapes into meta-food-webs and I subsequently used this model in **Chapters 1, 2 & 3** to uncover general mechanisms in meta-food-webs and to investigate interactive effects of global change drivers on biodiversity.

Integration of trophic and dispersal networks: mechanisms driving the coexistence of species in trophic metacommunities

One general mechanism that is, in its essence, recovered in all three chapters, is the drainage effect and its influence on trophic dynamics. In general, this effect describes a loss of biomass or energy through dispersal. In this sense, the drainage effect is the counterpart of the rescue effect which describes a biomass gain through dispersal. Thus, both effects are driven by the magnitude and the sign of net-dispersal. If there is more biomass emigrating from a population than immigrating to it, the population experiences the drainage effect, and vice-versa, if there is more biomass immigrating then emigrating, the population experiences a rescue effect. In meta-food-webs, this additional biomass flow through space then interacts with local trophic dynamics, which then feeds back again on dispersal. Food-web research has shown that the dynamics in an ecological network are strongly influenced by the rate at which energy flows through its links (Brose, 2008; Rall et al., 2008; Rip and McCann, 2011; Strogatz, 2001). Thus, the drainage and the rescue effect can shift a trophic system along the axis of the paradox of enrichment (**Chapter 2**) or result in a total energy flux that can support higher trophic levels or drive them to extinction (**Chapters 1, 2 & 3**). As an illustrative example, a simple animal community consisting of mice, weasels and lynxes (i.e. weasels are preying on mice and lynxes are preying on weasels) may coexist in an equilibrium state in a given patch. Increasing the drainage effect on these populations, for example due to increasing isolation and thus increasing loss during dispersal, all three populations may shrink as a result of more emigration than immigration. Then, because the mouse population is smaller, the weasels have less to eat, and thus the lynxes have even less to eat. This could drive the lynx population to extinction because of starvation. For instance, this is demonstrated in **Chapter 1** where isolation leads to the loss of top predators through cumulative losses throughout the food web. As a result of reduced predation pressure, lower trophic levels can recover or even increase despite increased isolation and thus more drainage. This highlights the non-linear responses to isolation across trophic levels that arise from interacting spatial and trophic processes. However, if the previously illustrated animal community resides in a eutrophic habitat with a lot of energy available, and thus coexists in an unstable oscillating state as illustrated in the introduction, the drainage effect can reduce this excess energy and reduce oscillations or even shift the system to a stable equilibrium (**Chapter 2**). In contrast, the rescue effect can result in opposite effects. Through an additional influx of biomass and thus energy for a trophic system, small populations in for example nutrient poor locations can persist despite of an insufficient local energetic basis. However, in a habitat that is not energy limited and in line with the principle of energy fluxes

(Rip and McCann, 2011), sideways influx of additional energy can push a trophic system into unstable oscillations and subsequent extinctions (**Chapter 2**) or support higher trophic levels on small well-connected patches, if they are present in the metacommunity. This energetic support of a local food web on small well-connected patches is responsible for the negative species-area relationships observed in **Chapter 3**.

Food-web research has shown that the strength of interactions, the size of the energetic basis (i.e. the amount of energy flowing), and the food-web structure (i.e. the pathways this energy is taking) affects stability and shapes patterns of biodiversity (Montoya et al., 2006; Otto et al., 2007; Paine, 1969; Rall et al., 2008; Rip and McCann, 2011; Rosenzweig, 1971; Stouffer and Bascompte, 2011; Thébault and Fontaine, 2010). Therefore, it is not surprising that the impact of drainage and rescue effects depends on the food-web structure they interact with. For instance, in **Chapter 3** I show that food-web structures interact with species-area-isolation relationships. There, potential meta-food-webs, that is all possible species and interactions of the initial metacommunity, with lower maximum trophic levels show shallower species-area relationships for negative as well as for positive relationships. This is because rescue effects affect the highest trophic levels the most, and in food webs without species occupying these high trophic levels, the effects are weaker. Species-area relationships are also shallower in food webs with a high modularity. This is because species are less affected by dispersal of other species that are not part of their own module and indirect effects are less likely to propagate across modules. In turn, species are also more restricted in their prey rendering their own dispersal less important. Other food-web metrics also interact with species-area relationships suggesting, that for some meta-food-web structures, the relative importance of dispersal compared to local trophic constraints may vary. Furthermore, meta-food-web structures do not only affect species-area-isolation relationships, but they can change them in a different direction depending on the landscape configuration. This suggests a complex interaction among landscapes and food webs in shaping biodiversity and could not have been uncovered in simple food chains.

At its core, landscape configurations and context as well as patch conditions affect the asymmetry of emigration and immigration, which gives rise to drainage and rescue effects and also influences the magnitude of these effects. In **Chapter 2**, I show that landscape heterogeneity in terms of nutrient conditions on patches, gives rise to drainage effects on eutrophic patches that buffer against extinctions, and to rescue effects on oligotrophic patches increasing species persistence on single patches and in the whole landscape. In **Chapter 3**, landscapes that contain patches with randomly distributed areas allow for strongly asymmetrical dispersal as a small patch neighbouring a large patch receives much more immigrating biomass than is emigrating from it. This results in higher population densities and thus, in the support of higher trophic levels which then produces negative species-area relationships in these types of landscapes. Essentially, the random distribution of patch areas gives rise to another level of heterogeneity, as opposed to when patch sizes are distributed spatially autocorrelated, which provides another mechanistic explanation for how heterogeneity promotes biodiversity. Thus, depending on landscape context, dispersal can overwrite local area effects and buffer against eutrophication or starvation of populations by interacting with local trophic dynamics.

Dispersal can also act synchronizing on population dynamics (i.e. population densities oscillate synchronous), which increases the risk of correlated extinction (Blasius et al., 1999; Gouhier et al., 2010) through stochastic events such as hurricanes or fires, and therefore threatens biodiversity. Thus, when two populations of a species in two different locations, for example two islands, oscillate in synchrony, and a hurricane hits both islands when both populations are at low densities, they both may go extinct. Dispersal can also reduce oscillations (Gounand et al., 2014) or result in compensatory dynamics (McCann et al., 2005) and buffer against extinctions. In this case, the two populations may exhibit stable equilibrium dynamics and be less likely to be driven to extinction by a hurricane. The two populations could also be oscillating asynchronously. For example, when one population is at low density, the other is at high density and therefore more likely to persist following the hurricane. In **Chapter 2**, I demonstrate, that with increasing isolation in a two-patch system, dispersal links are weakened, and with a decrease in coupling strength, first amplitudes of oscillating populations get decoupled and then also frequencies, which results in chaotic oscillation patterns with subsequent extinctions. In an ongoing collaboration I aim to understand how more complex landscape structures and configurations influence synchrony by applying the model presented here to food chains in dendritic river networks (see Outlook).

In a nutshell, the interaction of strong and weak trophic and spatial fluxes that arise from local conditions, food-web structures and landscape configurations shape biodiversity.

Global change

In addition to uncovering general mechanisms in meta-food-webs, this thesis also addresses interactive effects of global change by applying the meta-food-web model to several prominent biodiversity threats. Land-use intensification driven by growing demands for production of food and other goods, for gathering resources and energy and for space to expand settlements is causing accelerated habitat fragmentation, loss and isolation, eutrophication and homogenisation at global scales. Yet, we barely understand how they combine to affect ecosystems and shape biodiversity. These global change drivers may amplify or buffer each other in non-additive ways.

In **Chapter 1**, the exploration of interactive effects of isolation and the number of habitat fragments, that is the number of nodes in the spatial network, in meta-food-webs reveals that isolation particularly threatens species occupying high trophic levels while the number of fragments in a landscape did not uncover any effect. However, in **Chapter 2**, I demonstrate that increasing isolation or landscape hostility, essentially anything that increases dispersal losses, can buffer against extinctions when interacting with eutrophication. This reveals that the effect of habitat fragmentation with increasing isolation is context-dependent and, in some cases, even beneficial for biodiversity. In turn, nutrient heterogeneity in the landscape results in eutrophic patches supporting oligotrophic patches and oligotrophic patches buffer eutrophic patches, but only at low to intermediate isolation. This is because the dispersal loss due to isolation on the one hand increases the drainage effect, but on the other hand, decreases the rescue effect. Thus, at high isolation, eutrophic patches may still provide enough energy despite the increased dispersal loss, but oligotrophic patches lose the biomass support through dispersal (i.e. rescue effect) and their net migration also becomes negative. Eutrophication by itself increases dispersal fluxes through mass effects, but only up to a point where local extinctions occur due to unstable oscillations. At low isolation, this excess biomass can spill over to mesotrophic patches and cause unstable top-heavy biomass pyramids that also yield unstable oscillations. Then, **Chapter 3** reveals, that small patches, depending on the landscape configuration and the degree of isolation can even support species belonging to higher trophic levels that cannot persist anywhere else in the landscape. Responsible for this pattern is again the magnitude of dispersal fluxes relative to local trophic energy fluxes and the asymmetry of dispersal causing either positive or negative net migration. In principle, the global changes investigated here, except of the neutral effect of the number of habitat nodes in the spatial network, all modify drainage and rescue effects in different ways. In addition, drainage and rescue effects subsequently shape metacommunities and thus biodiversity depending on trophic structures and the species pool in the landscape. In a nutshell, this thesis reveals highly non-linear and context dependent responses in meta-food-web dynamics and resulting biodiversity changes via interacting global changes.

Biodiversity conservation

The mechanisms and interactive effects of global change drivers on meta-food-webs suggest that mitigation strategies against biodiversity loss should be context-dependent and account the complexity of trophic metacommunities on metaecosystem scales. For instance, wildlife bridges that decrease dispersal mortality by providing a bypass across roads could be detrimental for biodiversity in eutrophic landscapes but beneficial when they support connectivity in heterogeneous landscapes or between oligotrophic habitats. Then, high connectivity in predominantly eutrophic landscapes, i.e. intensive agricultural fields, may lose pest control, which, however, could be maintained if connectivity is lower or by increasing nutrient heterogeneity by adding energy sinks. Eutrophic agricultural fields, even without direct spill-over of nutrients, may destabilize adjacent mesotrophic habitats through dispersal of organisms, for example in nature reserves. Furthermore, negative species-area-isolation relationships observed in **Chapter 3**, may argue in favour of also conserving small patches that are well connected to larger patches, as they could uniquely harbour species occupying higher trophic levels. In general, broadscale landscape configuration such as the distribution of patch sizes and the spatial autocorrelation of patch connectivity and size, have the potential to shape local communities and metacommunities. The spatially non-random method of land-use change caused by humans, for example the historical trend of settlements being built along rivers or progressing deforestation that leads to spatially autocorrelated patch sizes (García et al., 2005; Taubert et al., 2018) may thus deserve attention in predicting future biodiversity loss.

Overall, this thesis presents a flexible and mechanistic meta-food-web model capable of simulating realistic complexity of landscapes and food webs, uncovers general mechanisms that only arise as a consequence of integrating spatial and trophic processes, and reveals complex context-dependent effects of interacting global changes on trophic metacommunities.

Future directions

All organisms need energy to live and thus, trophic interactions are a fundamental part of life. In this thesis, I highlight the importance of integrating spatial and trophic interactions as many of the described mechanisms and patterns only arise in a meta-food-web framework. However, there are other types of species interactions that occur in nature and are important drivers of biodiversity (Kéfi et al., 2012; Sauve et al., 2016) that could be integrated in the future. One prominent example are seed-dispersal networks. Interestingly, in seed-dispersal interactions, a plant essentially uses the mobility, and thus the spatial network of an animal species. In light of its architecture, the model presented in this thesis is highly suited to the integration of seed-dispersal interactions. Another example are mutualistic interaction networks such as plant-pollinator networks. For instance, a recent study has integrated pollination into food webs and thereby shown that mutualism increases stability, diversity and function in multiplex networks (Hale et al., 2020). Furthermore, at this stage, the model ignores evolutionary processes as they act on different time scales. However, recent advances have achieved building eco-evolutionary food-web models (Allhoff et al., 2015b, 2015a) that could, in the future, be integrated into the model presented here.

