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

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Abstract

Habitat fragmentation is threatening global biodiversity. To date, there is only limited understanding of how habitat fragmentation or any alteration to the spatial structure of a landscape in general, affects 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 explore how habitat fragmentation, defined as a decrease of habitat availability and an increase of habitat isolation, affects the species diversity patterns of complex food webs (α-, β-, γ-diversity), and specifically test whether there is a trophic dependency in the effect of habitat fragmentation on species diversity. In our model, habitat isolation is the main driver causing species loss and diversity decline. Our results emphasise 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.

Keywords— Food webs, allometry, bioenergetic model, metacommunity dynamics, dispersal mortality, landscape structure

Introduction

Understanding the impact of habitat fragmentation on biodiversity is crucial for ecology and conservation biology [1–4]. 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 [5–7]. However, most conclusions regarding the effect of fragmentation are based on single species or competitively interacting species (see [8, 9] and references therein). There is thus limited understanding how species embedded in complex food webs with multiple trophic levels respond to habitat fragmentation [6, 10–13], even though these networks are a central organising theme in nature [14–16].

The stability of complex food webs is, amongst others, determined by the number and strength of trophic interactions [17]. While it is broadly recognised that habitat fragmentation can have substantial impacts on such feeding

relationships [18–20], we lack a comprehensive and mechanistic understanding of how the disruption or loss of these interactions will affect species persistence and food web stability [13, 18, 21, 22]. Assuming that a loss of habitat and the increasing isolation of the remaining habitat patches disrupt or weaken trophic interactions [9], thereby causing species extinctions [13, 19], 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 [23–25].

Successful dispersal between habitat patches might be able to prevent local extinctions (spatial rescue effects), and thus, ensure species persistence at the landscape scale [26, 27]. 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) [28]. With progressing habitat fragmentation, suitable habitat becomes scarce and the remaining habitat fragments increasingly isolated [4, 29, 30]. 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 [3]. Also, habitat fragmentation often increases the hostility of the habitat matrix, e.g. due to human land use and landscape degeneration [4, 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 [28, 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.

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, the loss of habitat connectivity, which characterises the ability of organisms to move across a fragmented landscape, prevents spatial rescue effects buffering against local extinctions. Decreasing habitat connectivity might therefore 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 [6, 35–38]. 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 habitat loss and habitat fragmentation [13, 39–43]. Using tri-trophic food chains on a patch-dynamic framework, Liao *et al.* [41, 44] for example, show that increasing habitat fragmentation leads to

faster extinctions of species at higher trophic levels. They ascribe this loss to constraints of resource availability for top species, whereas Davies *et al.* [43] attribute the observed loss of top species in their fragmentation experiment to the unstable population dynamics of top species under environmental change. In summary, the division and loss of suitable habitat are likely to reduce food chain length and result in unpredicted changes in the food web structure [39, 41].

To understand how habitat fragmentation affects the diversity of communities organised in complex food webs requires knowledge of the interplay between their local (trophic) and spatial (dispersal) dynamics. Despite its relevance, a realistic picture and comprehensive understanding of how natural food webs might respond to progressing habitat fragmentation and any alteration to the spatial configuration of habitat in general, are lacking. 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 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. Our model setup further allows us to disentangle the two key aspects of habitat fragmentation, habitat availability and habitat isolation, in ways not possible with empirical studies. Here, we ask how habitat availability and habitat isolation impact the diversity patterns in complex food webs and 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 habitat fragmentation. Based on the substantial variation in both dispersal abilities and energy requirements among species and across trophic levels [6, 43, 45], we expect species at different trophic levels to vary in their response to habitat fragmentation strongly. 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 fragmentation. We test our expectations using Whittaker's classical approach of α-, β-, and γ-diversity [46] - a commonly used measure to test for the effect of habitat fragmentation on species diversity at different scales. In this approach, α- and γ-diversity describe the species richness at the local and regional scale, respectively, and β-diversity accounts for differences in community composition between habitat patches.

