# Food web persistence in fragmented landscapes

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# Food web persistence in fragmented landscapes

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# Abstract

Habitat destruction, characterized by patch loss and fragmentation, is a key driver of biodiversity loss. There has been some progress in the theory of spatial food webs, however to date practically nothing is known about how patch configurational fragmentation influences multi-trophic food web dynamics. We develop a spatially extended patch-dynamic model for different food webs by linking patch connectivity with trophic-dependent dispersal (i.e. higher trophic levels displaying longer-range dispersal). Using this model, we find that species display different sensitivities to patch loss and fragmentation, depending on their trophic position and the overall food web structure. Relative to other food webs, omnivory structure significantly increases system robustness to habitat destruction, as feeding on different trophic levels increases the omnivore's persistence. Additionally, in food webs with a dispersal-competition tradeoff between species, intermediate levels of habitat destruction can enhance biodiversity by creating refuges for the weaker competitor. This demonstrates that maximizing patch connectivity is not always effective for biodiversity maintenance, as in food webs containing indirect competition doing so may lead to further species loss.

**Keywords**: food webs, species dispersal, patch fragmentation, competition-dispersal tradeoff, patch-dynamic model.

# Introduction

Ecological communities across the world are under threat from ongoing habitat destruction, a leading driver of biodiversity loss [1]. Resulting from land use change, pollution, over-exploitation and climate change, habitat destruction can be characterized into two components: patch loss and patch fragmentation [2]. The first, patch loss, is simply a decrease in the total habitable area, which naturally reduces population sizes and thus increases the probability of species extinction. The latter, patch fragmentation, is the division of the habitable area into disconnected or poorly connected sub-patches [3], which is also known to increase species extinction risk, as the resulting sub-patches are smaller and the sub-populations inhabiting them are more isolated [2-5]. Drivers of patch fragmentation also include natural barriers (e.g. rivers and deserts) as well as anthropogenic barriers (e.g. roads, dams, and fences) [6-8].

While it is clear that ecological communities are damaged by habitat destruction, its precise impact on a community is much harder to predict. There has been extensive research, encompassing both empirical and theoretical studies, into the separate effects of patch loss and fragmentation [2-5,9,10], while studies on their interactive effects are relatively rare. Additionally, it is readily apparent that the effects of fragmentation on a given species strongly depend on its dispersal ability [2,11-16]. In particular, species with greater dispersal capability are less affected by patch fragmentation, as greater dispersal range allows wider barriers to be bypassed, directly counteracting the effects of fragmentation [17]. Furthermore, the interactions between species in a given community can be a key determinant for the effects of habitat destruction [1,18-22]. It has often been found that species at higher trophic levels are the first to go extinct undergoing habitat loss [23-26], in accordance with the trophic rank hypothesis [27]. But omnivorous species do not necessarily follow this paradigm [28,29] and indirect interactions between species in lower trophic levels, such as exploitative or apparent competition, may also modify the sensitivity of their predators to habitat destruction [29-32].

To get insights into trophically-linked communities in fragmented landscapes, further theoretical study should address all of these factors: patch loss and fragmentation, variation in species dispersal characteristics, and the trophic structure. Pillai *et al.* [31] developed a modelling framework for complex food web structures to describe the patch dynamics of the various trophic links instead of individual species. However, their framework is spatially implicit, in which any species can access to any habitat patch with prey species. Habitat destruction creates spatial fragmented landscapes for which this spatially implicit framework is insufficient. Hiebeler [11] has already characterized such landscapes in terms of the densities of two habitat types (suitable and unsuitable) and their clumping degrees, thus allowing the effects of habitat loss and habitat fragmentation to be investigated separately by using a pair approximation approach [33-37]. In addition, Liao *et al.* [12,13,38] used this approach to explore how a species dispersal capability affects its survival in landscapes subject to habitat destruction. Thus, there exist modelling techniques to fully describe the effects of landscape fragmentation on complex trophically-linked communities, yet very few studies have done so to date.