Another future direction of the model literally lies within the patch. While the dispersal part of the model accounts for species' size to define dispersal ranges and thus species-specific networks, larger animals may also perceive a patch on a different scale than small animals. Future work could thus define habitat patches in a nested manner scaled with species body size and include multi-patch functional responses (McCann et al., 2005). Furthermore, the model presented here does not allow for nutrients to be moved in space. Nutrient spill-over from a eutrophic to an oligotrophic location may decrease spatial heterogeneity (Gounand et al., 2014), increase local productivity and food-chain length (Gravel et al., 2010) or destabilize food-chains (Gounand et al., 2014) in line with the paradox of enrichment. Cross-ecosystem nutrient fluxes, for example from terrestrial habitats to rivers, can also change community composition (Harvey et al., 2020). The meta-food-web approach presented here provides an opportunity to extend such metaecosystem frameworks with complex food webs.

Similar to the concept of key-stone species (Paine, 1969), some patches in a landscape may have a disproportionately large impact on the metacommunity, which could be due to their properties, such as size or nutrient conditions, their position in the spatial network and how strongly they are connected to other patches, or both. Thus far, this thesis only addresses spatial networks as a whole, and for example, how nutrient conditions or patch sizes are distributed in the landscape. An extension of the meta-food-web approach to address what is driving "keystoneness" in patches (and thus keystone communities (Mouquet et al., 2013)), or how the removal of single patches cascades through meta-food-webs could further improve our understanding of ecological mechanisms shaping biodiversity and provide refined strategies for conservation efforts to mitigate biodiversity loss with increasing land-use change.

Furthermore, and despite the model being parameterised largely by empirically informed body mass relationships, some parameters remain relatively uncertain. Even though the modelling approach as presented in this thesis remains practically the only option to investigate the high-dimensionality and complexity of meta-food-webs and interacting global change drivers, it lies in the nature of modelling that they, strictly speaking, only provide evidence based on their assumptions. Furthermore, uncertainties in parameters and processes scale up with the complexity of a model. However, there are several levels at which the model can be empirically informed and validated.

Firstly, the better parameters are informed by empirical evidence, the lower is the uncertainty of resulting patterns. For instance, the movement mode of organisms, i.e. running, flying or swimming, will most likely influence how dispersal ranges scale with body mass as it also influences an organisms' maximum speed (Hirt et al., 2017a). Then, the underlying theory to predict food-web structures based on a species' body size is predominantly focused on individual-based interactions. Non-individual based interactions such as baleen whales consuming several prey individuals at once may change food-web dynamics. Thus, additional trait-axes such as movement speed or predator strategies could extend the prediction of food-web structures and interaction strengths beyond body masses to create even more realistic food webs in the model (see Outlook). Moreover, and especially to move towards using such models for predictions, quantitative effects of global change drivers on processes and parameters are needed. An example would be the extent to which light pollution is affecting activity patterns, movement behaviour and therefore encounter rates (see Outlook).

Secondly, patterns resulting from model simulations could be compared to ecosystem-scale patterns observed in nature to further validate the model. While some patterns uncovered in the chapters of this thesis do match with empirical examples, other empirical patterns lack specific information about some assumptions made in the model. For instance, many empirical studies of habitat fragmentation lack trophic structures or broad scale landscape configurations. In light of the complexity of real ecosystems, this is completely understandable. This, in turn, highlights another benefit of a modelling approach. On top of being able to distil mechanisms and dissect complex interactions with the power of *in silico* replication, modelling results can subsequently become sophisticated hypotheses and point empirical research towards measuring specific patterns and parameters.

Outlook

This thesis presents a complex meta-food-web model and explores general mechanisms and interactive global change drivers in trophic metacommunities on metaecosystem scales. In the process, it also highlights further gaps of knowledge and provides a flexible tool for further research of other global change drivers and in different systems.

As outlined in the discussion, population synchrony is an additional aspect of meta-food-web dynamics and has implications for ecosystem stability. Different ecosystem types may have different constraints for dispersal pathways and therefore on synchrony. Furthermore, dendritic river networks are an interesting type of spatial networks with distinct rules. River networks are flow-connected, which shapes connectivity. Thus, classical distance measures have less meaning in river networks. Also, due to the nature of flowing water, they inherently create asymmetrical dispersal fluxes as it is harder and more costly to swim against the current than with it. In an ongoing collaboration, I applied the meta-food-web model presented in this thesis to food chains in dendritic river networks. In this collaboration, we address population synchrony depending on river network complexity and dispersal capabilities of organisms. Furthermore, we aim to compare simulation results to a large data set of empirical timeseries of fish populations across Europe to isolate the most important mechanisms that create real patterns in population synchrony. With a similar approach and in another project in this collaboration, I included disturbances affecting fish mortality with different levels of intensity and duration in the model. Here, we aim to understand how different types of disturbances influence synchrony and interact with river network structure. These two projects are aimed at contributing to better understand mechanisms driving synchrony in trophic metacommunities and exploring the fascinating nature of river networks. By comparing simulation results to empirical data, we can on the one hand isolate the most important driving mechanisms, and on the other hand strengthen model assumptions and similarity to real world situations, given that patterns match.

In another project collaboration we aim to develop an eco-mechanical model to predict food-web structure based on mechanical and physiological traits (i.e. body mass and movement mode), physical properties of ecosystem types and basic laws of physics. This could further improve our ability to predict food-web structures based on two key functions that are metabolism and locomotion. This could then be integrated into the meta-food-web model presented in this thesis to further improve the food-web aspects of the model.

Moreover, the role of single patches and their network properties for meta-food-web dynamics and stability is still unclear. For example, the centrality of a patch in the spatial network or its degree (i.e. the number of spatial links) may affect local communities and have implications for neighbouring patches or the whole spatial network. By applying the concept of key-stone patches and through single patch removal to the meta-food-web model, I aim t understand single patch contributions to stability and biodiversity in a spatial network context. This could uncover further mechanisms in meta-food-webs and provide yet another basis for targeted habitat conservation and restoration.

Another global change driver that is receiving more and more attention is light pollution. With more than 60% of arthropods being at least partially night active (Hölker et al., 2010) and half of the planet being dark at any one time, light pollution has a large potential to affect biodiversity. In a current experiment, we aim to investigate the effect of different intensities of artificial light on activity patterns and movement of insect species. In a mesocosm setup with a simple landscape structure of four patches separated by bare ground, and a grid of RFID-readers installed in the ground we will track the movement of insects that have RFID-chips mounted on them. In twelve chambers with different intensities of artificial light and an astronomically accurate simulated moon light, we aim to infer activity patterns, patch bridging behaviour and encounter rates as a function of light pollution intensity. Subsequently, we will inform the meta-food-web model with these empirically measured effects to generalize and predict biodiversity changes and ecosystem functions in trophic metacommunities under light pollution. In a nutshell, this current project further improves the predictability of the meta-food-web model by empirically quantified effects on underlying processes and could shed light onto the effect of yet another global change driver.

This outlook highlights that the contributions from this thesis already find further application and integration to better understand complex ecosystems and global change consequences and foster biodiversity synthesis research.

Closing words

Developing and executing ideas for my thesis provided me with the opportunity to satisfy and foster my curiosity in complex systems and mechanisms in ecology. The deeper understanding of scientific methods and theories I gained during my PhD also provide a good filter and funnel for that curiosity for my future career and life. I hope that this thesis contributes to conserving the complexity of biodiversity so that also future generations can experience such curiosity and amazement as Aristotle did more than two millennia ago.

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Appendix

Supplement Chapter 1

Supplement to "The biggest losers: Habitat isolation deconstructs complex food webs from top to bottom"

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body masses of plant species from the inclusive interval $(0, 6)$ (for empirical examples see [6]). This step makes the model inherently stochastic, but from hereon, all other steps are completely deterministic. The model is designed such that animal consumers feed on resources, which can be both plants and other animal species that are smaller than themselves. Body masses further determine the interaction strengths of feeding links as well as the metabolic demands of species.

Data from empirical feeding interactions are used to parametrise the functions that characterise the optimal prey body mass and the location and width of the feeding niche of a predator. From each m_i a unimodal attack kernel, called feeding efficiency, L_{ij}, is constructed which determines the probability of consumer species i to attack and capture an encountered resource species j. We model L_{ij} as an asymmetrical hump-shaped Ricker's function (equation T1-4) that is maximised for an energetically optimal resource body mass (optimal consumer-resource body mass ratio $R_{opt} = 100$) and has a width of $\gamma = 2$. The maximum of the feeding efficiency L_{ij} equals 1. Table S1 list the full set of equation and table S2 is an overview of the standard parameter set for the equations. See also Schneider *et al.* [1] for further information regarding the allometric food web model.

S1 Food web and local population dynamics

We consider a multitrophic metacommunity consisting of 40 species on a varying number of randomly positioned habitat patches, Z (the meta-food-web, figure 1b). All patches have the same abiotic conditions and each patch can potentially harbour the full food web, consisting of 10 basal plant and 30 animal consumer species. The feeding links (i.e. who eats whom) are constant over all patches (figure 1a,b) and are as well as the feeding dynamics determined by the allometric food web model by Schneider *et al.* [1]. We integrate dispersal as species-specific biomass flow between habitat patches (figure 1b,d).

Using ordinary differential equations to describe the feeding and dispersal dynamics, the rate of change in biomass density, $B_{i,z}$, of species i on patch z is given by

$$\frac{dB_{i,z}}{dt} = T_{i,z} - E_{i,z} + I_{i,z}\,, \tag{1}$$

with $T_{i,z} = \upsilon_{i,z} \cdot B_{i,z}$ as the rate of change in biomass density determined by local feeding interactions (where $\upsilon_{i,z}$ is the per capita growth rate), $E_{i,z}$ as the total emigration rate of species i from patch z (equation (2)), and $I_{i,z}$ as the total rate of immigration of species i into patch z (equation (4)).

Local food web dynamics

We use an allometric trophic network model (ATN model) based on the work of Schneider *et al.* [1] & Kalinkat *et al.* [2] to simulate the trophic dynamics of local populations ($T_{i,z}$ in equation (1)). Regarding this term, we distinguish between animal species (Equation T1-1) and basal plant species (Equation T1-6). In each patch, the biomass dynamics of animal species (biomass densities $A_{i,z}$) is given by the differences between growth due to consumption of animal or plant species and losses due to mortality through predation and metabolic demands. The rate of change in plant biomass densities, $P_{i,z}$, depends on the uptake of the two resources, mortality through grazing, and also accounts for metabolic losses. We used a dynamic nutrient model (equation T1-8) with two nutrients (concentrations $N_{l,z}$) of different importance as the energetic basis of our food web [1, 3].

The topological network model is an extension of the niche model originally introduced by Williams & Martinez [4] and accounts for allometric degree distributions and recent data on scaling relationships for species body mass and trophic levels [5]. Each species i is fully characterised by its average adult body mass m_i. We sampled $\log_{10}$ body masses of animal species randomly with a uniform probability density from the inclusive interval $(2, 12)$ and the $\log_{10}$

Table S1: Ordinary differential equations describing the local population dynamics driven by feeding interactions (see Schneider *et al.* [1]. We use the same allometric constraints and parameter ranges.