Methods

Model

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.* [47]. We integrate dispersal as species-specific biomass flow between habitat patches (figure 1b,d). See the corresponding sections and the supplement for further information.

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 $T_{i,z}$ as the rate of change in biomass density determined by local feeding interactions (see the supplement, table S1), $E_{i,z}$ 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

Following the allometric food web model by Schneider *et al.* [47], 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 $\log_{10}$ body masses of plant species from the inclusive interval $(0, 6)$. 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. We use a nutrient model with two nutrients of different importance as the energetic basis of our food web [47, 48]. See the supplement and Schneider *et al.* [47] for further information regarding the allometric food web model and table S1 for the ordinary differential equations describing the local population dynamics.

Dispersal 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 [11]. Thus, biomass flows dynamically between local populations and the dispersal dynamics directly influence local population dynamics and vice versa [49]. 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 (see the supplement, figure S1), x_i, the inflection point determined by the metabolic demands per unit biomass of species i (for animals, $x_i = x_A m_i^{-0.25}$ with scaling constant $x_A = 0.314$ and for plants, $x_i = x_P m_i^{-0.25}$ with $x_P = 0.138$), 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 [49]. For each simulation run, a was sampled from a Gaussian distribution with mean $\mu = 0.1$, s.d. $\sigma = 0.03$, and cut off $\theta = 3 \cdot \sigma$; b was sampled from an integer uniform distribution within the inclusive limits $\mu_C = (0, 19)$ for consumer species and $\mu_P = (-20, 19)$ for plant species. The different intervals reflect different dispersal triggers for animals and plants. See the supplement, section S3 for the underlying assumptions for animal and plant dispersal.

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). 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.

Based on empirical observations (e.g. [37]) and previous theoretical frameworks (e.g. [6, 10, 34, 50]), we assume that the maximum dispersal distance δ_i of animal species increases with their body mass. Thus large-bodied animal species at high trophic positions can disperse further than smaller animals at lower trophic levels. As plants are passive dispersers, we model their maximum dispersal distance as random and body mass independent. For both plant and animal species, we set the highest possible maximum dispersal distance to $\delta_{max} = 0.5$. Additionally, we tested a null model in which all species have the same maximum dispersal distance of $\delta_i = \delta_{max}$. See the supplement, sections S4 and S6 for further information on the maximum dispersal distance and the additional simulations, respectively.

Numerical simulations

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 habitat availability 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 the supplement, section S2 for further information). With this approach, we generated landscapes with different degrees of fragmentation which we then related to each other, i.e. larger landscapes with fewer patches have larger mean patch distances, and are thus more isolated than smaller landscapes with more habitat patches (figure 1c). 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. 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% (see the supplement, section S7 for further information).

For each simulation run, we initialised our model with random conditions, provided that the full food web of 40 species exists in the regional species pool. In the initial setup, each habitat patch z holds a random selection of 21 to 40 species. We initialised each local population with a biomass density $B_{i,z}$, which we randomly sampled with uniform probability density within the interval $(0, 10)$. Nutrient concentrations N_l ($l \in 1, 2$) were initialised with random values uniformly distributed between $S_l/2$ and S_l, with S_l as the supply concentration of nutrient l. Supply concentrations S_l are drawn from normal distributions with mean $\mu_S = 10$ and s.d. $\sigma_S = 2$, provided that $S_l > 0$, and can differ between nutrients but are, for each nutrient, constant on all habitat patches. See the supplement, table S1 and Schneider *et al.* [47] for further information on the nutrient dynamics.