In this study we develop a spatially extended patch-dynamic model for different food webs in fragmented landscapes, based on the existing modelling frameworks of Pillai *et al.* [31]. Since it is not feasible to consider the full diversity of possible food web structure, we restrict our attention to four common trophic modules consisting of three species: a simple food chain, omnivory, exploitative competition, and apparent competition (figure 1). These typical modules describe the most important interaction types among species and form a basis for studying more complex food webs. In addition, we assign species dispersal ranges to reflect the common observation that a species' dispersal range increases with its trophic level [39-42]. Using this model, we first investigate how patch loss and fragmentation separately and interactively affect the persistence of species embedded in each of these trophic structures, and then explore whether species feeding preference/pressure can modify the effects of landscape fragmentation on community patterns.

# Methods

### *Landscape structure*

We model the landscape as an infinite lattice of cells (i.e. sites), each representing a patch that can be either empty or occupied by a specific set of trophically linked species. To introduce habitat destruction, we assume the landscape consists of two types of habitat patch: suitable ($s$) and unsuitable ($u$), where only $s$-patches ($s$ – patch availability) can permit species colonization, while $u$-patches ($u$ – patch loss) are unsuitable for any species establishment ($s+u=1$). According to Hiebeler [11], the clustering degree of a given patch (for example $s$) can be characterized by the local density $q_{s/s}$ (so-called patch connectivity), representing the conditional probability that the neighbour of a randomly chosen $s$-patch is also an $s$-patch, with $q_{s/s} = \rho_{ss} / \rho_s$. The pair density $\rho_{ss}$ denotes the probability that a randomly chosen pair of neighbouring patches are both $s$-patches. Thus, the fragmentation degree of $s$-patches is inversely related to the clustering degree, defined as 1- $q_{s/s}$. According to the orthogonal neighbouring correlation method for landscape generation (using von Neumann neighbourhood; see details in Hiebeler [11,43]), we have

$$2-1/s < q_{s/s} < 1. \qquad (1)$$

In particular, the suitable patches are randomly distributed at $s = q_{s/s}$.

### *Coupling dispersal range to trophic level*

We consider four trophic modules containing three species (species 1, 2 and 3; illustrated in figure 1): a simple food chain (basal species 1✂✍intermediate consumer 2✂✍top predator 3), a food web with an omnivorous top predator (omnivory), two competing species feeding on one prey species (exploitative competition), and one species feeding on two competing prey species (apparent competition). To reflect the fact that species dispersal range increases with trophic level/body size (as commonly observed in [39-42]), we assign each species a different dispersal mode: (i) species 1 can only colonize the neighbouring *s*-patches (neighbour dispersal; using von Neumann neighbourhood with $z$=4); (ii) species 2 has uniform probability to colonize any *s*-patch within a habitat fragment (so-called patch cluster that consists of a group of connected patches; within fragment dispersal), thus species 2's dispersal range is highly correlated with patch connectivity; (iii) species 3 has uniform probability to colonize any *s*-patch in the landscape (global dispersal). As such, the *u*-patches as barriers (e.g. rivers, roads, dams and fences) can only limit the dispersal of species 1 and 2, while the spread of species 3 is not affected. Therefore, we can describe the dynamics of: (i) species 1 with a pair approximation (PA) model, which has already proven qualitatively useful in characterizing spatial correlation between neighbours in lattice-structured landscapes [11-13,33-38,43-47]; (ii) species 2 with a modified mean-field approximation (MFA) incorporating patch clustering degree $q_{s/s}$ (as demonstrated in [38]); and (iii) species 3 with a MFA model [31].

Following Liao *et al.* [38], we can describe the patch dynamics of a simple food chain subject to the colonization-extinction-predation processes (models for other trophic modules shown in appendix A, electronic supplementary material)

$$\frac{d\rho_1}{dt} = \underbrace{c_1(\rho_1 - \rho_{1u} - \rho_{11})}_{\text{Neighbour dispersal}} \underbrace{-e_1\rho_1}_{\text{Extinction}} \underbrace{-\mu_{21}\rho_{(1,2)}}_{\text{Predation}}, \tag{2}$$

