This is a repository copy of *Food web persistence in fragmented landscapes*.

Article:

PROCEEDINGS B

Food web persistence in fragmented landscapes

SCHOLARONE™
Manuscripts

1   # Food web persistence in fragmented landscapes

2   Jinbao Liao[1*], Daniel Bearup[2,3], Bernd Blasius[3]

3   [1] Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed Research,

4   Jiangxi Normal University, Ziyang Road 99, 330022 Nanchang, China

5   [2] Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield, S10 2TN, UK

6   [3] University of Oldenburg, Institute for Chemistry and Biology of the Marine Environment

7   (ICBM), Carl-von-Ossietzky-Strasse 9-11, D-26111 Oldenburg, Germany

8

9   [*] **Corresponding author:** Dr. Jinbao Liao (jinbaoliao@163.com)

10   Address: Ziyang Road 99, 330022 Nanchang, Jiangxi Province, China.

11   Tel.: +86-(0)791-88133622   Fax: +86-(0)791-88120538

12

Abstract

13

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

Introduction

32

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

3

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 ρ_{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    $2-1/s < q_{s/s} < 1$.   (1)

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

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→intermediate consumer 2→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)

6

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

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

125     $$\frac{d\rho_{(2,3)}}{dt} = \underbrace{c_3\rho_{(2,3)}(\rho_{(1,2)} - \rho_{(2,3)})}_{\text{Global dispersal}} - (\underbrace{e_1 + e_2 + e_3}_{\text{Extinction}} + \underbrace{\mu_{21} + \mu_{32}}_{\text{Predation}})\rho_{(2,3)},$$ (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 $\rho_{1s} = (\rho_1 - \rho_{1u} - \rho_{11})$, 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 ρ_{11} and ρ_{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, ψ, and the feeding

158   pressure on species 1, ω, 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.

8

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 2*a*), 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 2*b*), 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 1→3 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 2*c*). 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→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 2*d*). 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 4*d*). 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 3*d*).

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 2*c*, 2*d*).

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 2*a*), 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 2*c* 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

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

340   **Funding**

341   This study was supported by the DFG through grant FOR 1748, the Opening Fund of Key

342   Laboratory of Poyang Lake Wetland and Watershed Research (Jiangxi Normal University),

343   Ministry of Education (No. PK2015004 and TK2016002), Jiangxi Provincial Education

344   Department (No. GJJ160274), and the Doctoral Scientific Research Foundation of Jiangxi

345   Normal University (No. 12017778).

346

347   **Acknowledgements**

348   We would like to thank Kevin S. McCann, Jordi Bascompte and Shaopeng Wang for their useful

349   comments on early versions of the manuscript.

350

351   **Supplementary Material**

352   Electronic supplementary material accompanies this manuscript is also supplied.

References

1. Pimm SL, Raven P. 2000 Biodiversity: extinction by numbers. *Nature* **403**, 843-845. (doi:10.1038/35002708)

2. Fahrig L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.* **34**, 487-515. (doi:10.1146/annurev.ecolsys.34.011802.132419)

3. Fahrig L, *et al.* 2011 Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* **14**, 101-112. (doi:10.1111/j.1461-0248.2010.01559.x)

4. Fahrig L. 2002 Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol. Appl.* **12**, 346-353. (doi:10.1890/1051-0761(2002)012[0346:EOHFOT]2.0.CO;2)

5. Ewers RM, Didham RK. 2006 Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* **81**, 117-142. (doi:10.1017/S1464793105006949)

6. Andrews A. 1990 Fragmentation of habitat by roads and utility corridors: a review. *Aust. Zool.* **26**, 130-141. (doi:10.7882/AZ.1990.005)

7. Jaeger JAG, Fahrig L. 2004 Effects of road fencing on population persistence. *Conserv. Biol.* **18**, 1651-1657. (doi:10.1111/j.1523-1739.2004.00304.x)