Starting from these random initial conditions, we numerically simulated local food web and dispersal dynamics over 250,000 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} [51, 52]). 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 parameters

We recorded the following output parameters 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 to capture oscillations, $\overline{B}_{i,z}$; (2) habitat availability, i.e. the number of habitat patches in a landscape, Z; (3) habitat isolation, i.e. the mean distance between all habitat patches, $\overline{\tau} = \frac{\sum_{n,m=1}^{Z} \tau_{nm}}{Z^2 - Z}$, where τ_{nm} is the absolute distance between patches n and m, and the denominator, $(Z^2 - Z)$, is the total number of potential directed links between all Z habitat patches; and (4) the landscape connectance of each species i, $\rho_i = \frac{L_i}{Z^2 - Z}$, with L_i, the number of directed dispersal links of species i. Thus, ρ_i determines the species-specific habitat fragmentation, i.e. the ability of a species to connect habitat patches in a fragmented landscape.

Analysis

Out of the 2160 simulations we started, 374 were terminated by reaching the maximum usage time of the high-performance-cluster we used [53]. We further deleted 31 simulations as they had entirely isolated landscapes. We

performed all statistical analyses in R version 3.3.2. [54] using the output of the remaining 1755 simulations, except for the analysis of β-diversity in which we excluded 111 additional simulations as all species went extinct, and thus these simulations could not be used to calculate β-diversity.

Species diversity We quantified Whittaker's α-, β-, and γ-diversity [46] using presence-absence data derived from the recorded mean biomass densities, $\overline{B}_{i,z}$, counting species i present on patch z when $\overline{B}_{i,z} > 10^{-8}$. 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 [46]. We relate α, β and γ to each other using multiplicative partitioning [46], i.e. $\alpha \cdot \beta = \gamma$, and thus, $\beta = \frac{\gamma}{\alpha}$. 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.

Statistical models We tested for correlation between initialised and emerged β-diversity, which was however not the case (see the supplement, section S9). Further, we used generalised additive mixed models (GAMM) from the mgcv package in R [55] to investigate the impact of habitat availability and habitat isolation on species diversity. To fit the model assumptions, we logit-transformed $\overline{\alpha}$-diversity, and log-transformed β- and γ-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. We used the mean patch distance, $\overline{\tau}$, as fixed effect and the food web ID (1 - 30) as random effect.

Results

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 in landscapes in which habitats are highly isolated. This species decline applies both to the averaged local diversity, $\overline{\alpha}$, and regional diversity, γ (figure 2, left and right panel, respectively). Habitat availability (the number of habitat patches in a landscape, Z, figure 2, y-axis)

only marginally affected this pattern. Contrary to the simple decrease of $\overline{\alpha}$- and γ-diversity with increasing habitat isolation, β-diversity (figure 2, middle panel), which describes differences in the community composition between patches, shows a more complicated pattern. The most prominent feature is a local maximum of β around $\log_{10}\overline{\tau} \approx 0.25$, which becomes more pronounced with more patches Z. When approximating the two extreme cases (i.e. landscapes with no dispersal mortality, $\log_{10}\overline{\tau} < -2$, and fully isolated landscapes with a 100% dispersal mortality, $\log_{10}\overline{\tau} > 1$), β-diversity declines towards lower values approaching 1. The additional simulations of the two extreme cases that we performed support this pattern. In both cases, β-diversity is approximately 1, i.e. all patches within the landscape have the same or a very similar community composition (see the supplement, 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 characterised by reduced food webs with fewer species and fewer trophic levels (see the supplement, figure S2).

Differences among trophic levels

As the number of patches only marginally affects 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. 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 have higher population biomass densities than smaller consumers (figure 3a,c). This pattern is reversed if habitat isolation increases. With expanding distances between habitat patches, large-bodied consumers at high trophic positions (figure 3a, red to blue lines) show a particularly strong decrease in population biomass densities. Small consumer species (figure 3a, orange to yellow lines) and basal plant species (figure 3b) on the other hand, are generally less affected by increasing habitat isolation, with only a minor decrease of their biomass densities over the full gradient of habitat isolation. 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 3c). Despite this dispersal advantage, intermediate-sized and large animal species (figure 3a, red to blue lines) lose biomass in landscapes in which they still have the potential to fully connect (almost) all habitat patches (figure 3c). In our simulations, the smallest plant species has the overall highest population biomass averaged over all food webs,