$$\frac{d\rho_{(1,2)}}{dt} = \underbrace{c_2\rho_{(1,2)}(\rho_1 - \rho_{(1,2)})q_{s/s}}_{\text{Within fragment dispersal}} \underbrace{-(e_1 + e_2)\rho_{(1,2)}}_{\text{Extinction}} \underbrace{-(\mu_{21}\rho_{(1,2)} + \mu_{32}\rho_{(2,3)})}_{\text{Predation}}, \tag{3}$$

$$\frac{d\rho_{(2,3)}}{dt} = \underbrace{c_3\rho_{(2,3)}(\rho_{(1,2)} - \rho_{(2,3)})}_{\text{Global dispersal}} - (\underbrace{e_1 + e_2 + e_3}_{\text{Extinction}} + \underbrace{\mu_{21} + \mu_{32}}_{\text{Predation}})\rho_{(2,3)}, \tag{4}$$

where all parameters are interpreted in Table 1 (see details in [38]). Note that this model mainly focuses on describing the patch occupancy of trophic links or subcommunities (i.e. 1, 1X✍2, or 1X✍2X✍3) rather than those of individual species [31].

Here we emphasize that: (i) species 1 is restricted to colonizing its adjacent *s*-patches, represented in equation (2) by taking the pair density of neighbouring patches (1-*s*) available for colonization equal to $\rho_{1s} = (\rho_1 - \rho_{1u} - \rho_{11})$, as there are three possible neighbour states for an occupied 1-patch: 1, *u* or *s*. In order to construct a closed system, we further derive the dynamics of $\rho_{11}$ and $\rho_{1u}$ as shown in equations (B5-B6) (electronic supplementary material, appendix B). (ii) In the equation (3) for 1X✍2 links, we multiply the colonization term by the patch clustering coefficient $q_{s/s}$ to estimate the limited dispersal of species 2, which has proven effective in spatially correlated landscapes [38]. The coefficient $q_{s/s}$ can be regarded as a measure of the average size of habitat fragment (i.e. an area of connected *s*-patches) [12,13,33,34]. Thus, our modified term can be interpreted as allowing species 2 to disperse only within habitat fragments. (iii) The equation (4) for 2X✍3 links is unmodified from the framework of Pillai *et al.* [31], as species 3 disperses globally.

### *Numerical simulations*

Using this spatially extended model, we first investigate how patch loss and fragmentation separately affect species persistence in trophically linked communities. In these food webs where species compete, we introduce a tradeoff between competition and dispersal range (as commonly used in ecological models to analyze species coexistence [29,32]), i.e. the species with a greater dispersal range is a poorer competitor and vice versa (scenarios with no competition-dispersal tradeoff shown in electronic supplementary material, figures S5-S6 in appendix D). When species 3 can feed on both species 1 and 2, we assume species 3 prefers to consume species 2 if both prey species are present in a local patch. We quantify this preference by comparing the intrinsic extinction rate of species 3 when preying on species 1 or 2, $\psi = e_{31} / e_{32} \geq 1$ ($e_{31} \geq e_{32}$; see Table 1). Additionally, when species 2 and 3 compete for feeding on the same prey species 1, species 3 is assumed to require a larger nutrient input than species 2, reflecting the body size gradient that is commonly observed in food webs [39-42,48]. To represent this, we assume there is a higher feeding pressure on species 1 when consumed by species 3 than by species 2, quantified by comparing the top-down extinction rate of species 1 in such links $\omega = \mu_{31} / \mu_{21} \geq 1$ ($\mu_{31} \geq \mu_{21}$). Thus, we further consider how species 3's feeding preference, $\psi$, and the feeding pressure on species 1, $\omega$, modify the effects of habitat destruction on spatial food web dynamics.

Here we use numerical methods to derive the non-trivial stable equilibrium states for system simulations, therefore determining which species can be expected to survive and which to go extinct. Note that our results are qualitatively robust for a broad range of parameter combinations (electronic supplementary material, figures S1-S14 in appendices C-F) and that, as such, we use symmetrical parameter combinations as a representative reference parameter set throughout.