Equation No.	Model equations	Description
Equation T1-1	Animal population dynamics $\frac{dA_{i,z}}{dt} = e_P A_{i,z} \sum_j F_{ij,z} + e_A A_{i,z} \sum_k F_{ik,z} - \sum_k A_{k,z} F_{ki,z} - x_i A_{i,z}$	Rate of change of biomass density of animal species i on patch z; with conversion efficiency $e_P = 0.545$ typical for herbivory [7]; conversion efficiency $e_A = 0.906$ typical for carnivory [7]; feeding rate $F_{ij,z}$ of consumer i on resource j on patch z; metabolic demands per unit biomass for animals $x_i = x_A m_i^{-0.305}$ with scaling constant $x_A = 0.314$ [8, 9]. The first sum goes over all plant resources j, the second over all animal resources k and the third over all animal predators k of animal species i.
Equation T1-2	Functional response $F_{ij,z} = \frac{\omega_i \kappa_{i,j} R_{j,z}^{1+q}}{1 + cA_{i,z} + \omega_i \sum_k \kappa_{ik} h_{ik} R_{k,z}^{1+q}} \cdot \frac{1}{m_i}$	Per unit biomass feeding rate of consumer i as function of its own biomass density, A_i, (taking interference competition c, which is the time lost due to intraspecific encounters, sampled from a normal distribution with mean $\mu_c = 0.8$ and s.d. $\sigma_c = 0.2$ for each food web), and biomass density of the resource R_j (either animal A_j or plant species P_j); with ϕ_{ij}, resource specific capture coefficient (Eq. T1-3); h_{ij}, resource-specific handling time (Eq. T1-5); $\omega_i = 1/(\text{number of resource species of } i)$, relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.

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Table S1 – continued from previous page

Equation No.	Model equations	Description
Equation T1-3	Capture coefficient $\kappa_{ij} = \lambda_l m_i^{\beta_i} m_j^{\beta_j} L_{ij}$	Resource specific capture coefficient of consumer species i on resource species j scaling the feeding kernel L_{ij} by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed. We sample the exponents β_i and β_j from normal distributions (mean $\mu_{\beta_i} = 0.42$, s.d. $\sigma_{\beta_i} = 0.05$; $\mu_{\beta_j} = 0.19$, s.d. $\sigma_{\beta_j} = 0.04$, respectively [10]). We divide here the group of consumer species into the subgroup of carnivorous and herbivorous species each comprising a constant scaling factor for their capture coefficients λ_l with $l \in 0, 1$ ($\lambda_0 = 40$ for carnivorous species and $\lambda_1 = 5000$ for herbivorous species); For plant resources, $m_j^{\beta_j}$ was replaced with the constant value of 1 (as plants do not move).
Equation T1-4	Feeding efficiency $L_{ij} = \left(\frac{m_i}{m_j R_{opt}} e^{1 - \frac{m_i}{m_j R_{opt}}} \right)^{\gamma}$	The probability of consumer i to attack and capture an encountered resource j (which can be either plant or animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width $\gamma = 2$ centered around an optimal consumer-resource body mass ratio $R_{opt} = 100$.
Equation T1-5	Handling time $h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j}$	The time consumer i needs to kill, ingest and digest resource species j, with scaling constant $h_0 = 0.4$ and allometric exponents η_i and η_j drawn from normal distributions with means $\mu_{\eta_i} = -0.48$ and $\mu_{\eta_j} = -0.66$, and standard deviations $\sigma_{\eta_i} = 0.03$ and $\sigma_{\eta_i} = 0.02$, respectively [11].

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Table S1 – continued from previous page

Equation No.	Model equations	Description
Equation T1-6	Plant population dynamics $\frac{dP_{i,z}}{dt} = r_i G_i P_{i,z} - \sum_k A_{k,z} F_{ki,z} - x_i P_{i,z}$	Rate of change of biomass density of plant species i on patch z; with predation loss $F_{ki,z}$ summed over all consumer species k feeding on plant species i; metabolic demands per unit biomass for plants $x_i = x_P m_i^{-0.25}$ with $x_P = 0.138$; intrinsic growth rate $r_i = m_i^{-0.25}$; species specific growth factor G_i (Eq. T1-7).
Equation T1-7	Growth factor for plants $G_i = min\left(\frac{N_1}{K_{i,1} + N_1}, \frac{N_2}{K_{i,2} + N_2}\right)$	Species-specific growth factor of plants determined dynamically by the most limiting nutrient $l \in 1, 2$; with $K_{i,l}$, half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species i and nutrient l (uniform distribution within (0.1, 0.2)). The term in the minimum operator approaches 1 for high nutrient concentrations.
Equation T1-8	Nutrient dynamics $\frac{dN_{l,z}}{dt} = D(S_l - N_l) - \nu_l \sum_{i,z} r_i G_i P_{i,z}$	Rate of change of nutrient concentration N_l of nutrient $l \in \{1, 2\}$ on patch z, with global turnover rate $D = 0.25$, determining the rate at which nutrients are refreshed; supply concentration S_l, determining the maximum nutrient level of each nutrient, l, drawn from normal distributions with mean $\mu_S = 50$ and standard deviation $\sigma_S = 2$ (provided $S_l > 0$); relative nutrient content in plant species biomass ν_l ($\nu_1 = 1$, $\nu_2 = 0.5$).

S2 Generating landscapes

We generated differently fragmented landscapes, represented by random geometric graphs [12], by randomly drawing the locations of Z patches from a uniform distribution between 0 and 1 for x- and y-coordinates respectively. We created landscapes of different size by scaling the maximum dispersal distance of all organisms δ_{max} with a factor, Q, to represent landscape sizes with edge lengths between 0.01 and 10. We obtained the number of patches, Z, by using a stratified random sampling approach, i.e. we added a random number drawn from an integer uniform distribution between 0 and 9 to a series of numbers of $10, 20, \ldots, 60$. Similarly, we set the landscape size, Q, by adding a random number drawn from a uniform distribution between 0 and 1 (respectively 0 and 0.1 for landscape sizes below 1) to a series of numbers of $0.01, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9, 1, 3, 5, 7, 9$.

S3 Dispersal

We model dispersal between local communities as a dynamic process of emigration and immigration, assuming dispersal to occur at the same timescale as the local population dynamics [13]. Thus, biomass flows dynamically between local populations and the dispersal dynamics directly influence local population dynamics and vice versa [14]. Similar approaches have been used by e.g. Abrams & Ruokolainen [15] and Ims & Andreassen [16]. We model a hostile matrix between habitat patches that does not allow for feeding interactions to occur during dispersal, and thus, assume the biomass lost to the matrix to scale linearly with the distance travelled.

Emigration The total rate of emigration of species i from patch z is

$$E_{i,z} = d_{i,z} B_{i,z}, \tag{2}$$

with $d_{i,z}$ as the corresponding per capita dispersal rate. We model $d_{i,z}$ as

$$d_{i,z} = \frac{a}{1 + e^{b(x_i - \upsilon_{i,z})}}, \tag{3}$$

with a, the maximum dispersal rate, b, a parameter determining the shape of the dispersal rate (figure S1), x_i, the inflection point determined by the metabolic demands per unit biomass of species i, and $\upsilon_{i,z}$, the per capita net growth rate of species i on patch z. We chose to model $d_{i,z}$ as a function of each species' per capita net growth rate to account for emigration triggers such as resource availability, predation pressure and inter- and intraspecific competition [14, 17]. If for example an animal species' net growth is positive, there is no need for dispersal and emigration will be low. However, if the local environmental conditions deteriorate, the growing incentives to search for a better habitat increase the fraction of individuals emigrating. For plants, we assumed an additional scenario as there are examples of different life history strategies. There are for example plant species which disperse from their local habitat when they are doing well, i.e. they have a high net growth rate, as they can allocate more resources into reproduction resulting in higher seed dispersal [18]. However, there are also examples where plants reallocate resources into reproduction when they are doing poorly [19] (figure S1b).

For each simulation run, a was sampled from a Gaussian distribution (μ_{aS}, σ_{aS}) and b was sampled from an integer uniform distribution within inclusive limits that differed between consumer and plant species (see table S2). The different intervals reflect different dispersal triggers for animals and plants.

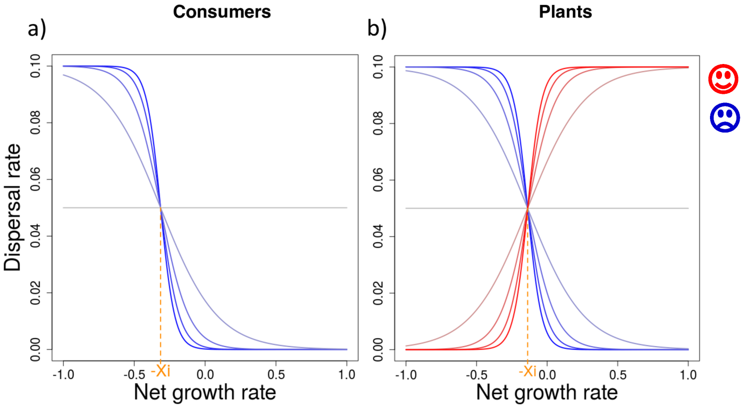

Figure S1: Functions illustrating the dispersal rate d_i for animal (a) and plant species (b), where x_i marks the inflection point for each species i determined by the metabolic demands (x_i) per unit biomass of species i (see Table S1). The colours blue and red represent different dispersal strategies and the respective colour gradients depict the parameter range of b, which determines the slope of the dispersal rate (see equation (3)). For the purpose of illustration, we set the maximum dispersal rate to $a = 0.1$ and for animals and plants $x_{i_A} = 0.314$ and $x_{i_P} = 0.1384$, respectively.

Immigration The rate of immigration of biomass density of species i into patch z follows

$$I_{i,z} = \sum_{n \in N_z} E_{i,n}(1 - \delta_{i,nz}) \frac{1 - \delta_{i,nz}}{\sum_{m \in N_n} 1 - \delta_{i,nm}}, \tag{4}$$

where N_z and N_n are the sets of all patches within the dispersal range of species i on patches z and n, respectively. In this equation, $E_{i,n}$ is the emigration rate of species i from patch n, $(1 - \delta_{i,nz})$ is the fraction of successfully dispersing biomass, i.e. the fraction of biomass not lost to the matrix, and $\delta_{i,nz}$ is the distance between patches n and z relative to species i's maximum dispersal distance δ_i (see below paragraph Maximum dispersal distance). The term $\frac{1-\delta_{i,nz}}{\sum 1-\delta_{i,nm}}$ determines the fraction of biomass of species i emigrating from source patch n towards target patch z. This fraction depends on the relative distance between the patches, $\delta_{i,nz}$, and the relative distances to all other potential target patches m of species i on the source patch n, $\delta_{i,nm}$. Thus, the flow of biomass is greatest between patches with small distances. For numerical reasons, we did not allow for dispersal flows with $I_{i,z} < 10^{-10}$. In this case, we immediately set $I_{i,z}$ to 0.

Maximum dispersal distance Based on empirical observations (e.g. [20]) and previous theoretical frameworks (e.g. [10, 21–23]), we assume that the maximum dispersal distance δ_i of animal species increases with their body mass. For animal species, the body mass m_i determines how fast and how far they can travel through the matrix before needing to rest and feed in a habitat patch. Thus animal species at high trophic positions can disperse further than smaller animals at lower trophic levels. Each animal species perceives its own dispersal network dependent on its species-specific maximum dispersal distance

$$\delta_i = \delta_0 m_i^{\epsilon}, \tag{5}$$

where the exponent $\epsilon = 0.05$ determines the slope of the body mass scaling of δ_i. We chose a positive value for ϵ to account for a higher mobility of animals with larger body masses. The intercept $\delta_0 = 0.1256$ was chosen such that the animal species with the largest possible body mass of $m_i = 10^{12}$ had a maximum dispersal distance of $\delta_i = 0.5$. Thus, the animal species with the smallest possible body mass of $m_i = 10^2$ had a maximum dispersal distance of $\delta_i = 0.158$.