which is due to a minor bias of the allometric food web model in the assignment of consumers that favours plant species at the lower end of the body mass axis [47]. This pattern holds across all landscapes independent of habitat isolation. Biomass densities of large plant species (figure 3b, dark green lines) show a stronger response to habitat isolation than those of small plant species. This body mass dependent response to habitat isolation among plant species cannot be attributed to 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 (figure 3d). 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 supplement, figure S3).

Discussion

Habitat fragmentation is a major driver of global biodiversity decline, but to date, a comprehensive understanding of how fragmentation affects the diversity patterns of species embedded in complex ecological networks such as food webs is lacking [8, 13, 41]. In our simulation experiment we disentangle habitat fragmentation into habitat availability and habitat isolation. 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 fragmentation 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 at the verge of extinction 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: as habitat fragmentation progresses an increasing fraction of the biomass production of the lower trophic levels is lost due to mortality during dispersal and is thus no longer available to support the higher trophic levels. Our model adds a complementary perspective to previous research pointing towards a trophic-dependent extinction risk due to constraints in resource availability with increasing habitat fragmentation [41, 42].

Habitat isolation drives species loss The increasing isolation of habitat fragments poses a severe threat to species persistence. We demonstrate in our simulation experiment that the generally observed pattern of species loss with

increasing habitat isolation 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. In contrast to our expectations and previous research (see for instance Melian & Bascompte [8]), the observed diversity patterns were only marginally affected by the amount of available habitat in a landscape.

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 [4]. 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 fragmentation the larger a species is. Despite this, top predators and other large consumer species respond strongly to habitat 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 fragmentation is mediated by indirect effects originating from the local food web dynamics.

Local food web dynamics and energy limitation drive top predator loss To understand this finding, we need to consider the basic fact that in the 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% [56]. This energy limitation effectively controls the food chain length [57] and renders large species at high trophic levels vulnerable to extinction due to resource shortage [58]. Considering the way we modelled habitat fragmentation, energy availability decreases if habitat availability is low (fewer patches per total area) and habitat isolation is high (extended distances between habitat patches increase biomass loss during dispersal). The latter affects particularly small species at lower trophic levels as they generally have the highest metabolic costs per unit biomass and therefore the highest biomass losses per distance travelled [33, 47]. This 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, due 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, 59, 60] – 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 fragmentation progresses. We attribute this paradoxical finding to a release from top-down control as their consumers lose biomass and eventually go extinct, which counters the negative direct effect of habitat fragmentation. These arguments suggest that species-specific maximum dispersal distances 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 had the same maximum dispersal distance (and thus experienced the same level of dispersal mortality), which yielded similar results (see the supplement, figure S3).

We did not find a strong effect of habitat availability on $\overline{\alpha}$- and γ-diversity, even though it is also directly connected to the total energy availability of the meta-food-web. For plant and small animal species this can be understood easily, as these species are always able to persist even 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 density of their resources (and thus also the realised 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.

Spatial heterogeneity promotes β-diversity Apart from the decline of both $\overline{\alpha}$- and γ-diversity with increasing habitat isolation, one striking feature of our simulation results is the conspicuous peak of β-diversity around $\log_{10}$ mean patch distance $\overline{\tau} \approx 0.25$, on top of the overall trends of a decline in β-diversity with increasing mean patch distance and an increase with habitat availability (number of patches, Z). We suppose that this peak is related to a maximum in effective spatial heterogeneity of habitat that appears when the average distance between patches is large, but not so extreme that the patches are completely isolated.

