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## PROCEEDINGS B

### Food web persistence in fragmented landscapes

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1                                   **Food web persistence in fragmented landscapes**

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12

13 **Abstract**

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

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

30

31

## 32 **Introduction**

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

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

55 between species in lower trophic levels, such as exploitative or apparent competition, may also  
56 modify the sensitivity of their predators to habitat destruction [29-32].

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

71 In this study we develop a spatially extended patch-dynamic model for different food webs in  
72 fragmented landscapes, based on the existing modelling frameworks of Pillai et al. [31]. Since it  
73 is not feasible to consider the full diversity of possible food web structure, we restrict our  
74 attention to four common trophic modules consisting of three species: a simple food chain,  
75 omnivory, exploitative competition, and apparent competition (figure 1). These typical modules  
76 describe the most important interaction types among species and form a basis for studying more  
77 complex food webs. In addition, we assign species dispersal ranges to reflect the common

78 observation that a species' dispersal range increases with its trophic level [39-42]. Using this  
 79 model, we first investigate how patch loss and fragmentation separately and interactively affect  
 80 the persistence of species embedded in each of these trophic structures, and then explore whether  
 81 species feeding preference/pressure can modify the effects of landscape fragmentation on  
 82 community patterns.

83

## 84 **Methods**

### 85 **Landscape structure**

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

$$99 \quad 2 - 1/s < q_{s/s} < 1. \quad (1)$$

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

### 101 **Coupling dispersal range to trophic level**

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

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



$$123 \quad \frac{d\rho_1}{dt} = c_{1442443}(\rho_u - \rho_{1u} - \rho_{1s}) - e_1 \rho_1 - \mu_{14243} \rho_1, \quad (2)$$

$$124 \quad \frac{d\rho_{(1,2)}}{dt} = c_{144424443}^2 \rho_{(1,2)} (\rho_{1(1,2)} - \rho_{s/s}) q_{s/s} - (e_1 + e_2) \rho_{(1,2)} - (\mu_{21(1,2)} \rho_{(1,2)} + \mu_{32(2,3)} \rho_{(2,3)}), \quad (3)$$

$$125 \quad \frac{d\rho_{(2,3)}}{dt} = c_{314424443} \rho_{(2,3)} (\rho_{(1,2)} - \rho_{(2,3)}) - (e_1 + e_2 + e_3 + \mu_{21} + \mu_{32}) \rho_{(2,3)}, \quad (4)$$

126 where all parameters are interpreted in Table 1 (see details in [38]). Note that this model mainly  
 127 focuses on describing the patch occupancy of trophic links or subcommunities (i.e. 1, 1~~×~~2, or  
 128 1~~×~~2~~×~~3) rather than those of individual species [31].

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

141

## 142 Numerical simulations

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

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

## 164 **Results**

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

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

172 Similarly in the food web with an omnivorous top predator (figure 2b), all species can persist  
173 at high levels of patch availability and connectivity. However, in contrast to the simple food  
174 chain, as patch connectivity decreases, species 2 becomes extinct before species 3. In this case,  
175 both species 2 and 3 can feed directly on species 1 and thus have similar vulnerability to trophic  
176 cascading effects (bottom-up control). Yet, the dispersal superiority of species 3 allows it to  
177 survive in more fragmented landscapes where species 2 with limited dispersal is unable to persist.  
178 Thus, the maximum patch occupancy of 1X3 links occurs at intermediate patch availability and  
179 connectivity, more precisely along a boundary where species 2 just goes extinct (electronic  
180 supplementary material, figure S2 in appendix C). In highly connected landscapes, the dispersal  
181 advantage of species 3 diminishes, so species extinctions are once again predicted by the trophic  
182 rank hypothesis (that species at higher trophic levels go extinct sooner), as observed in simple  
183 food chains.

184 Unlike the food webs above, when species 2 and 3 compete for the same prey species 1  
185 (species 3 with a greater dispersal range is a poorer competitor), species 3 becomes extinct at  
186 high levels of patch availability and connectivity (figure 2c). In such situations, species 3 has no

187 dispersal advantage over species 2, but the competitive disadvantage of species 3 leads to its  
188 extinction. At intermediate patch connectivity, all species can survive as species 3's superior  
189 dispersal allows it to find patches where the dispersal-limited species 2 cannot access. Further  
190 decreasing patch connectivity causes species 2 to go extinct before species 3, as in omnivory  
191 food webs. Again, the patch occupancy of the 1 $\times$ 3 link (in this case equivalent to the patch  
192 occupancy of species 3) peaks at the extinction threshold of species 2 (electronic supplementary  
193 material, figure S3 in appendix C).