As plants are passive dispersers driven by e.g. wind with no clear relationship between body mass and dispersal distance, we model their maximum dispersal distance as random and body mass independent [20]. We sampled δ_i for each plant species from a uniform probability density within the interval $(0, 0.5)$. Thus, the best plant disperser can potentially have the same maximum dispersal distance as the largest possible animal species (table S2). Additionally, we tested a null model in which all species have the same maximum dispersal distance of $\delta_i = \delta_{max}$. See section S8 for further information on the additional simulations.

Table S2: Model parameters and output variables.

Parameter	Description	Value
	Trophic interactions between species	
e_A	conversion efficiency animal species	0.906; [7]
e_P	conversion efficiency plant species	0.545; [7]
x_A	scaling constant metabolic demands animal species	0.314; [9]
x_P	scaling constant metabolic demands plant species	0.138; [9]
μ_c, σ_c	mean and standard deviation for interference competition	0.8, 0.2
λ_0	scaling factor capture coefficient for carnivorous species	40
λ_1	scaling factor capture coefficient for herbivorous species	5000
μ_{β_i}, σ_{β_i}	mean and standard deviation allometric exponent for attack rates consumer	0.42, 0.05; [10]
μ_{β_j}, σ_{β_j}	mean and standard deviation allometric exponent for encounter of prey	0.19, 0.04; [10]
ω_i	relative consumption rate	$\frac{1}{\text{number of prey species } i}$
R_{opt}	optimal consumer-resource body mass ratio	100
γ	scaling exponent Ricker's function	2
h_0	scaling factor handling time	0.4
μ_{η_i}, σ_{η_i}	mean and standard deviation allometric exponent handling time consumer	-0.48, 0.03; [11]
μ_{η_j}, σ_{η_j}	mean and standard deviation allometric exponent handling time resource	-0.66, 0.02; [11]
μ_q, σ_q	mean and standard deviation hill coefficient	1.5, 0.2
	Nutrient dynamics	
K	half saturation density nutrient uptake	(0.1, 0.2)
D	nutrient turnover rate	0.25
μ_{S_l}, σ_{S_l}	mean and standard deviation of nutrient supply concentration	50, 2
ν_1, ν_2	relative nutrient content in plant species biomass	1, 0.5
	Dispersal dynamics	
δ_{max}	species-specific maximum dispersal distance	0.5
ϵ	scaling exponent for species-specific maximum dispersal distance	0.05
μ_{a_S}, σ_{a_S}	mean and standard deviation of max. emigration	0.1, 0.03
θ	cut off emigration function	$3 \cdot \sigma_{a_S}$
b	shape parameter of the emigration function	(0,19) (cons.) (-20,19) (plants)
	Output variables	
$\overline{\tau}$	mean distance between all habitat patches, with τ_{nm}, the absolute distance between patches n and m, and $(Z^2 - Z)$, the total number of potential directed links between all Z habitat patches	$\frac{\sum_{n,m=1}^{Z} \tau_{nm}}{Z^2 - Z}$
ρ_i	landscape connectance of species i, with L_i, the number of directed dispersal links of species i	$\frac{L_i}{Z^2 - Z}$

S4 Numerical simulations and data analysis

We constructed 30 model food webs, each comprising 10 plant and 30 animal species. To avoid confounding effects of different initial species diversities, we kept both the number of species S and the fraction of plants and animals constant among all food webs. For each simulation, we randomly generated a landscape of size Q (edge length of a square landscape) with Z randomly distributed habitat patches. To test each food web across a gradient of number of habitat patches and habitat isolation, we drew the number of habitat patches, Z, from the inclusive interval $(10, 69)$ and the size of the landscape, Q, from the inclusive interval $(0.01, 10)$ using a stratified random sampling approach (see also section S2 for further information). With this approach, we generated landscapes on two independent gradients covering two aspects of fragmentation, namely number of fragments and habitat isolation. To cover the full parameter range of Z and Q, we simulated each food web on 72 landscapes resulting in a total of 2160 simulations. We achieved a full range for the gradient of habitat isolation (landscape connectance ranging from 0 to 1, figure S3c). The upper limit for the number of patches was chosen to conform to the maximum usage time of 10 days per simulation on the high-performance-cluster we used [24]. Additionally, we performed dedicated simulation runs to reference the two extreme cases, i.e. (1) landscapes in which all patches are direct neighbours without a hostile matrix, and thus, no dispersal mortality, and (2) fully isolated landscapes, in which no species can bridge between patches, and thus, a dispersal mortality of 100% .

For each simulation run, we initialised our model with random conditions: Each habitat patch z holds a random selection of 21 to 40 species (with each of the 40 species of the full food web existing on at least one patch) and initial biomass densities $B_{i,z}$ and nutrient concentrations N_l ($l \in 1, 2$) were randomly sampled with uniform probability density within the intervals $(0, 10)$ for $B_{i,z}$ and $(S_l/2, S_l)$ for N_l, respectively. Here, S_l are the supply concentrations of the nutrients, which are constant on all habitat patches but differ between the two nutrients. See table S2, Equation T1-8 and Schneider *et al.* [1] for further information on the nutrient dynamics.

Starting from these random initial conditions, we numerically simulated local food web and dispersal dynamics over 50,000 time steps by integrating the system of differential equations implemented in C++ using procedures of the SUNDIALS CVODE solver version 2.7.0 (backward differentiation formula with absolute and relative error tolerances of 10^{-10} [25]). Successful dispersal between local populations thereby enabled species to establish populations on patches where they were initially absent. For numerical reasons, a local population was considered extinct once $B_{i,z} < 10^{-20}$, and $B_{i,z}$ was then immediately set to 0.

Output variables

We recorded the following output variables for each simulation run: (1) the mean biomass density of each species i on each habitat patch z over the last 20,000 time steps, $\overline{B}_{i,z}$; (2) the number of habitat patches in a landscape, Z; (3) habitat isolation, i.e. the mean distance between all habitat patches, $\overline{\tau}$ (see table S2); and (4) the landscape connectance of each species i, ρ_i (see table S2). Thus, ρ_i determines the ability of a species to connect habitat patches in a fragmented landscape.

Statistical models and data visualisation We tested for correlation between initialised and emerged β-diversity, which was however not the case (see section S9). Further, we used generalised additive mixed models (GAMM) from the mgcv package in R [26] to visualise the impact of number of patches and habitat isolation on species diversity. To fit the model assumptions, we logit-transformed $\overline{\alpha}$-diversity, and log-transformed β-diversity. We analysed each diversity index separately, with the number of patches Z (log-transformed), the mean patch distance $\overline{\tau}$ (log-transformed) and their interaction as fixed effects and the ID of the food web (1 - 30) as random factor (with normal distribution for $\overline{\alpha}$- and β-diversity, and binomial distribution for γ-diversity). Similarly, we analysed the mean biomass densities, $\overline{B}_{i,z}$ (log-transformed), and species-specific landscape connectance, ρ_i, for each species (ID 1 - 40) using GAMM with a normal distribution.

Analysis

Out of the 2160 simulations we started, 57 were terminated by reaching the maximum usage time of 10 days per simulation on the high-performance-cluster we used [24]. We further deleted 30 simulations as they had entirely isolated landscapes with no dispersal links. We performed all statistical analyses in R version 3.3.2. [27] using the output of the remaining 2073 simulations. See also section S8 for additional information.

Species diversity We quantified Whittaker's α-, β-, and γ-diversity [28] using presence-absence data derived from the recorded mean biomass densities, $\overline{B}_{i,z}$, counting species i present on patch z when $\overline{B}_{i,z} > 10^{-20}$. In Whittaker's approach, α accounts for the local species richness, β is the component of regional diversity that accumulates from compositional differences between local communities, and γ is the regional diversity, i.e. the species richness at the landscape scale [28]. We relate α, β and γ to each other using multiplicative partitioning [28], i.e. $\alpha \cdot \beta = \gamma$. Here, we use α averaged over all habitat patches Z (which we hereafter refer to as $\overline{\alpha}$) to get a measure at the landscape level comparable to β and γ.

S5 Maximum trophic level

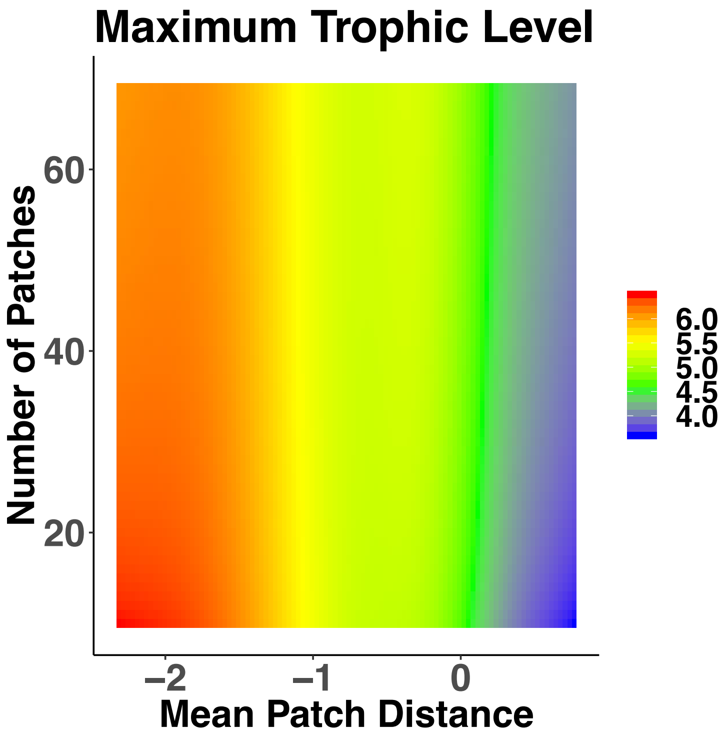

Figure S2: Heatmap visualising the maximum trophic level within a food web (colour-coded; z-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis) and the number of habitat patches (Z; y-axis). The heatmap was generated based on the statistical model predictions. The loss of species diversity driven by habitat isolation also translates into a loss of the maximum trophic level.

S6 Additional simulations with a constant maximum dispersal distance

We repeated all simulations with a constant maximum dispersal range for all species of $\delta_{const.} = 0.5$, i.e. all species have the same spatial network, to understand the effect of the dispersal advantage of larger animals. The results from these simulations are very similar to the results with the species-specific scaling of dispersal ranges, showing the same biomass density drop of larger animals at low mean distances (figure S3).

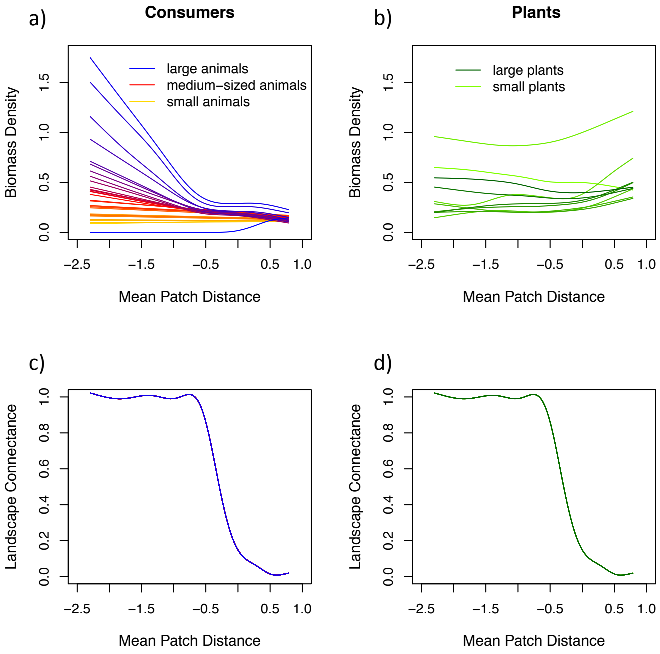

Figure S3: Top row: Mean biomass densities of consumer (a) and plant species (b) over all food webs (B_i, $\log_{10}$-transformed; y-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Each colour depicts the biomass density of species i averaged over all food webs: (a) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (b) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; y-axis) for consumer species (c) and plant species (d) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis), using the same maximum dispersal distance for all species, $\delta_{const} = 0.5$.