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 structure of the dispersal network. One way for such different conditions to emerge is the disintegration of the dispersal network into several smaller clusters, what appears to happen right before β-diversity reaches its maximum. 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 of at least 0.5. This dispersal advantage easily allows them to connect all patches to a single network component, thereby providing some homogenisation for the meta-food-web. However, as the mean patch distance increases further up to $\log_{10} \overline{\tau} \approx 0.25$, 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 size and mean patch distance within the cluster, the level of dispersal mortality experienced by the species on the different clusters can also vary considerably. Given that in our simulations dispersal mortality is a key factor determining species persistence and diversity, this might explain the observed increase in β-diversity. Any further increase in mean patch distance beyond $\log_{10} \overline{\tau} = 0.25$ causes the landscape connectance to drop to nearly zero for all species and the average cluster size approaches one. At this point, all clusters are from a network point of view trivially identical and β-diversity declines again.

By contrast, communities in landscapes with either no dispersal mortality (i.e. all pathces are direct neighbours) or dispersal mortality of a 100% (i.e. fully isolated patches), showed no β-diversity (see the supplement, section S7), suggesting that in such extreme cases local food web dynamics conserve similar communities. Given current land use practices, these findings point towards a high risk of biotic homogenisation in fragmented landscapes, in which the remaining habitat fragments often have the same or very similar environmental conditions.

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 [47] with a fixed number of 40 species – a typical value in dynamic food web modelling (e.g. [61, 62]). We based all model parameters on allometric principles [33, 63] allowing for a simple adaptation of our modelling approach to other trophic networks such as empirically sampled food webs [64] or other food web models such as the niche model [65]. Moreover, empirical patch networks (e.g. the coordinates of meadows in a forest landscape) or other dispersal mechanisms [8, 66] 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 [67, 68] 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.

Synthesis and outlook

Our simulation experiment demonstrates that fragmentation reduces species diversity in complex food webs in general, with differences in the effect across trophic levels. In increasingly fragmented landscapes, energy becomes limited, which prevents large consumers from persisting. These primary extinctions may result in a cascade of secondary extinctions, given the importance of top predators for food web stability [25, 69]. The increased risk of network downsizing, i.e. simple food webs with fewer and smaller species [12, 70], 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, conservation strategies are mostly designed based on single species or competitive interactions and do not consider the complex network of interactions in natural communities [12]. However, the patterns we presented here clearly support previous studies (e.g. [39, 41, 42]) and 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 stabilise food webs [25, 69], the loss of top predators might entail unpredictable consequences for adjacent trophic levels, destabilise food webs, reduce species diversity and trophic complexity and ultimately compromise ecosystem functioning [23, 25, 71]. Our results suggest that bottom-up energy limitation due to habitat isolation is the critical factor driving species loss and the reduction of trophic complexity. The extent of this loss strongly depends on the spatial context (see also [8]). Our results further emphasise that in fragmented landscapes a strategically planned spatial configuration of habitats can potentially foster β-diversity, and thus, mitigate the risk of biotic homogenisation, which poses a severe threat to biodiversity in human-dominated landscapes [72]. 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 focus on decreasing 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. Therefore, 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.

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Author contributions

All authors conceived and designed the modelling framework; JH and RR ran the simulations on the high-performance-cluster; RR analysed the data with support from all other authors; all authors contributed to interpreting the results; JH wrote the first draft of the manuscript with support from RR and MS and led the editing. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Upon acceptance, we will upload the corresponding C- and R-code to an online repository (e.g. Dryad).

Competing interests

The authors declare no competing interests.