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

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

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

207 While increasing species feeding preference ( $\psi = e_{31}/e_{32} > 1$  in both omnivory and apparent  
208 competition) or feeding pressure ( $\omega = \mu_{31}/\mu_{21} > 1$  in both omnivory and exploitative competition)  
209 slightly increases the extinction risk of species 2 (despite the fact that species 2 is not directly

210 affected by either of changes), it greatly accelerates the extinction of species 3 following habitat  
211 destruction (figures 3 and 4). This is explained by the fact that the extinction of species 1 can  
212 cascade and cause the extinction of species 3. However, these negative effects of increasing  
213 feeding preference or pressure are reduced when species 3 is an omnivore, as it feeds primarily  
214 on species 2 rather than species 1 at low levels of habitat destruction. In the food webs with  
215 exploitative or apparent competition, we do not observe this moderating effect when increasing  
216 feeding pressure or preference respectively. In the case of exploitative competition this is due to  
217 the fact that species 3 must consume species 1 and consequently increasing feeding pressure  
218 always increases species 3's sensitivity to the trophic cascade (bottom-up control), leading to a  
219 significant shrink in its survival region of landscape space (figure 4d). For apparent competition  
220 the mechanism is similar: species 1 outcompeting species 2 in the majority of landscapes results  
221 in species 3 only feeding on prey species 1 (figure 3d).

222

## 223 **Discussion**

224 Traditional metacommunity theory for food webs mostly considers models of the relative  
225 occurrence of species within patches across a landscape (i.e. spatially implicit patch models)  
226 while ignoring the details of local dispersal and patch connectivity. Here we propose a spatially  
227 extended patch-dynamic model for food webs by incorporating patch connectivity with trophic-  
228 dependent dispersal (i.e. species at higher trophic levels displaying longer-range dispersal [39-  
229 42]). Our model provides a new approach to study trophic networks in space. Using this model,  
230 we demonstrate that dispersal across space can play a critical role in maintaining trophic  
231 complexity. For example, the dispersal-competition tradeoff allows the competing species to

232 coexist on the regional scale (despite competitive exclusion on the local scale) in fragmented  
233 landscapes (figure 2c, 2d).

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

254 [16], but instead is a complex function of species dispersal and interactions (e.g. competition and  
255 predation) with other species in the community.

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

268 In the food webs with exploitative or apparent competition, we find that intermediate  
269 landscape fragmentation maximizes species diversity while low or high fragmentation leading to  
270 the loss of one or more species (figure 2c and d). The peak observed in species richness at  
271 intermediate patch fragmentation represents a compromise between competition and dispersal  
272 mediated by patch fragmentation. In particular, when species compete for the same resource,  
273 high levels of habitat fragmentation severely limit the colonization opportunities and therefore  
274 patch occupancy of poor dispersers, allowing the inferior competitor with longer range dispersal  
275 to survive on the landscape. By contrast, in highly connected landscapes, species even with short  
276 range dispersal are able to access to most of the available habitat and, as such, the poor

277 competitor is driven to extinction. If this tradeoff holds in nature, moderate patch fragmentation  
278 could promote the survival of long-range dispersers (e.g. increased patch occupancy of species 3  
279 in figure S3). This suggests habitat heterogeneity as a critical factor for biodiversity maintenance,  
280 as it can provide refuges for the poor competitor (via long-range dispersal) that the strong  
281 competitor with dispersal limitation is unable to access (i.e. a competition-dispersal tradeoff  
282 commonly used in traditional metapopulation models [29,32,54,55]).

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

295 In our model, we have made two simplifying assumptions. Firstly, we only considered three  
296 ideal types of dispersal scaling (i.e. neighbour dispersal, dispersal within fragments and global  
297 dispersal), with higher trophic level displaying longer-range dispersal (as commonly observed in  
298 [39-42]). In such case, species dispersal ranges are essentially categorical, which is relatively  
299 restrictive as species in nature show a broad range of movement behaviors [42,63-65]. Such



300 categorical description can be naturally linked to the effects of fragment size and patch  
301 connectivity, but it does eliminate the effect of distance between fragments [2-5,42]. Thus, this  
302 omission could be further explored by comparing our predictions with those models using more  
303 realistic dispersal ranges. A second simplification used in this model is the division of habitat  
304 into suitable and unsuitable habitats. In fact, real landscapes rarely consist of neatly divided  
305 patches of “habitat” and “non-habitat” [9,13], instead habitat degradation coincides with  
306 reduction in habitat quality, so that most landscapes display at least some level of habitat  
307 variegation (i.e. varying suitability for species). To account for this, future study could include  
308 the range of possible habitat types, and apply more complex metrics to characterize the overall  
309 spatial landscape structure.