S7 Additional simulations of the two extreme cases

To explore the extreme cases of fragmentation in our model framework, we conducted additional simulations with emigration but no immigration on patches to represent completely isolated patches (disconnected), and landscapes with patches containing all species of the meta-food-web and neither emigration nor immigration to represent one joint landscape with no fragmentation (joint). For the disconnected scenario we simulated 12 replicates for each of the 30 food webs covering in the same stratified random gradient of patch numbers between 10 and 69 as in the main simulations and were also initialised with a subset of species (see section S4). For the joint scenario we simulated 20 replicates for each food web containing 2 independent patches initialised with all species and no dispersal.

(1) Joint scenario with no dispersal mortality $\overline{\alpha}$-diversity is on average 37.621, γ-diversity 37.172 and β-diversity 1.004 (figure S4, purple triangle).

(2) Fully isolated scenario with 100% dispersal mortality $\overline{\alpha}$-diversity is on average 11.945, γ-diversity 32.801 and β-diversity 2.876 (figure S4, orange triangle).

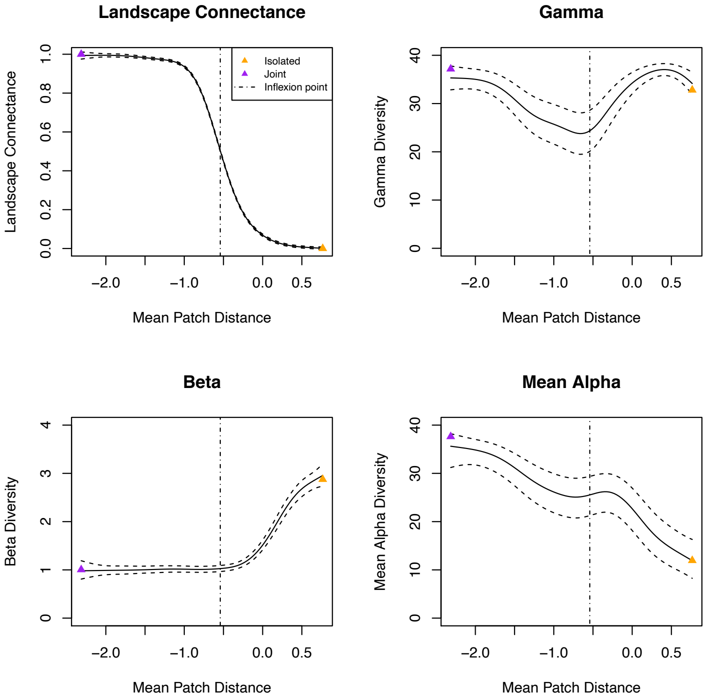

Figure S4: Shown are model predictions for landscapes with 40 patches across the whole gradient of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Top-left panel shows the landscape connectance averaged over all species (y-axis) as response to the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Subsequent panels show γ-diversity, β-diversity and $\overline{\alpha}$-diversity (y-axes) in response to the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Purple triangles represent reference points from dedicated simulations in a joint scenario and orange triangles for fully isolated scenarios (see section S7).

S8 Sensitivity analysis

We tested the effect of randomly drawn dispersal parameters (maximum dispersal rate, a, and the shape of the dispersal function, b; equation (3)) on $\overline{\alpha}$-, β- and γ-diversity for consumers and plants respectively. We used generalised additive mixed models (GAMM) from the mgcv package in R for all sensitivity analyses. To fit the model assumptions, we logit-transformed $\overline{\alpha}$-diversity, and log-transformed β- and γ-diversity.The emigration parameters were separately used as fixed effects and the ID of the food web (1 - 30) as random factor (with normal distribution for $\overline{\alpha}$- and β-diversity, and binomial distribution for γ-diversity). Both parameters show no strong effect in all tested cases (figure S5 - S7). Only the maximum emigration rate a of consumers shows a small negative effect on $\overline{\alpha}$-diversity (figure S5). As a higher maximum emigration rate results in an overall larger loss term due to dispersal, this fits to our general findings.

Additional sensitivity analysis for interference competition, allometric exponent for attack rates of consumer species, exponents for handling time, hill coefficient and nutrient turnover rate were omitted as they were tested thoroughly in Schneider *et al.* [1]. There, the dynamics of the food web model were shown to be robust to changes in model parameters. For each of the 2073 simulation runs the parameters of the trophic interactions were independently sampled from appropriate probability distributions within ecologically reasonable limits (see table 1). To account for the stochastic nature of the algorithm provided by Schneider *et al.* [1] by which food web topologies are created, we generated an ensemble of 30 food webs by randomly sampling 30 sets of species body masses.

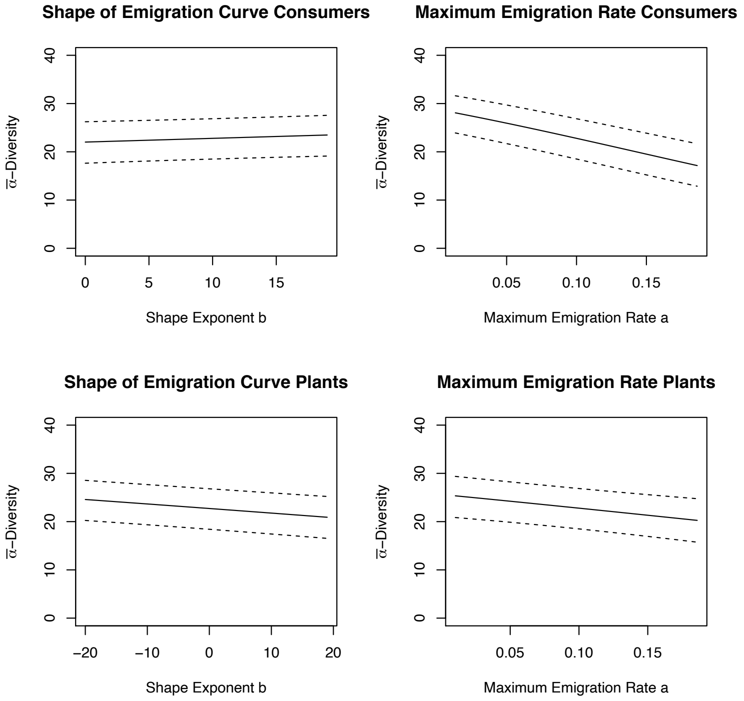

Figure S5: $\overline{\alpha}$-diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, *a*, and the shape of the emigration function, *b* respectively (x-axes).

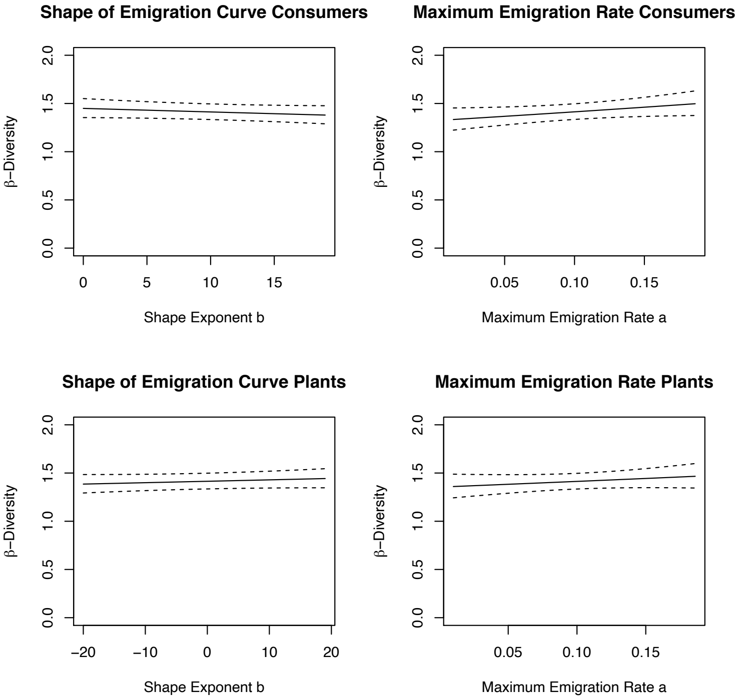

Figure S6: β-diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, *a*, and the shape of the emigration function, *b* respectively (x-axes).

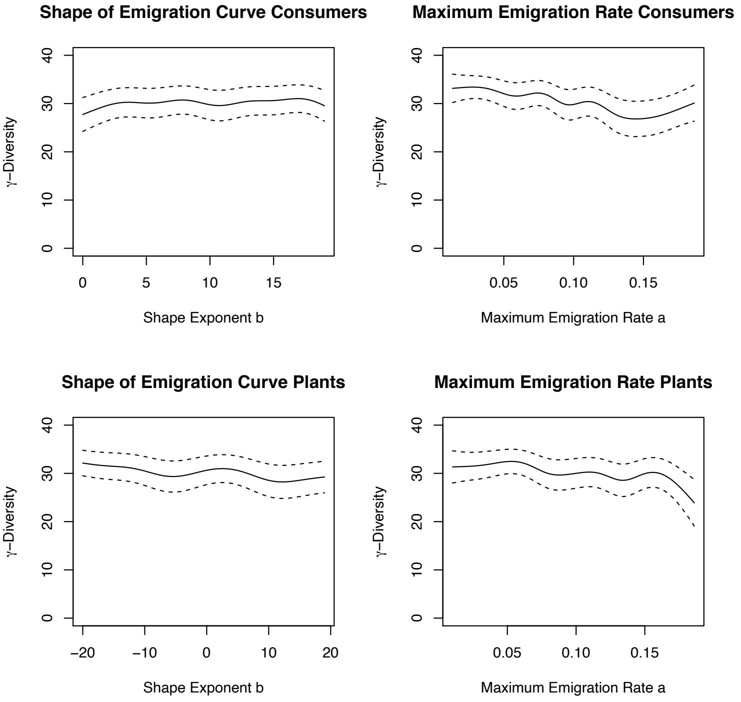

Figure S7: $\gamma-$diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, a, and the shape of the emigration function, b respectively (x-axes).

S9 Initial and post-simulation β-diversity

To see how the initialised β-diversity (see section S4) influenced the post-simulation β-diversity we performed a generalised additive mixed model (GAMM) from the mgcv package in R with the initial β-diversity as fixed effect and the post-simulation β-diversity as the response variable. Both were log-transformed to fit model assumptions. The post-simulation β-diversity and initial β-diversity were not correlated. This suggests that the initial β-diversity which is due to initialising the patches in the landscape with only a subset of species from the regional species pool does not

193 influence the post-simulation β-diversity detectably (approximate p-value: 0.518) (figure S8).

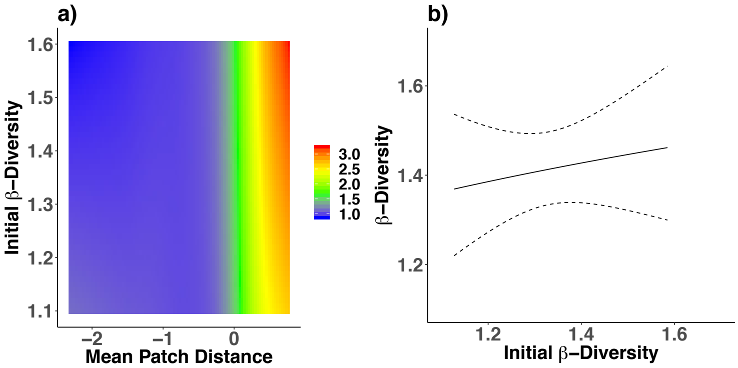

Figure S8: (a) Heatmap visualising β-diversity (colour-coded; z-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis) and the initial β-diversity (y-axis). The heatmap was generated based on the statistical model predictions. (b) The post-simulation β-diversity (y-axis) and the initial β-diversity (x-axis) were not correlated. In strongly isolated landscapes β-diversity increases slightly with higher initial β-diversity. However, post-simulation β-diversity is higher than the initial β-diversity.