8. Di Giulio M, Holderegger R, Tobia S. 2009 Effects of habitat and landscape fragmentation on humans and biodiversity in densely populated landscapes. *J. Environ. Manage.* **90**, 2959-2968. (doi:10.1016/j.jenvman.2009.05.002)

9. Mortelliti A, Amori G, Boitani L. 2010 The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. *Oecologia* **163**, 535-547. (doi:10.1007/s00442-010-1623-3)

10. Legrand D, *et al.* 2017 Eco-evolutionary dynamics in fragmented landscapes. *Ecography* **40**, 9-25. (doi:10.1111/ecog.02537)

11. Hiebeler D. 2000 Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. *Ecology* **81**,1629-1641. (doi:10.1890/0012-9658(2000)081[1629:POFLWS]2.0.CO;2)

12. Liao J, *et al.* 2013a Modelling plant population size and extinction thresholds from habitat loss and fragmentation: effects of neighbouring competition and dispersal strategy. *Ecol. Model.* **268**, 9-17. (doi:10.1016/j.ecolmodel.2013.07.021)

13. Liao J, *et al.* 2013b Species persistence in landscapes with spatial variation in habitat quality: a pair approximation model. *J. Theor. Biol.* **335**, 22-30. (doi:10.1016/j.jtbi.2013.06.015)

14. Carrara F, Altermatt F, Rodriguez-Iturbe I, Rinaldo A. 2012 Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *Proc. Natl. Acad. Sci. USA* **109**, 5761-5766. (doi:10.1073/pnas.1119651109)

15. Carrara F, Rinaldo A, Giometto A, Altermatt F. 2014 Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. *Am. Nat.* **183**, 13-25. (doi:10.1086/674009)

16. Cote J, *et al.* 2017 Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography* **40**, 56-73. (doi:10.1111/ecog.02538)

18

392   17. Prugh LR, Hodges KE, Sinclair AR, Brashares JS. 2008 Effect of habitat area and isolation
393   on fragmented animal populations. *Proc. Natl. Acad. Sci. USA* **105**, 20770-20775.
394   (doi:10.1073/pnas.0806080105)

395   18. Holt RD. 2002 Food webs in space: on the interplay of dynamic instability and spatial
396   processes. *Ecol. Res.* **17**, 261-273. (doi:10.1046/j.1440-1703.2002.00485.x)

397   19. Amarasekare P. 2008 Spatial dynamics of food webs. *Annu. Rev. Ecol. Syst.* **39**, 479-500.
398   (doi:10.1146/annurev.ecolsys.39.110707.173434)

399   20. McCann KS, Rooney N. 2009 The more food webs change, the more they stay the same.
400   *Philos. T. Roy. Soc. B* **364**, 1789-1801. (doi:10.1098/rstb.2008.0273)

401   21. Gonzalez A, Rayfield B, Lindo Z. 2011 The disentangled bank: how loss of habitat
402   fragments and disassembles ecological networks. *Am. J. Bot.* **98**, 503-516.
403   (doi:10.3732/ajb.1000424)

404   22. Hagen M, *et al.* 2012 Biodiversity, species interactions and ecological networks in a
405   fragmented world. *Adv. Ecol. Res.* **46**, 89-210. (doi:10.1016/B978-0-12-396992-7.00002-2)

406   23. Dobson A, *et al.* 2006 Habitat loss, trophic collapse, and the decline of ecosystem services.
407   *Ecology* **87**, 1915-1924. (doi:10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2)

408   24. Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M. 2009 Habitat fragmentation and
409   species loss across three interacting trophic levels: Effects of life‐history and food‐web
410   traits. *Conserv. Biol.* **23**, 1167-1175. (doi:10.1111/j.1523-1739.2009.01214.x)

411   25. Fenoglio MS, Salvo A, Videla M, Valladares GR. 2010 Plant patch structure modifies
412   parasitoid assemblage richness of a specialist herbivore. *Ecol. Entomol.* **35**, 594-601.
413   (doi:10.1111/j.1365-2311.2010.01218.x)