## Results

### *Effects of patch availability and connectivity on species persistence in food webs*

We find that species' responses to patch availability and connectivity depend on their trophic position and the food web structure (figure 2). In simple food chains (figure 2*a*), increasing patch availability or connectivity increases species persistence and thus system robustness (i.e. higher patch occupancy; electronic supplementary material, figure S1 in appendix C). Species at higher trophic levels display higher sensitivity to patch loss and fragmentation, which go extinct first when patch availability and connectivity decrease due to trophic cascading effect.

Similarly in the food web with an omnivorous top predator (figure 2*b*), all species can persist at high levels of patch availability and connectivity. However, in contrast to the simple food chain, as patch connectivity decreases, species 2 becomes extinct before species 3. In this case, both species 2 and 3 can feed directly on species 1 and thus have similar vulnerability to trophic cascading effects (bottom-up control). Yet, the dispersal superiority of species 3 allows it to survive in more fragmented landscapes where species 2 with limited dispersal is unable to persist. Thus, the maximum patch occupancy of 1✂✍3 links occurs at intermediate patch availability and connectivity, more precisely along a boundary where species 2 just goes extinct (electronic supplementary material, figure S2 in appendix C). In highly connected landscapes, the dispersal advantage of species 3 diminishes, so species extinctions are once again predicted by the trophic rank hypothesis (that species at higher trophic levels go extinct sooner), as observed in simple food chains.

Unlike the food webs above, when species 2 and 3 compete for the same prey species 1 (species 3 with a greater dispersal range is a poorer competitor), species 3 becomes extinct at high levels of patch availability and connectivity (figure 2*c*). In such situations, species 3 has no dispersal advantage over species 2, but the competitive disadvantage of species 3 leads to its extinction. At intermediate patch connectivity, all species can survive as species 3's superior dispersal allows it to find patches where the dispersal-limited species 2 cannot access. Further decreasing patch connectivity causes species 2 to go extinct before species 3, as in omnivory food webs. Again, the patch occupancy of the 1✂✍3 link (in this case equivalent to the patch occupancy of species 3) peaks at the extinction threshold of species 2 (electronic supplementary material, figure S3 in appendix C).

In the food web with apparent competition between species 1 and 2, species 1 outcompetes species 2 in most landscape types because of its competitive superiority (figure 2*d*). Species 2 is able to survive only in a relatively small region of the landscape space characterized by low connectivity (around $q_{s/s} = 0.2$) and intermediate patch availability (around $s$=0.5) (electronic supplementary material, figure S4 in appendix C). Species 3 persists in landscapes with sufficiently high habitat availability as it can easily switch preys between species 1 and 2, again reflecting its sensitivity to a trophic cascade (bottom-up control).

Comparing system robustness to habitat destruction across these trophic structures, we find that the omnivory food web allows the complete community to survive on the widest range of landscape types. This range decreases for the simple food chain and the food web with exploitative competition. The food web with apparent competition has the smallest region where all species can survive.

### *Species feeding preference/pressure modifying community patterns in fragmented landscapes*

While increasing species feeding preference ($\psi = e_{31}/e_{32} > 1$ in both omnivory and apparent competition) or feeding pressure ($\omega = \mu_{31}/\mu_{21} > 1$ in both omnivory and exploitative competition) slightly increases the extinction risk of species 2 (despite the fact that species 2 is not directly affected by either of changes), it greatly accelerates the extinction of species 3 following habitat destruction (figures 3 and 4). This is explained by the fact that the extinction of species 1 can cascade and cause the extinction of species 3. However, these negative effects of increasing feeding preference or pressure are reduced when species 3 is an omnivore, as it feeds primarily on species 2 rather than species 1 at low levels of habitat destruction. In the food webs with exploitative or apparent competition, we do not observe this moderating effect when increasing feeding pressure or preference respectively. In the case of exploitative competition this is due to the fact that species 3 must consume species 1 and consequently increasing feeding pressure always increases species 3's sensitivity to the trophic cascade (bottom-up control), leading to a significant shrink in its survival region of landscape space (figure 4*d*). For apparent competition the mechanism is similar: species 1 outcompeting species 2 in the majority of landscapes results in species 3 only feeding on prey species 1 (figure 3*d*).