S10 Standard errors in biomass densities

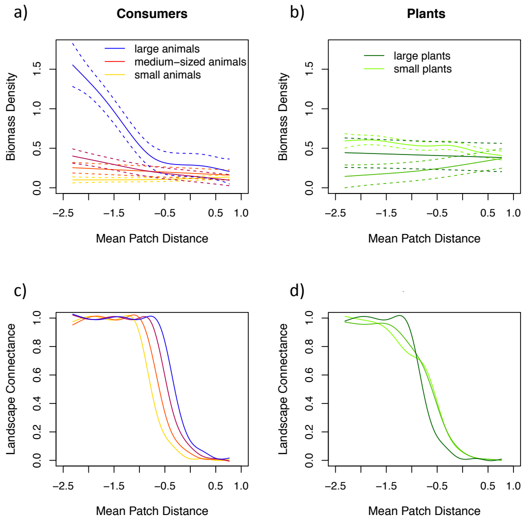

Figure S9: Top row: Mean biomass densities [$\log_{10}$(biomass density +1)] with standard errors [± 2*SE] for four exemplary animal consumer species (a) and three exemplary basal plant species (b) over all food webs (B_i, $\log_{10}$-transformed; y-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Each colour depicts the biomass density of species i averaged over all food webs: (a) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (b) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; y-axis) for consumer (c) and plant species (d) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis).

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Supplement Chapter 2

Supplement:

Landscape heterogeneity buffers biodiversity of meta food webs under global change through rescue and drainage effects

Remo Ryser, Myriam R. Hirt, Johanna Häussler, Björn C. Rall, Dominique Gravel, Ulrich Brose

Model

The model has been adapted from Ryser et al. 2019 (Ryser et al., 2019). The feeding links (i.e. who eats whom) are constant over all patches and are as well as the feeding dynamics determined by the allometric food web model by Schneider et al. 2016 (Schneider et al., 2016) We integrate dispersal as species-specific biomass flow between habitat patches. Using ordinary differential equations to describe the feeding and dispersal dynamics, the rate of change in biomass density $B_{i,z}$ of species *i* on patch *z* is given by

$$\frac{dB_{i,z}}{dt} = B_{i,z} \sum_j e_j F_{ij,z} - \sum_j B_{j,z} F_{ji,z} - x_i B_{i,z} - E_{i,z} + I_{i,z} \qquad \text{(for animals)} \qquad (1)$$

$$\frac{dB_{i,z}}{dt} = r_i G_i B_{i,z} - \sum_j B_{j,z} F_{ji,z} - x_i B_{i,z} \qquad \text{(for plants)} \qquad (2)$$

with the first three terms describing local trophic dynamics and the last two terms describing emigration, $E_{i,z}$ (equation 9), and immigration, $I_{i,z}$ (equation 11). For simplicity, we do not let plants disperse. Trophic dynamics are driven by following three processes. First, predation or herbivory on species *j* with assimilation efficiency *e* (e_j = 0.545, if *j* is a plant, typical for herbivory; e_j = 0.906 if *j* is an animal, typical for carnivory(Lang et al., 2017)) and the functional response $F_{ij,z}$ (equation 3) for animals, and a nutrient dependent growth (equation 7) for plants. Second, losses due to predation or herbivory respectively. Third, losses by metabolic demands with $x_i = x_A m^{-0.305}$ with scaling constant $x_A = 0.141$ (tenfold laboratory metabolic rate (Ehnes et al., 2011) at a temperature of 20° Celsius to represent field metabolic rates) for animals and $x_i = x_P m^{-0.25}$ with $x_P = 0.138$ for plants. We used a dynamic nutrient model (equation 8) as the energetic basis of our food web. Each species *i* is fully characterized by its average adult body mass m_i. Body masses determine the interaction strengths of feeding links as well as the metabolic demands of species. Data from empirical feeding interactions are used to parametrize the functions that characterize the optimal prey body mass and the location and width of the feeding niche of a predator (Schneider et al., 2016). From each m_i a unimodal attack kernel, called feeding efficiency L_{ij} is constructed which determines the probability of consumer species *i* to attack and capture an encountered resource species *j*. We model L_{ij} as an asymmetrical hump-shaped Ricker's function (equation 5) that is maximized for an energetically optimal resource body mass (optimal consumer-resource body mass ratio R_{opt} = 100) and has a width of γ. The maximum of the feeding efficiency L_{ij} equals 1. Table A2.TS1 is an overview of the standard parameter set for the equations. See also Schneider et al. 2016 (Schneider et al., 2016) for further information regarding the allometric food web model.

Functional response

$$F_{ij,z} = \frac{\omega_i b_{i,j} R_{j,z}^{1+q}}{1+cA_{i,z}+\omega_i \sum_k b_{ik} h_{ik} R_{k,z}^{1+q}} \cdot \frac{1}{m_i} \tag{3}$$

Per unit biomass feeding rate of consumer *i* as function of its own biomass density, A_i, (taking interference competition *c*, which is the time lost due to intraspecific encounters,), and biomass density of the resource R_j, with $b_{i,j}$, resource specific capture coefficient (equation 4); $h_{i,j}$, resource-specific handling time (equation 6); ω_i = 1/(number of resource species of *i*), relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.

Capture coefficient

$$b_{ij} = f a_k m_i^{\beta_i} m_j^{\beta_j} L_{ij} \tag{4}$$

Resource specific capture coefficient of consumer species *i* on resource species *j* scaling the feeding kernel L_{ij} by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed. We differentiate between carnivorous and herbivorous interactions with each comprising a constant scaling factor for their capture coefficients a_k with $k \in 0, 1$ (a_0 = 15 for carnivorous species and a_1 = 3500 for herbivorous species). For plant resources, $m^{\beta j}$ was replaced with the constant value of 1 (as plants do not move).

Feeding efficiency

$$L_{i,j} = \left(\frac{m_i}{m_j R_{opt}} e^{1-\frac{m_i}{m_j R_{opt}}}\right)^{\gamma} \tag{5}$$

The probability of consumer *i* to attack and capture an encountered resource *j* (which can be either plant or animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width γ centered around an optimal consumer-resource body mass ratio R_{opt} = 100 (Schneider et al., 2016).

Handling time

$$h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j} \tag{6}$$

The time consumer *i* needs to kill, ingest and digest resource species *j*, with scaling constant h_0 = 0.4 and allometric exponents η_i = −0.48 and η_j = −0.66.

Growth factor for plants

$$G_i = \frac{N}{K_i + N} \tag{7}$$

Species-specific growth factor of plants determined dynamically by the nutrient; with K_i, half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species *i* and (uniform distribution within (0.1, 0.2)). The term in the minimum operator approaches 1 for high nutrient concentrations.

Nutrient dynamics

$$\frac{dN_z}{dt} = D(S - N) - \sum\nolimits_{i,z} r_i G_i P_{i,z} \tag{8}$$

Rate of change of nutrient concentration *N* of nutrient on patch *z*, with global turnover rate *D* = 0.25, determining the rate at which nutrients are refreshed and the nutrient supply concentration *S*.

Generating landscapes

We generated different fragmented landscapes, represented by random geometric graphs, by randomly drawing the locations of Z patches from a uniform distribution between 0 and 1 for x- and y-coordinates respectively.

Dispersal

We model dispersal between local communities as a dynamic process of emigration and immigration, assuming dispersal to occur at the same timescale as the local population dynamics. Thus, biomass flows dynamically between local populations and the dispersal dynamics directly influence local population dynamics and vice versa. We model a hostile matrix between habitat patches that does not allow for feeding interactions to occur during dispersal. The total rate of emigration of animal species *i* from patch *z* is

$$E_{i,z} \; = d_{i,z}B_{i,z} \tag{9}$$

with $d_{i,z}$ as the corresponding per capita dispersal rate. We model $d_{i,z}$ as

$$d_{i,z} = \frac{a}{1+\mathrm{e}^{b(x_i - v_{i,z})}} \tag{10}$$

with *a*, the maximum dispersal rate, *b* = 10, a parameter determining the shape of the dispersal rate, x_i, the inflection point determined by the metabolic demands per unit biomass of species *i*, and $\upsilon_{i,z}$, the per capita net growth rate of species *i* on patch *z*. We chose to model $d_{i,z}$ as a function of each species' per capita net growth rate to account for emigration triggers such as resource availability, predation pressure and inter- and intraspecific competition. If for example an animal species' net growth is positive, there is no need for dispersal and emigration will be low. However, if the local environmental conditions deteriorate, the growing incentives to search for a better habitat increase the fraction of individuals emigrating.

Immigration

The rate of immigration of biomass density of species *i* into patch *z* follows

$$I_{i,z} = \sum\nolimits_{n \,\epsilon\, N_z} E_{i,n}(1 - \; \delta_{i,nz}) \frac{1-\; \delta_{i,nz}}{\sum_{m \,\epsilon\, N_n} 1-\; \delta_{i,nm}} \tag{11}$$

where N_z and N_n are the sets of all patches within the dispersal range of species *i* on patches *z* and *n*, respectively. In this equation, $E_{i,n}$ is the emigration rate of species *i* from patch n, $(1 - \delta_{i,nz})$ is the fraction of successfully dispersing biomass, i.e. the fraction of biomass not lost to the matrix, and $\delta_{i,nz}$ is the distance between patches n and z relative to species i's maximum dispersal distance δ_i (see below paragraph Maximum dispersal distance). The term $\frac{1-\; \delta_{i,nz}}{\sum_{m \,\epsilon\, N_n} 1-\; \delta_{i,nm}}$ determines the fraction of biomass of species *i* emigrating from source patch n towards target patch *z*. This fraction depends on the relative distance between the patches, $\delta_{i,nz}$, and the relative distances to all other potential target patches m of species *i* on the source patch *n*, $\delta_{i,nm}$. Thus, the flow of biomass is greatest between patches with small distances.

For numerical reasons, we did not allow for dispersal flows with $I_{i,z} < 10^{-10}$. In this case, we immediately set $I_{i,z}$ to 0. We assume that the maximum dispersal distance δ_i of animal species increases with their body mass. For animal species, the body mass m_i determines how far they can travel through the matrix. Thus, animal species at high trophic positions can disperse further than smaller animals at lower trophic levels. Each animal species perceives its own dispersal network dependent on its species-specific maximum dispersal distance

$$\delta_i = \delta_0 m_i^{\epsilon} \tag{12}$$

where the exponent $\varepsilon = 0.05$ determines the slope of the body mass scaling of δ_i. We chose a positive value for ε to account for a higher mobility of animals with larger body masses.