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List of Figures

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 habitat fragmentation by manipulating the patch number and the mean distance between habitat patches (c). 22

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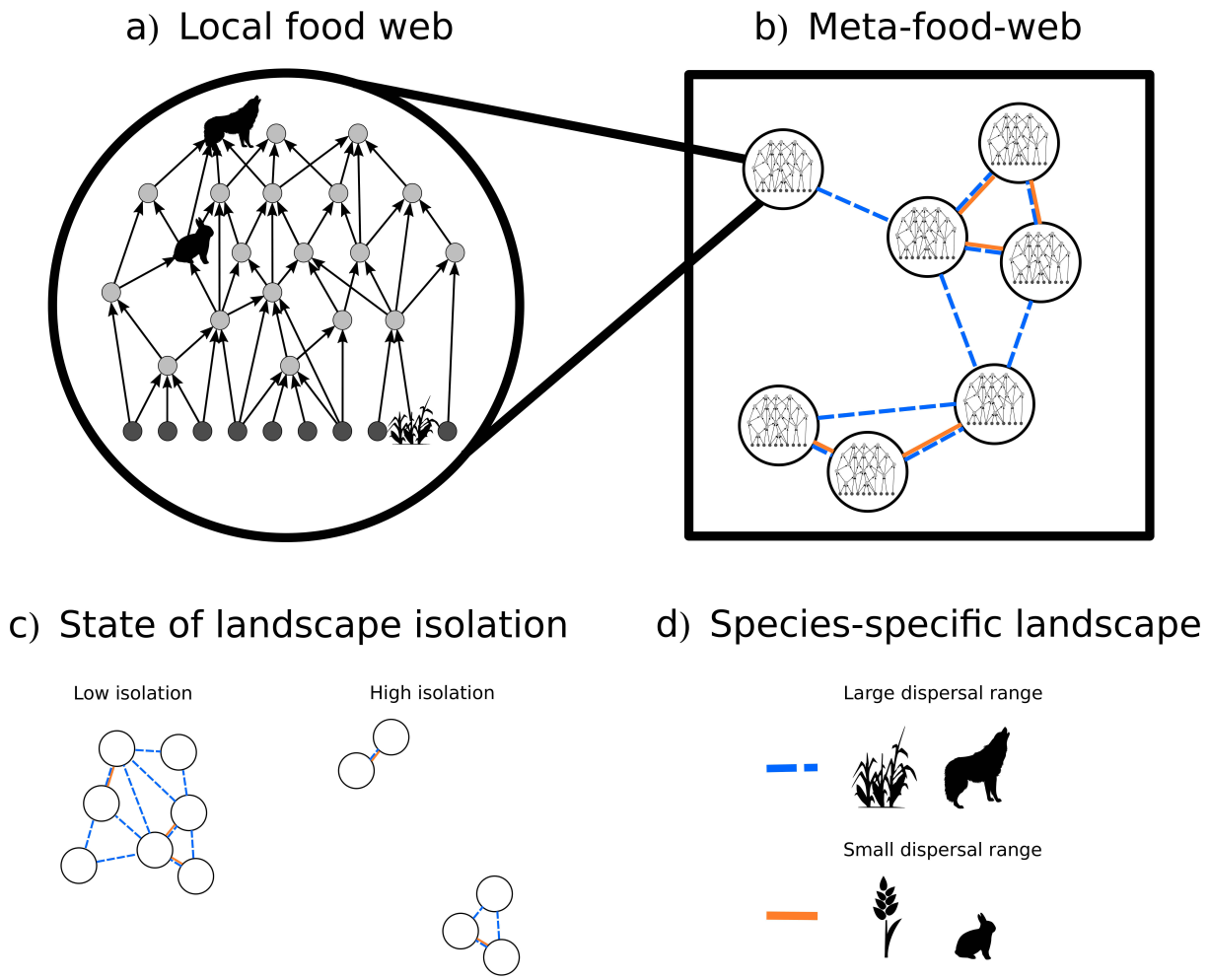