## Discussion

Traditional metacommunity theory for food webs mostly considers models of the relative occurrence of species within patches across a landscape (i.e. spatially implicit patch models) while ignoring the details of local dispersal and patch connectivity. Here we propose a spatially extended patch-dynamic model for food webs by incorporating patch connectivity with trophic-dependent dispersal (i.e. species at higher trophic levels displaying longer-range dispersal [39-42]). Our model provides a new approach to study trophic networks in space. Using this model, we demonstrate that dispersal across space can play a critical role in maintaining trophic complexity. For example, the dispersal-competition tradeoff allows the competing species to coexist on the regional scale (despite competitive exclusion on the local scale) in fragmented landscapes (figure 2*c*, 2*d*).

Ignoring trophic interactions, previous metapopulation models predicted that species with poor dispersal ability are more likely to become extinct in fragmented landscapes [5,12,13,49]. In our model, however, incorporating trophic interaction into the metacommunity system may reverse this prediction, resulting in different species sensitivities to habitat destruction (figure 2). In a simple food chain, species at higher trophic levels are found to be more vulnerable to patch loss and fragmentation despite of their dispersal superiority (figure 2*a*), in accordance with the trophic rank hypothesis (a trophic cascade [27,50-52]). In the omnivory structure, however, the intermediate consumer with limited dispersal has greatest sensitivity to patch fragmentation, while the omnivorous top predator with dispersal superiority is able to persist in more fragmented landscapes by switching feeding on the basal species. But in highly connected landscapes, the intermediate consumer has very similar dispersal abilities to the top predator and consequently we observe a return to the typical paradigm where the top predator is most sensitive to habitat loss. Interestingly, in the exploitative competition, species 2 monotonously decreases with habitat destruction, whereas species 3 displays diverse (positive as well as negative) responses. In particular, species 3 does not survive in highly connected landscapes due to competitive exclusion; instead it can persist at intermediate patch loss and fragmentation because of a dispersal-competition tradeoff. In the apparent competition, species 2 is competitively excluded by species 1 in most landscapes types, resulting in a bi-trophic system where species 3 shows more sensitivity to habitat destruction than species 1. In summary, the sensitivity of species to habitat fragmentation is not always monotonic with its dispersal ability

[16], but instead is a complex function of species dispersal and interactions (e.g. competition and predation) with other species in the community.

By extension, our results suggest that system robustness, defined as the ability of a trophic community to tolerate habitat destruction without suffering species extinctions, depends strongly on the trophic structure of that community. As we would expect, competition between species significantly reduces robustness of the overall system, since it prevents all species from surviving on the same patch. In contrast, increased diet breadth for higher trophic-level species, e.g. the module with an omnivorous top predator, significantly increases system robustness, as the typically more vulnerable species is allowed to survive by switching their feeding behavior (adaptive feeding behavior). This indicates that the omnivore can modify its diet dependent on prey availability, either by switching prey or by adjusting the proportion of each in a mixed diet in response to patch fragmentation [53]. Essentially, feeding on different trophic levels (omnivory) increases the number of available habitat patches accessible to the omnivorous top predator, thus offering more opportunities for its survival [29,32].

In the food webs with exploitative or apparent competition, we find that intermediate landscape fragmentation maximizes species diversity while low or high fragmentation leading to the loss of one or more species (figure 2*c* and *d*). The peak observed in species richness at intermediate patch fragmentation represents a compromise between competition and dispersal mediated by patch fragmentation. In particular, when species compete for the same resource, high levels of habitat fragmentation severely limit the colonization opportunities and therefore patch occupancy of poor dispersers, allowing the inferior competitor with longer range dispersal to survive on the landscape. By contrast, in highly connected landscapes, species even with short range dispersal are able to access to most of the available habitat and, as such, the poor competitor is driven to extinction. If this tradeoff holds in nature, moderate patch fragmentation could promote the survival of long-range dispersers (e.g. increased patch occupancy of species 3 in figure S3). This suggests habitat heterogeneity as a critical factor for biodiversity maintenance, as it can provide refuges for the poor competitor (via long-range dispersal) that the strong competitor with dispersal limitation is unable to access (i.e. a competition-dispersal tradeoff commonly used in traditional metapopulation models [29,32,54,55]).