TS1: Table of parameters

Symbol	Parameter	Value
e_A	Conversion efficiency animal species	0.906
e_P	Conversion efficiency plant species	0.545
x_A exp	Scaling constant and exponent metabolic rate animal species	0.141 -0.305
x_P exp	Scaling constant and exponent metabolic rate plant species	0.138 -0.25
c	Interference competition	0
a_0	Scaling factor capture coefficient for carnivorous links	15
a_1	Scaling factor capture coefficient for herbivorous links	3500
β_i; β_j	Allometric exponent for encounter rates	Carnivorous: 0.42; 0.42 Herbivorous: 0.19; 1 (Hirt et al., 2017a)
R_{opt}	Optimal consumer-resource body mass ratio	100
γ	Exponent Ricker's function	Foodchain: 2 Foodweb: 6
h_0	scaling factor handling time	0.4
η_i η_j	Allometric exponent handling time (*i*: consumer, *j*: resource)	-0.48 -0.66 (Rall et al., 2012)
q	Hill coefficient	Foodchain: 1 Foodweb: 1.1
K	Half saturation density for nutrient uptake	Foodchain: 0.1 Foodweb: (0.1,0.2)
D	Nutrient turnover rate	0.25
S	Nutrient supply concentration	variable
d_{max}	Maximum dispersal distance	0.5
ε δ_0	Scaling factor and exponent for species-specific dispersal distance	0.05 0.1256
a_S	Maximal emigration rate	Variable (Fig2b main text), 0.05
b	Shape parameter of emigration function	10
f	Additional scaling factor for capture rates for stability	0.05

Results

Rescue effect

Increased dispersal loss (hostility) or the coupling with an oligotrophic patch (heterogeneity) essentially increases the strength of the drainage effect from the perspective of a eutrophic patch. However, while heterogeneity also increases the strength of the rescue effect from the perspective of an oligotrophic patch (Figure S1, left to right), dispersal loss decreases the strength of the rescue effect (Figure S1, bottom to top) except at high heterogeneity where the pattern is slightly more complex. Here (Figure S1, top-left), the weakened coupling with a eutrophic patch induces oscillations (see section on dynamical interference).

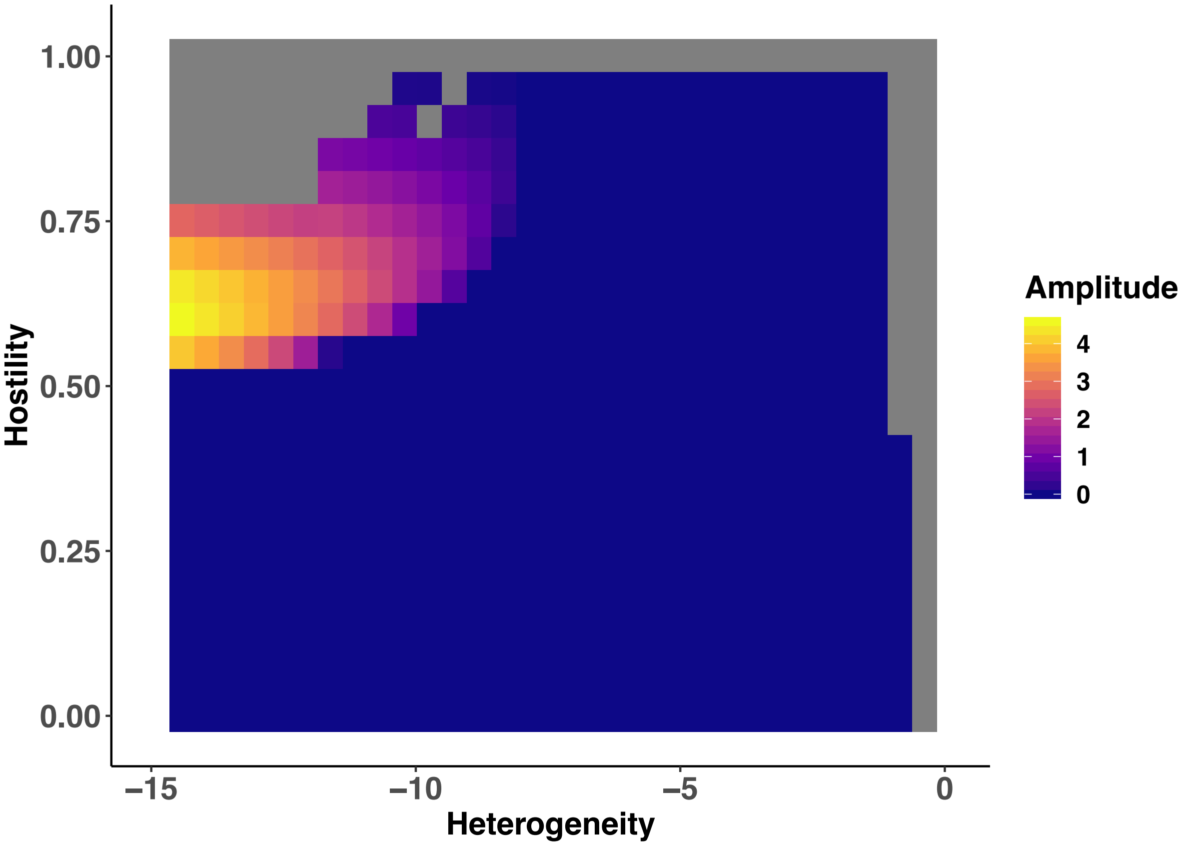
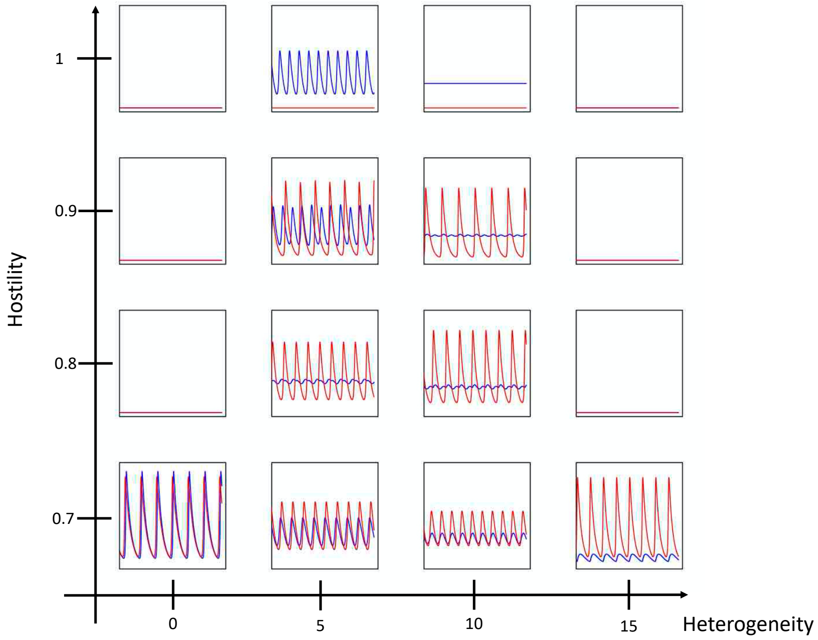


Figure S1: Rescue effect under different levels of landscape heterogeneity and hostility. Heat map showing the amplitude of biomass density oscillations in the predator (z-axis; colour coded) on the (always) oligotrophic patch across gradients of landscape heterogeneity (x-axis; difference in nutrient supply concentration between the two patches) and matrix hostility (y-axis). Amplitudes of 0 (blue) stand for an equilibrium state of the predator. Grey areas are where the predator went extinct.

Dynamical interference

When the hostility effect is very large, the coupling of the dynamics is weakened, which results in more chaotic oscillations as the frequencies get decoupled (Blasius et al., 2003). This in turn can lead to increased oscillations in the whole system that arise not from increased biomass fluxes but from dynamical interference (top quarter in Figure 3 and top-left corner in Figure S1). This suggests that there is a lower threshold in strength of spatial links where instability arises from causes beyond the drainage and rescue effect. This becomes apparent in the top four rows in Figure S2. As soon as the frequencies get decoupled, the reduction of amplitudes due do the drainage effect is overwritten and amplitudes increase again on the eutrophic patch (red).



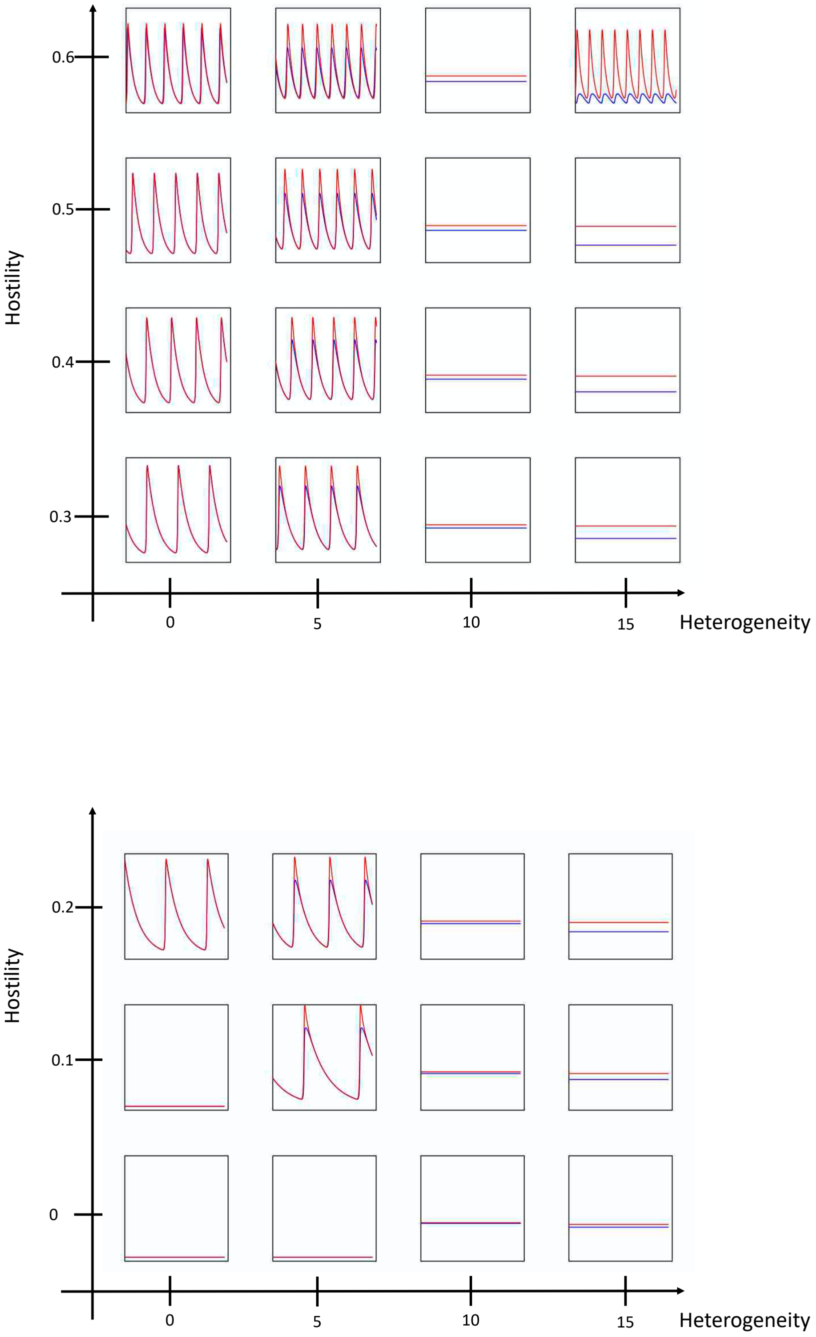


Figure S2: Predator population synchrony under different levels of landscape heterogeneity and hostility. Each plot represents biomass densities of the predator (y-axis) over time (x-axis) on the eutrophic patch (red) and on the variable patch (blue). Plots are arranged in a grid with the x-axis representing the landscape heterogeneity (delta nutrient supply of the eutrophic and the variable patch) and the y-axis representing the matrix hostility corresponding to Figure 3 in the main manuscript.

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Supplement Chapter 3

Supplement: Landscape configurations and trophic network structures interactively drive species-area relationships in meta food webs

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Modularity

The modularity of the initial food web (i.M) changes species-area-isolation relationships in all landscapes. Food webs that have a high modularity are less affected by patch area and isolation and generally show a lower persistence than food webs with low modularity (Figure S1). This could be due to lower probabilities of encountering a prey species on a different patch as consumers belonging to one module depend on having their module present.