414   26. Valladares G, Cagnolo L, Salvo A. 2012 Forest fragmentation leads to food web contraction.
415   *Oikos* **121**, 299-305. (doi:10.1111/j.1600-0706.2011.19671.x)

416   27. Kruess A, Tscharntke T. 1994 Habitat fragmentation, species loss, and biological control.
417   *Science* **264**, 1581-1584. (doi:10.1126/science.264.5165.1581)

418   28. Patterson BD. 1984 Mammalian extinction and biogeography in the Southern Rocky
419   Mountains. In: *Extinctions* (ed. Nitecki M) University of Chicago Press, Chicago, pp. 247-
420   293.

421   29. Melián CJ, Bascompte J. 2002 Food web structure and habitat loss. *Ecol. Lett.* **5**, 37-46.
422   (doi:10.1046/j.1461-0248.2002.00280.x)

423   30. Fox JW, Olsen E. 2000 Food web structure and the strength of transient indirect effects.
424   *Oikos* **90**, 219-226. (doi:10.1034/j.1600-0706.2000.900202.x)

425   31. Pillai P, Loreau M, Gonzalez A. 2010 A patch-dynamic framework for food web
426   metacommunities. *Theor. Ecol.* **3**, 223-237. (doi:10.1007/s12080-009-0065-1)

427   32. Pillai P, Gonzalez A, Loreau M. 2011 Metacommunity theory explains the emergence of
428   food web complexity. *Proc. Natl. Acad. Sci. USA* **108**, 19293-19298.
429   (doi:10.1073/pnas.1106235108)

430   33. Matsuda H, Ogita N, Sasaki A, Sato K. 1992 Statistical mechanics of population: the lattice
431   Lotka-Volterra model. *Progr. Theor. Phys.* **88**, 1035-1049. (doi:10.1143/ptp/88.6.1035)

432   34. Harada Y, Iwasa Y. 1994 Lattice population dynamics for plants with dispersing seeds and
433   vegetative propagation. *Res. Popul. Ecol.* **36**, 237-249. (doi:10.1007/BF02514940)

434   35. Levin SA, Durrett R. 1996 From individuals to epidemics. *Philos. T. Roy. Soc. B* **351**, 1615-
435   1621. (doi:10.1098/rstb.1996.0145)

436   36. Ives AR, Turner MG, Pearson SM. 1998 Local explanations of landscape patterns: Can
437   analytical approaches approximate simulation models of spatial processes? *Ecosystems* **1**, 35-
438   51. (doi:10.1007/s100219900004)

439   37. Ovaskainen O, Sato K, Bascompte J, Hanski I. 2002 Metapopulation models for extinction
440   threshold in spatially correlated landscapes. *J. Theor. Biol.* **215**, 95-108.
441   (doi:10.1006/jtbi.2001.2502)

442   38. Liao J, Chen J, Ying Z, Hiebeler DE, Nijs I. 2016a An extended patch-dynamic framework
443   for food chains in fragmented landscapes. *Sci. Rep.* **6**, 33100. (doi:10.1038/srep33100)

444   39. Peters RH. 1983 *The Ecological Implications of Body Size*. Cambridge University Press,
445   Cambridge.

446   40. McCann KS, Rasmussen JR, Umbanhowar J. 2005 The dynamics of spatially coupled food
447   webs. *Ecol. Lett.* **8**, 513-523. (doi:10.1111/j.1461-0248.2005.00742.x)

448   41. Greenleaf SS, Williams NM, Winfree R, Kremen C. 2007 Bee foraging ranges and their
449   relationship to body size. *Oecologia* **153**, 589-596. (doi:10.1007/s00442-007-0752-9)

450   42. Stevens VM, *et al.* 2014 A comparative analysis of dispersal syndromes in terrestrial and
451   semi-terrestrial animals. *Ecol. Lett.* **17**, 1039-1052. (doi:10.1111/ele.12303)