310

## 311 **Conclusions**

312 We develop a spatially extended patch-dynamic model to include spatial heterogeneity in order  
313 to investigate how trophic communities, characterized by different food webs, differ in their  
314 responses to habitat destruction. Each module produces unique species survival patterns in  
315 fragmented landscapes. As such, we suggest that, in conservation efforts, the community  
316 structure to be preserved must be considered in combination with habitat configurational  
317 fragmentation [10,14-16,62,66]. In particular, we find that, in food webs with a dispersal-  
318 competition tradeoff between species, the greatest species diversity is achieved at intermediate  
319 levels of habitat destruction. Thus, the common recommendation to mitigate negative impacts of  
320 landscape fragmentation on biodiversity by increasing habitat connectivity [61,67], could, in fact,  
321 be detrimental to some communities. This calls for particular caution when designing

322 conservation strategies for biodiversity maintenance in trophically-linked communities, as  
323 species loss resulting from habitat management will simultaneously influence multiple species  
324 across trophic levels, possibly resulting in the collapse of the entire community. Our model  
325 further demonstrates that differential sensitivities to patch loss and fragmentation are closely  
326 related to species traits (e.g. dispersal, competition and trophic position), thus identification of  
327 these traits from empirical data would contribute to the setting of conservation priorities in  
328 applied ecology. Experimental tests of these predictions could be performed in natural or  
329 laboratory-based model systems (e.g. microcosms and field observations) that allow the direct  
330 manipulation of metacommunity size and patch connectivity [14,15,66,68]. Overall, our  
331 extended modelling framework offers a promising way to advance the spatial food web theory in  
332 fragmented landscapes and provides new insights into biodiversity conservation.

333

334 **Authors' contributions**

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

337

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

339

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350

351 **Supplementary Material**

352 Electronic supplementary material accompanies this manuscript is also supplied.

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516 **Figure captions**

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

522  
 523 **Figure 2.** Interactive effects of patch availability and patch connectivity on species regional  
 524 coexistence in different food webs, simultaneously considering species dispersal (1 – neighbour  
 525 dispersal, 2 – within fragment dispersal, and 3 – global dispersal). Four food web structures are  
 526 included: (a) a simple food chain, (b) omnivory, (c) exploitative competition, and (d) apparent  
 527 competition. Invalid region: see equation (1). Parameter values: species colonization rate  $c_i=c_{ji}=1$ ,  
 528 intrinsic extinction rate  $e_i=e_{32}=0.05$  and species feeding preference cost  $\psi=e_{31}/e_{32}=3$ , top-  
 529 down extinction rate  $\mu_{ji}=0.025$  ( $i, j = 1, 2, 3$ ).

530  
 531 **Figure 3.** Effect of variation in species feeding preference cost ( $\psi=e_{31}/e_{32}=1, 3, 5, 7$  at fixed  
 532  $e_{32}=0.05$ ) on species extinction risk in omnivory versus apparent competition, simultaneously by  
 533 varying both patch availability and patch connectivity. Again, species dispersal ranges: 1 –  
 534 neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal. Invalid region: see  
 535 equation (1). Other parameter values seen in figure 2.

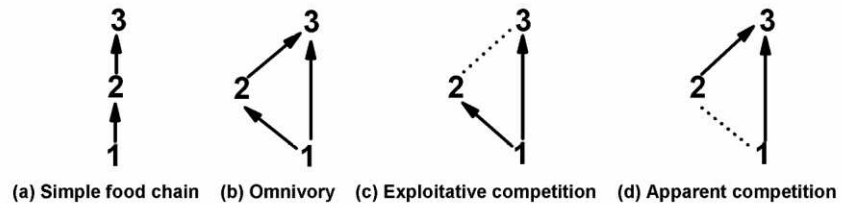
536  
 537 **Figure 4.** Effect of variation in species top-down extinction rate ( $\omega=\mu_{31}/\mu_{21}=1, 3, 5, 7, 9$  at fixed  
 538  $\mu_{21}=0.025$ ) on species persistence in omnivory versus exploitative competition, while again  
 539 varying both patch availability and connectivity. Species dispersal ranges: 1 – neighbour  
 540 dispersal, 2 – within fragment dispersal, and 3 – global dispersal. Other parameter values: see  
 541 figure 2. Invalid region seen in equation (1).