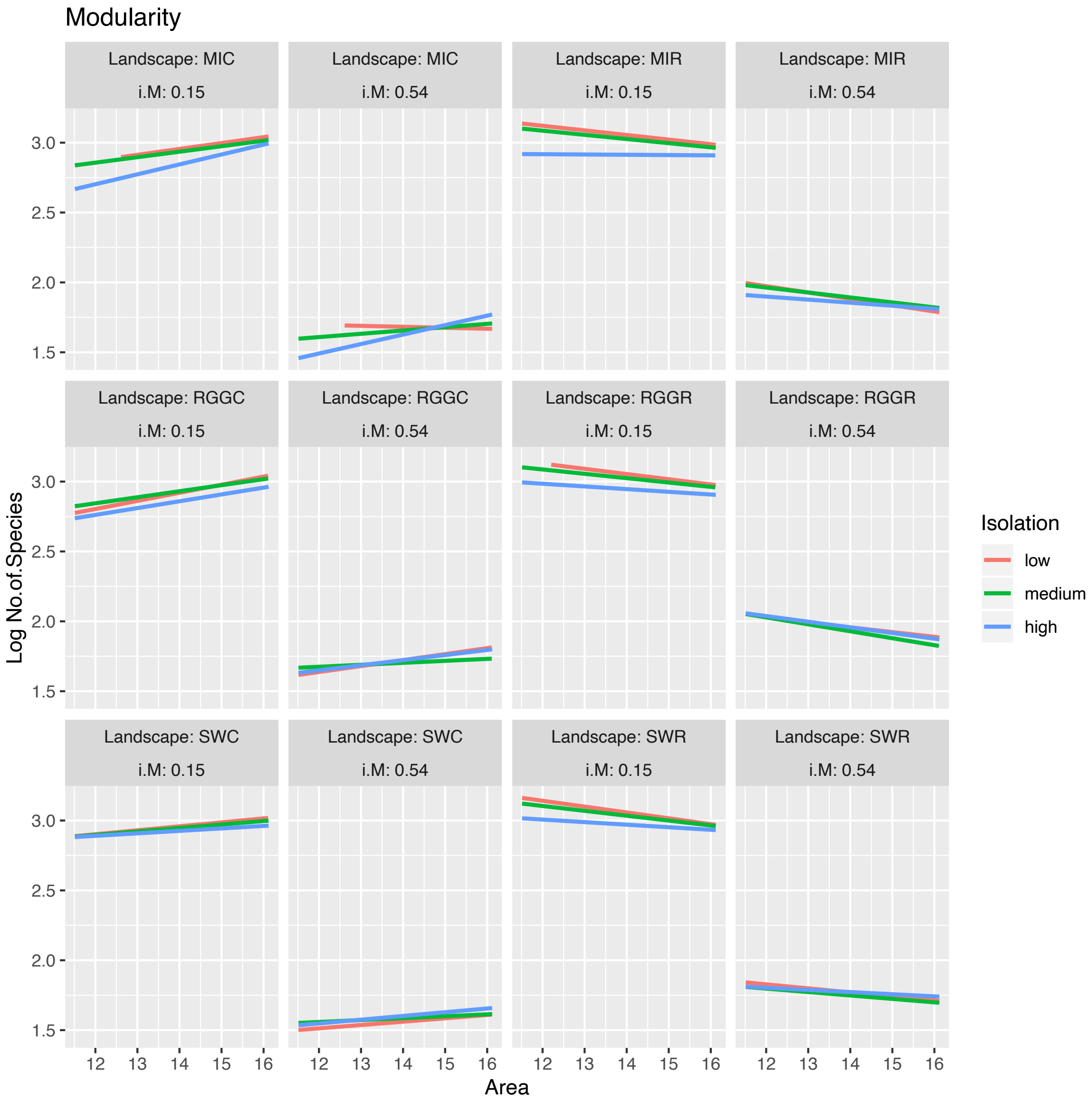

Figure S1: Food-web modularity modifies species-area relationships. Species-area-isolation relationships under different landscape configuration (left two columns: correlated patch size distribution, right two columns: random patch size distribution, rows: 1: Mainland-Island, 2: Random Graph, 3: Small-World; see Figure 3.1 in the main text) with low and high modularity of the initial food web (i.M).

Trophic Level

The maximal trophic level of the initial food web. (i.TL) also affects how strongly a food web reacts to patch area and isolation in the different landscapes (Figure S2). For landscapes in which the patch size distribution is correlated, the positive species-area relationship tends to be weakened or disappear for food webs that do not contain species of high trophic levels. It is precisely these species that are lost on small patches and suffer the most from isolation, thus, if they are not there from the beginning, this effect cannot arise. Similarly, in landscapes with random patch size distributions where we found negative species-area-relationships, food webs with a low maximum trophic level do not show this. As it is also in this case, that it is the species occupying higher trophic levels that drive the negative species-area relationships, this effect does not occur when these species are not there from the beginning.

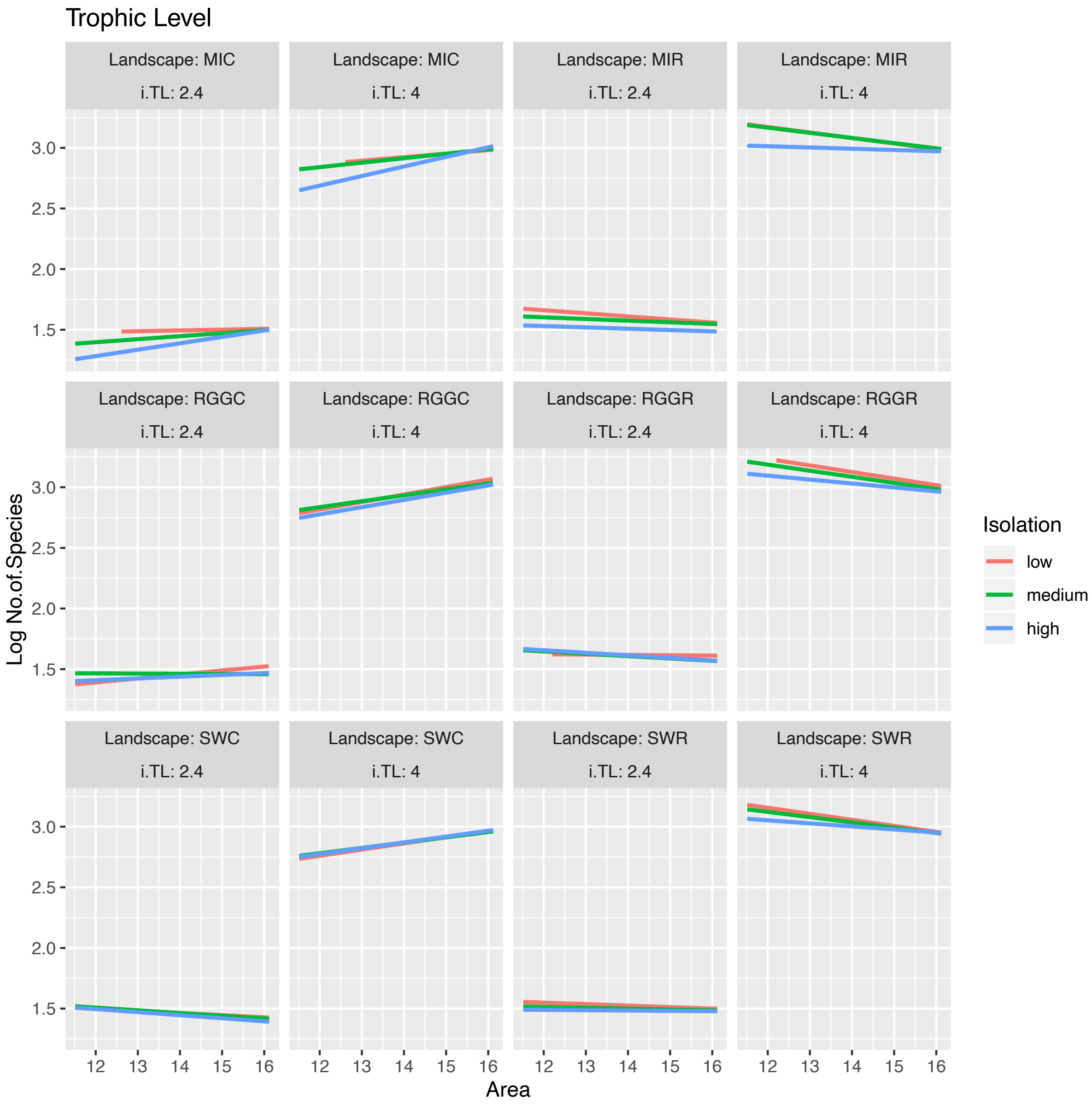

Figure S2: Maximum trophic level of food-webs change species-area relationships. Species-area-isolation relationships under different landscape configuration (left two columns: correlated patch size distribution, right two columns: random patch size distribution, rows: 1: Mainland-Island, 2: Random Graph, 3: Small-World; see Figure 3.1 in the main text) with low and high maximum trophic level of the initial food web (i.TL).

Table TS1: Slopes of species-area relationships in the different landscapes and under different isolation and in the null model, and 95% confidence interval.

landscape	isolation	slope	CI 2.5%	CI 97.5%
MIC	medium	0.0326759	0.02842044	0.03693135
MIC	high	0.06959087	0.0639753	0.07520643
MIC	low	0.0211429	0.01586693	0.02641887
MIR	medium	-0.0322681	-0.0360448	-0.0284914
MIR	high	-0.0104791	-0.0179546	-0.0030036
MIR	low	-0.03817	-0.0416827	-0.0346572
RGGC	medium	0.03075076	0.02577538	0.03572615
RGGC	high	0.04353735	0.03971272	0.04736198
RGGC	low	0.05143004	0.04442447	0.05843561
RGGR	medium	-0.0391027	-0.0440884	-0.0341171
RGGR	high	-0.02835	-0.032431	-0.024269
RGGR	low	-0.0358237	-0.044551	-0.0270967
SWC	medium	0.02006224	0.01467519	0.02544927
SWC	high	0.02155136	0.01471328	0.0283894
SWC	low	0.0264604	0.02161679	0.03130403
SWR	medium	-0.0304646	-0.0349375	-0.0259918
SWR	high	-0.017062	-0.0232033	-0.0109206
SWR	low	-0.0362151	-0.04039	-0.0320401
Null	Null	0.11575032	0.10930631	0.12219433

Food-web parameters

Table TS2: Food-web parameters. This table shows all food-web parameters depicted in Figure 3.4 and a short description.

parameter	abbreviation	description
species richness	i.S	Number of initial species
generality	i.G	Average number of prey (incoming trophic links) per species
sd generality	i.sdG	Standard deviation of generality across species
vulnerability	i.V	Average number of predators (outgoing trophic links) per species
sd vulnerability	i.sdV	Standard deviation of vulnerability across species
connectance	i.C	Number of links divided by the squared number of nodes (fraction of realised links out of all possible node to node connections)
sd linkedness	i.sdL	Standard deviation of outgoing and incoming trophic links per species
modularity	i.M	Strength of division of a network into clusters
mean trophic level	i.TLmean	Prey-averaged trophic level of all species
maximum trophic level	i.TL	Highest trophic level in the food web
sd trophic level	i.TLsd	Standard deviation of trophic levels across species

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Folgende Personen haben mich bei der Auswahl und Auswertung des Materials sowie bei der Herstellung der einzelnen Manuskripte unterstützt: Johanna Häussler, Markus Stark, Björn Rall, Christian Guill, Myriam Hirt, Benjamin Rosenbaum, Benoit Gauzens, Dominique Gravel, Jonathan Chase und Ulrich Brose.
Nähere Angaben sind den generellen Author Contributions sowie den jeweiligen Author Contributions der einzelnen Forschungskapitel zu entnehmen.

Diese Dissertation lag noch nicht als eine 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 hat.

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Leipzig, 27.05.2020