452   43. Hiebeler D. 2007 Competing populations on fragmented landscapes with spatially structured
453   heterogeneities: improved landscape generation and mixed dispersal strategies. *J. Math. Biol.*
454   **54**, 337-356. (doi:10.1007/s00285-006-0054-6)

455   44. Boots M, Sasaki A. 2000 The evolutionary dynamics of local infection and global
456   reproduction in host-parasite interactions. *Ecol. Lett.* **3**,181-185. (doi:10.1046/j.1461-
457   0248.2000.00139.x)

458   45. Ying Z, *et al.* 2014 Species coexistence in a lattice-structured habitat: Effects of species
459   dispersal and interactions. *J. Theor. Biol.* **359**, 184-191. (doi:10.1016/j.jtbi.2014.05.048)

460   46. Liao J, *et al*. 2015 Species extinction thresholds in the face of spatially correlated periodic
461   disturbance. *Sci. Rep.* **5**, 15455. (doi:10.1038/srep15455)

462   47. Liao J, *et al*. 2016b Coexistence of species with different dispersal across landscapes: a
463   critical role of spatial correlation in disturbance. *Proc. Roy. Soc. B* **283**, 20160537.
464   (doi:10.1098/rspb.2016.0537)

465   48. Brose U, *et al.* 2006 Consumer-resource body-size relationships in natural food webs.
466   *Ecology* **87**, 2411-2417. (doi:10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)

467   49. Hanski I, Ovaskainen O. 2000 The metapopulation capacity of a fragmented landscape.
468   *Nature* **404**, 755-758. (doi:10.1038/35008063)

469   50. Kruess A, Tscharntke T. 2000 Species richness and parasitism in a fragmented landscape:
470   experiments and field studies with insects on *Vicia sepium*. *Oecologia* **122**,129-137.
471   (doi:10.1007/PL00008829)

472   51. Terborgh J, *et al*. 2001 Ecological meltdown in predator-free forest fragments. *Science* **294**,
473   1923-1926. (doi:10.1126/science.1064397)

474   52. Scheid BE, Thies C, Tscharntke T. 2011 Enhancing rape pollen beetle parasitism within
475   sown flower fields along a landscape complexity gradient. *Agr. Entomol.* **13**, 173-179.
476   (doi:10.1111/j.1461-9563.2010.00516.x)

477   53. Kratina P, Lecraw RM, Ingram T, Anholt BR. 2012 Stability and persistence of food webs
478   with omnivory: is there a general pattern? *Ecosphere* **3**, 794-804. (doi:10.1890/ES12-00121.1)

479   54. Hastings A. 1980 Disturbance, coexistence, history and competition for space. *Theor. Pop.*
480   *Biol.* **163**, 491-504. (doi:10.1016/0040-5809(80)90059-3)

481   55. Tilman D. 1994 Competition and biodiversity in spatially structured habitats. *Ecology* **75**,
482   685-700. (doi:10.2307/1939377)

483   56. Quinn JF, Harrison SP. 1988 Effects of habitat fragmentation and isolation on species
484   richness: evidence from biogeographic patterns. *Oecologia* **75**, 132-140.
485   (doi:10.1007/BF00378826)

486   57. Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C. 2002 Contribution of small habitat
487   fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol.*
488   *Appl.* **12**, 354-363. (doi:10.1890/1051-0761(2002)012[0354:COSHFT]2.0.CO;2)

489   58. Fahrig L. 2017 Ecological responses to habitat fragmentation *per se*. *Annu. Rev. Ecol. Syst.*
490   **48**, in press. (doi:10.1146/annurev-ecolsys-110316-022612)

491   59. Elton CS. 2000 *The ecology of invasions by animals and plants*. University of Chicago Press.