542

543 **Tables**544 **Table 1.** Parameter interpretation

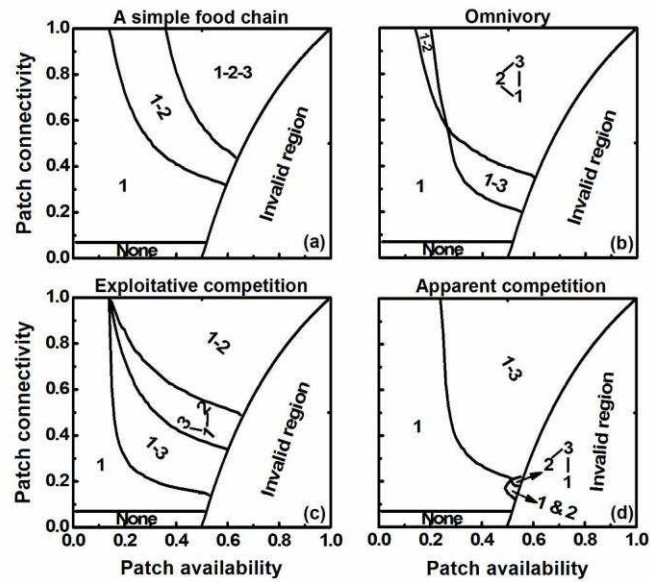
Parameter	Interpretation
$u$	Fraction of unsuitable patches (habitat patch loss)
$s$	Fraction of suitable patches (patch availability)
$c_i$	Colonization rate of species $i$
$e_i$	Intrinsic extinction rate of species $i$
$c_{ji}$	Colonization rate of species $j$ when feeding on prey species $i$
$e_{ji}$	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 $i \rightarrow j$ , 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; $i, j \in \{1,2,3,u,s\}$ )

545



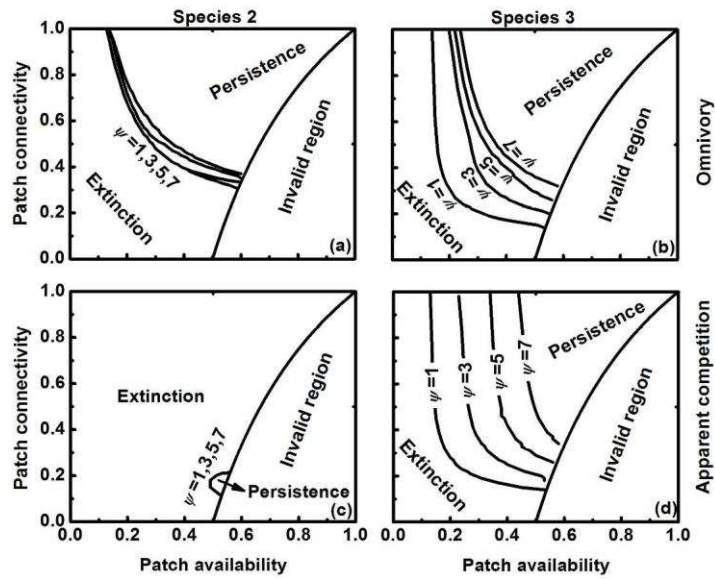
Four types of food web structures: (a) a simple food chain, (b) an omnivory food web, (c) exploitative competition, (d) apparent competition (arrow – predation and dotted line – competition). Each food web consists of three interacting species but with different dispersal traits: species 1 with neighbour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

201x264mm (300 x 300 DPI)



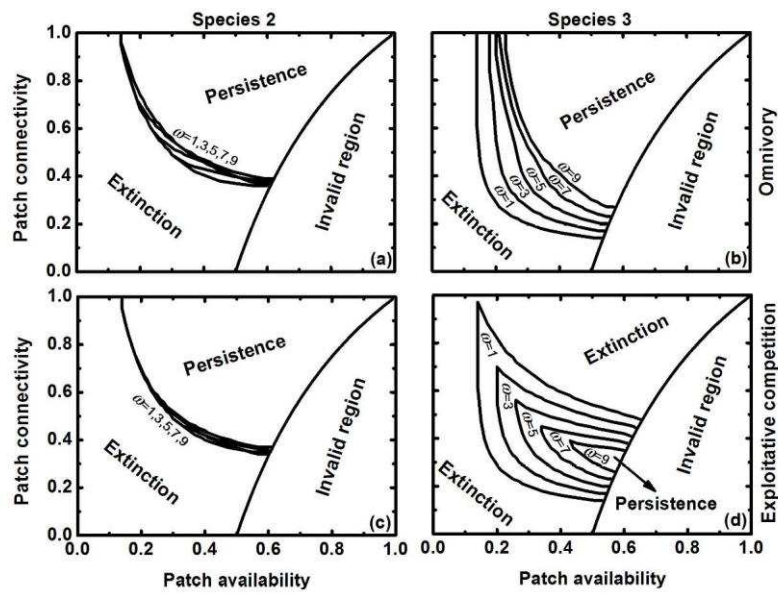
Interactive effects of patch availability and patch connectivity on species regional coexistence in different food webs, simultaneously considering species dispersal (1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal). Four food web structures are included: (a) a simple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

201x264mm (300 x 300 DPI)



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.

201x288mm (300 x 300 DPI)



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)