This is one example of a more general paradigm that landscape boundaries promote biodiversity, which has been observed frequently on the global scale [56-58]. An obvious example is the loss of biodiversity in Australia and the south Pacific that followed colonization from Europe due, in part, to the introduction of superior competitors from that continent [59,60]. Our results show that this paradigm extends to the smaller scale of an individual landscape, and thus increasing patch connectivity is not always the optimal strategy for biodiversity conservation. Indeed it may result in further species loss. This refutes previous suggestions that maximizing the connectivity of good-quality habitat patches is always an effective way to promote species diversity [4,5,9,61,62]. Instead, landscape fragmentation may, in some cases, lead to increases in species richness especially at modest levels, despite ultimately causing the collapse of the food web at more extreme levels (as shown by previous spatially implicit modelling studies [29,32]).

In our model, we have made two simplifying assumptions. Firstly, we only considered three ideal types of dispersal scaling (i.e. neighbour dispersal, dispersal within fragments and global dispersal), with higher trophic level displaying longer-range dispersal (as commonly observed in [39-42]). In such case, species dispersal ranges are essentially categorical, which is relatively restrictive as species in nature show a broad range of movement behaviors [42,63-65]. Such categorical description can be naturally linked to the effects of fragment size and patch connectivity, but it does eliminate the effect of distance between fragments [2-5,42]. Thus, this omission could be further explored by comparing our predictions with those models using more realistic dispersal ranges. A second simplification used in this model is the division of habitat into suitable and unsuitable habitats. In fact, real landscapes rarely consist of neatly divided patches of “habitat” and “non-habitat” [9,13], instead habitat degradation coincides with reduction in habitat quality, so that most landscapes display at least some level of habitat variegation (i.e. varying suitability for species). To account for this, future study could include the range of possible habitat types, and apply more complex metrics to characterize the overall spatial landscape structure.

## Conclusions

We develop a spatially extended patch-dynamic model to include spatial heterogeneity in order to investigate how trophic communities, characterized by different food webs, differ in their responses to habitat destruction. Each module produces unique species survival patterns in fragmented landscapes. As such, we suggest that, in conservation efforts, the community structure to be preserved must be considered in combination with habitat configurational fragmentation [10,14-16,62,66]. In particular, we find that, in food webs with a dispersal-competition tradeoff between species, the greatest species diversity is achieved at intermediate levels of habitat destruction. Thus, the common recommendation to mitigate negative impacts of landscape fragmentation on biodiversity by increasing habitat connectivity [61,67], could, in fact, be detrimental to some communities. This calls for particular caution when designing conservation strategies for biodiversity maintenance in trophically-linked communities, as species loss resulting from habitat management will simultaneously influence multiple species across trophic levels, possibly resulting in the collapse of the entire community. Our model further demonstrates that differential sensitivities to patch loss and fragmentation are closely related to species traits (e.g. dispersal, competition and trophic position), thus identification of these traits from empirical data would contribute to the setting of conservation priorities in applied ecology. Experimental tests of these predictions could be performed in natural or laboratory-based model systems (e.g. microcosms and field observations) that allow the direct manipulation of metacommunity size and patch connectivity [14,15,66,68]. Overall, our extended modelling framework offers a promising way to advance the spatial food web theory in fragmented landscapes and provides new insights into biodiversity conservation.

## Authors' contributions

J.L. conceived the study; J.L. and D.B. performed the analysis and discussed the results; J.L. wrote the manuscript; and D.B. and B.B improved the manuscript.

**Competing interests:** The authors declare no competing interests.

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## Supplementary Material

Electronic supplementary material accompanies this manuscript is also supplied.

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## Figure captions

**Figure 1.** Four types of food web structures: (a) a simple food chain, (b) an omnivory food web, (c) exploitative competition, (d) apparent competition (arrow – predation and dotted line – competition). Each food web consists of three interacting species but with different dispersal traits: species 1 with neighbour dispersal, species 2 having random dispersal within habitat fragments, and species 3 with global dispersal.