492   60. Davis MA. 2003 Biotic globalization: does competition from introduced species threaten
493   biodiversity? *Bioscience* **53**, 481-489.
494   (doi:10.1641/00063568(2003)053[0481:BGDCFI]2.0.CO;2)

495   61. Fischer J, Lindenmayer DB. 2007 Landscape modification and habitat fragmentation: a
496   synthesis. *Global Ecol. Biogeogr.* **16**, 265-280. (doi:10.1111/j.1466-8238.2007.00287.x)

497   62. Thompson PL, Rayfield B, Gonzalez A. 2017 Loss of habitat and connectivity erodes species
498   diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* **40**,
499   98-108. (doi:10.1111/ecog.02558)

500   63. Johst K, Brand R, Eber S. 2002 Metapopulation persistence in dynamic landscapes: the role
501   of dispersal distance. *Oikos* **98**, 263-270. (doi:10.1034/j.1600-0706.2002.980208.x)

502   64. Bertuzzo E, *et al.* 2011 Spatial effects on species persistence and implications for
503   biodiversity. *Proc. Natl. Acad. Sci. USA* **108**, 4346-4351. (doi:10.1073/pnas.1017274108)

504   65. Fennell M, Murphy JE, Armstrong C, Gallagher T, Osborne B. 2012 Plant spread simulator:
505   a model for simulating large-scale directed dispersal processes across heterogeneous
506   environments. *Ecol. Model.* **230**, 1-10. (doi:10.1016/j.ecolmodel.2012.01.008)

507   66. Altermatt F. 2013 Diversity in riverine metacommunities: a network perspective. *Aquat.*
508   *Ecol.* **47**, 365-377. (doi:10.1007/s10452-013-9450-3)

22

509   67. Heller NE, Zavaleta ES. 2009 Biodiversity management in the face of climate change: a
510   review of 22 years of recommendations. *Biol. Conserv.* **142**, 14-32.
511   (doi:10.1016/j.biocon.2008.10.006)

512   68. Chisholm C, Lindo Z, Gonzalez A. 2011 Metacommunity diversity depends on connectivity
513   and patch arrangement in heterogeneous habitat networks. *Ecography* **34**, 415-424.
514   (doi:10.1111/j.1600-0587.2010.06588.x)

515

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

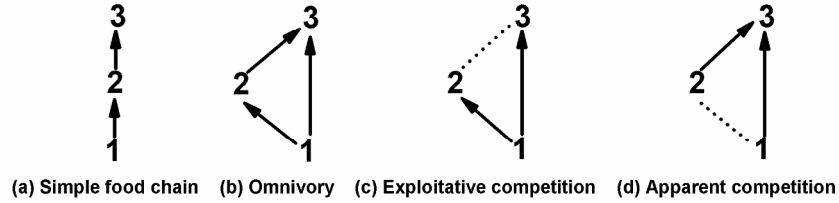535   equation (1). Other parameter values seen in figure 2.

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
μ_{ji}	The top-down extinction rate of species i eaten by species j
ρ_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
ρ_{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

24

(a) Simple food chain   (b) Omnivory   (c) Exploitative competition   (d) Apparent competition

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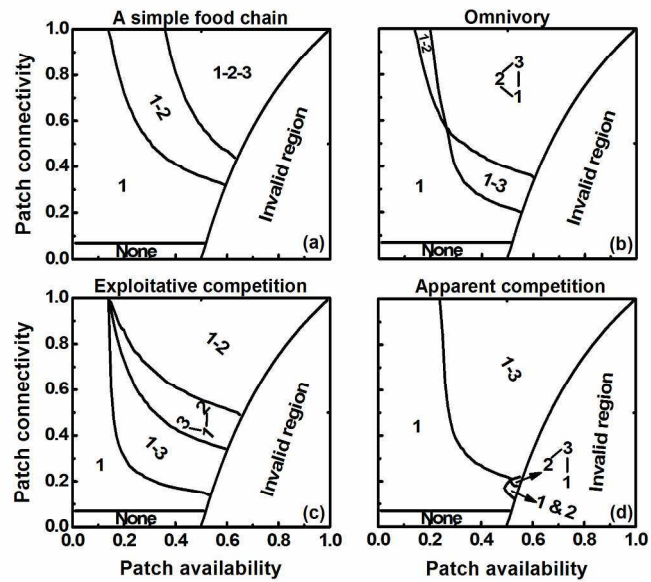
Interactive effects of patch availability and patch connectivity on species regional coexistence in different food webs, simultaneously considering species dispersal (1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal). Four food web structures are included: (a) a simple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