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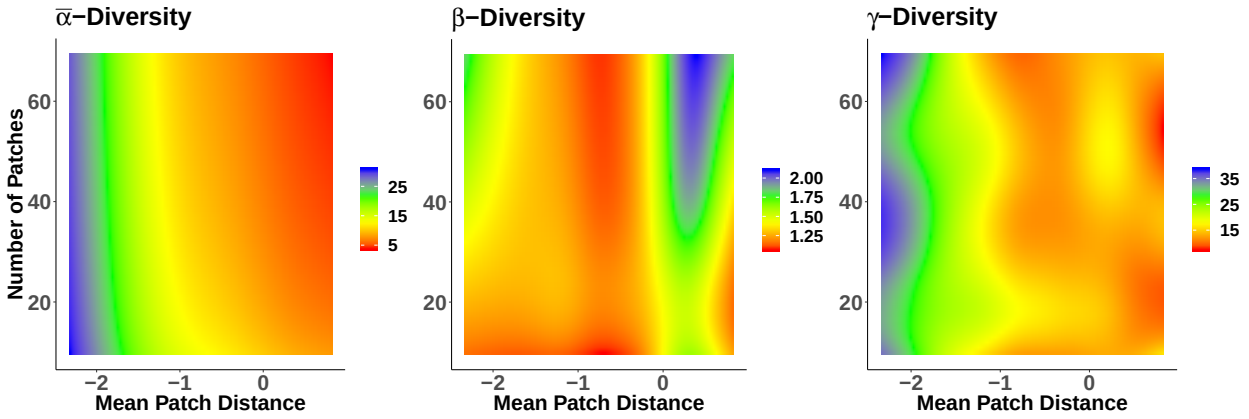

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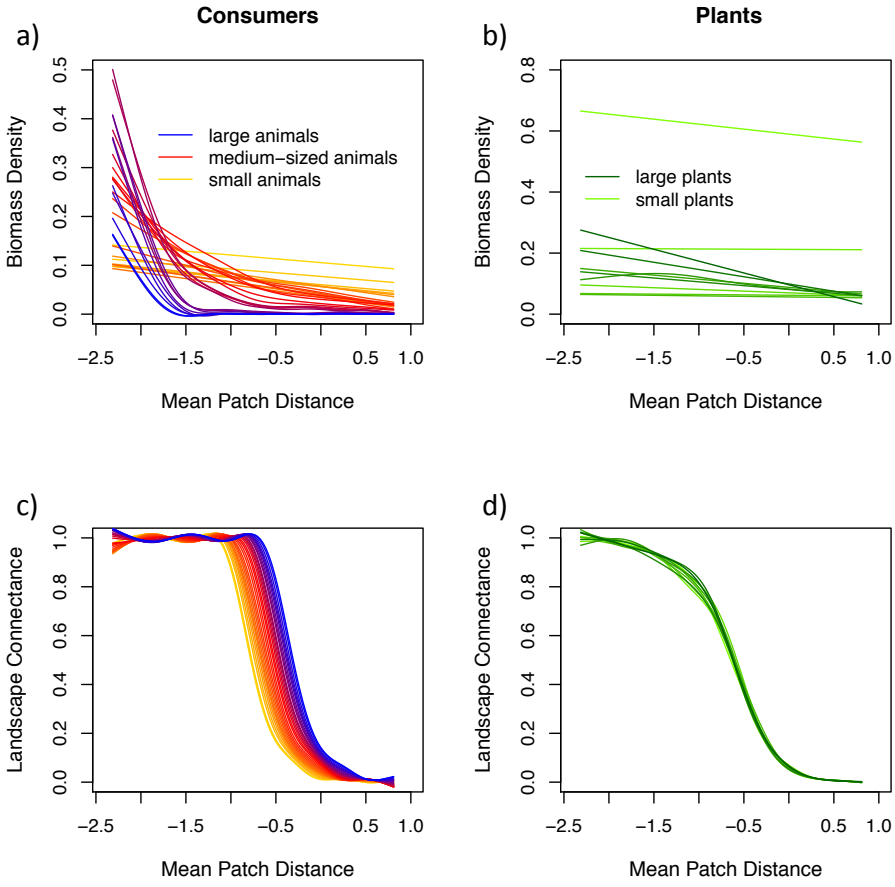

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