**Figure 2.** Interactive effects of patch availability and patch connectivity on species regional coexistence in different food webs, simultaneously considering species dispersal (1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal). Four food web structures are included: (a) a simple food chain, (b) omnivory, (c) exploitative competition, and (d) apparent competition. Invalid region: see equation (1). Parameter values: species colonization rate $c_i$=$c_{ji}$=1, intrinsic extinction rate $e_i$= $e_{32}$= 0.05 and species feeding preference cost $\psi = e_{31}/ e_{32}= 3$ , top-down extinction rate $\mu_{ji} = 0.025 \ \ (i, j = 1, 2, 3)$.

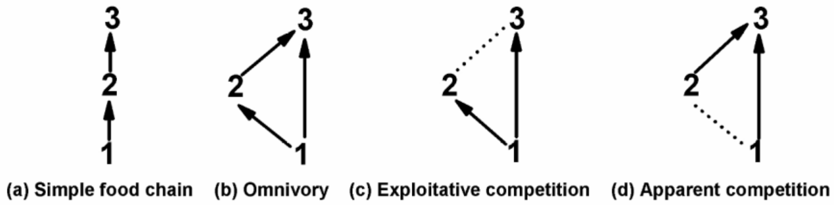
**Figure 3.** Effect of variation in species feeding preference cost ($\psi = e_{31} / e_{32}$ =1, 3, 5, 7 at fixed $e_{32}$ =0.05) on species extinction risk in omnivory versus apparent competition, simultaneously by varying both patch availability and patch connectivity. Again, species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal. Invalid region: see equation (1). Other parameter values seen in figure 2.

**Figure 4.** Effect of variation in species top-down extinction rate ($\omega$=$\mu_{31}$/$\mu_{21}$=1, 3, 5, 7, 9 at fixed $\mu_{21}$=0.025) on species persistence in omnivory versus exploitative competition, while again varying both patch availability and connectivity. Species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal. Other parameter values: see figure 2. Invalid region seen in equation (1).

## Tables

**Table 1.** Parameter interpretation

| Parameter | Interpretation |
|---|---|
| $u$ | Fraction of unsuitable patches (habitat patch loss) |
| $s$ | Fraction of suitable patches (patch availability) |
| $c_i$ | Colonization rate of species *i* |
| $e_i$ | Intrinsic extinction rate of species *i* |
| $c_{ji}$ | Colonization rate of species *j* when feeding on prey species *i* |
| $e_{ji}$ | Intrinsic extinction rate of species *j* when feeding on prey species *i* |
| $\mu_{ji}$ | The top-down extinction rate of species *i* eaten by species *j* |
| $\rho_i$ | Global patch occupancy of species *i* (*i*=1,2,3) |
| $\rho_{(i,j)}$ | Patch occupancy by the trophic link *i*✂✎*j*, with "(*i*, *j* )" indicating species *j* feeding on species *i* within a local patch |
| $\rho_{ij}$ | Probability of a randomly chosen pair of neighbouring patches that one is *i* and another is *j* (i.e. pair density; $i,\ j \in \{1,2,3,u,s\}$) |
| $q_{s/s}$ | Clustering degree of suitable patches (i.e. patch connectivity), indirectly indicating mean patch cluster size and habitat fragmentation |
| $q_{i/j}$ | Conditional probability that the neighbour of a *j*-patch is an *i*-patch (i.e. local density; $i,\ j \in \{1,2,3,u,s\}$) |



Four types of food web structures: (a) a simple food chain, (b) an omnivory food web, (c) exploitative competition, (d) apparent competition (arrow – predation and dotted line – competition). Each food web consists of three interacting species but with different dispersal traits: species 1 with neighbour dispersal, species 2 having random dispersal within habitat fragments, and species 3 with global dispersal.