201x264mm (300 x 300 DPI)
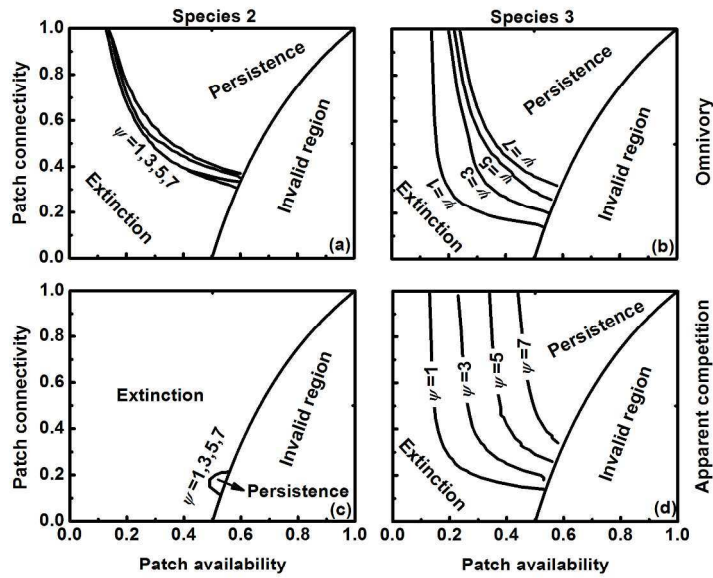
Effect of variation in species feeding preference cost on species extinction risk in omnivory versus apparent competition, simultaneously by varying both patch availability and patch connectivity. Again, species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal.

201x288mm (300 x 300 DPI)
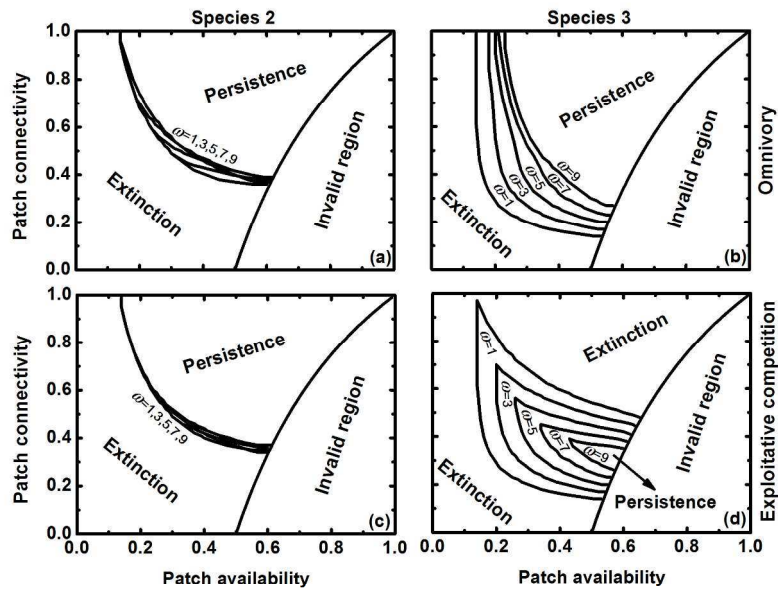
Effect of variation in species top-down extinction rate on species persistence in omnivory versus exploitative competition, while again varying both patch availability and connectivity. Species dispersal ranges: 1 – neighbour dispersal, 2 – within fragment dispersal, and 3 – global dispersal.

201x288mm (300 x 300 DPI)