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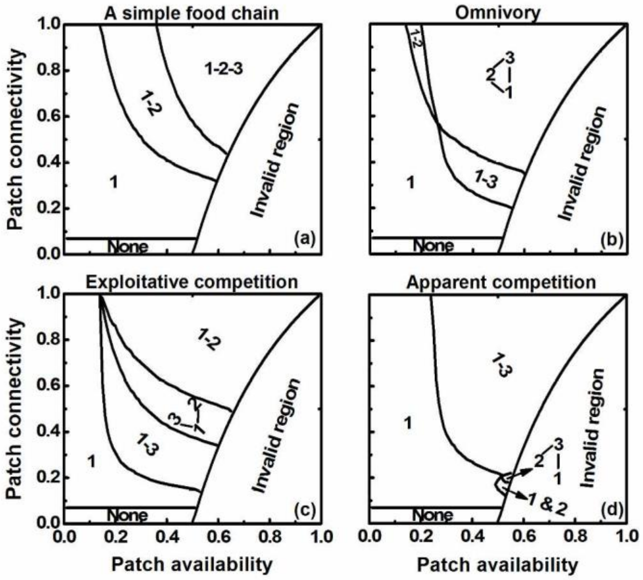

Interactive effects of patch availability and patch connectivity on species regional coexistence in different food webs, simultaneously considering species dispersal (1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal). Four food web structures are included: (a) a simple food chain, (b) omnivory, (c) exploitative competition, and (d) apparent competition. Invalid region: see equation (1).

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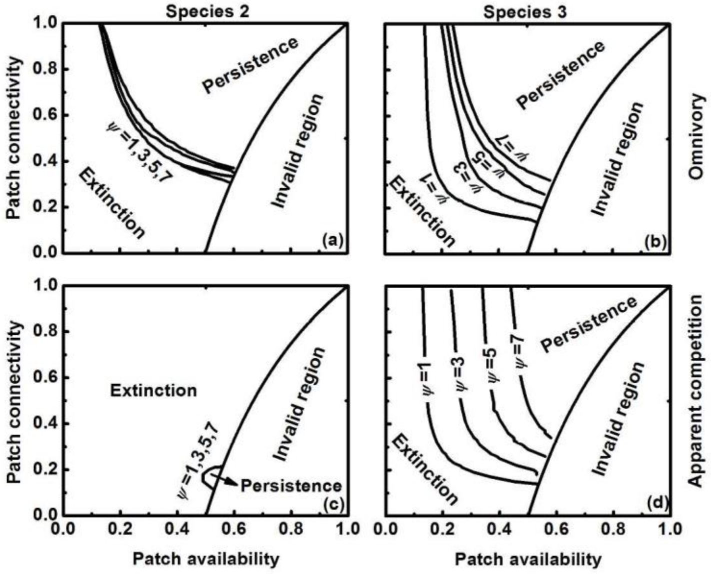

Effect of variation in species feeding preference cost on species extinction risk in omnivory versus apparent competition, simultaneously by varying both patch availability and patch connectivity. Again, species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal.

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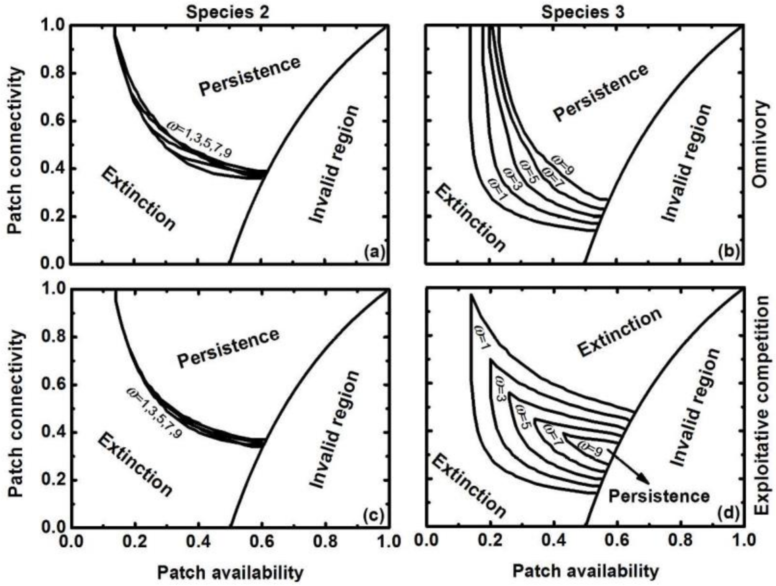

Effect of variation in species top-down extinction rate on species persistence in omnivory versus exploitative competition, while again varying both patch availability and connectivity. Species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal.

201x288mm (300 x 300 DPI)