DR. JINBAO LIAO (Orcid ID : 0000-0002-9520-3235)

Article type : Articles

Journal: Ecology

Manuscript type: Article

RUNNING HEAD: Robustness of omnivory structures

The role of omnivory in mediating metacommunity robustness to habitat destruction

Jinbao Liao[1,*], Daniel Bearup[2], William F. Fagan[3]

[1]Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed Research, School of Geography and Environment, Jiangxi Normal University, Ziyang Road 99, Nanchang 330022, China

[2]University of Kent, School of Mathematics, Statistics and Actuarial Sciences, Parkwood Road, Canterbury, CT2 7FS, UK

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/ECY.3026

[3]Department of Biology, University of Maryland, College Park, MD 20742, USA

[*]**Corresponding author:** E-mail: jinbaoliao@163.com

Abstract

Omnivores have long been known to play an important role in determining the stability of ecological communities. Recent theoretical studies have suggested that they may also increase the resilience of their communities to habitat destruction, one of the major drivers of species extinctions globally. However, these outcomes were obtained for minimal food webs consisting of only a single omnivore and its prey species, while much more complex communities can be anticipated in nature. In this study, we undertake a systematic comparative analysis of the robustness of metacommunities containing various omnivory structures to habitat loss and fragmentation using a mathematical model. We observe that, in general, omnivores are better able to survive facing habitat destruction than specialist predators of similar trophic level. However, the community as a whole does not always benefit from the presence of omnivores, as they may drive their intraguild prey to extinction. We also analyze the frequency with which these modules occur in a set of empirical food webs, and demonstrate that variation in their rate of occurrence is consistent with our model predictions. Our findings demonstrate the importance of considering the complete food web in which an omnivore is embedded, suggesting that future study should focus on more holistic community analysis.

Keywords: Omnivory, patch loss and fragmentation, patch-dynamic model, trophic-dependent dispersal, competition capability, food web persistence.

Introduction

There is a longstanding debate about the role of omnivorous species in mediating community stability (i.e., the ability of a system to return its original state after a small perturbation) and resilience (i.e., the return time to its original state after a small perturbation; see Landi et al. 2018). Early theory predicted that omnivory would destabilize food webs and therefore be rare in nature (Rosenheim et al. 1995, Holt and Polis 1997, Arim and Marquet 2004). This was supported by several empirical studies (e.g., Pimm and Lawton 1978, Pimm 1980, 1982, Cohen et al. 1990). The destabilizing mechanism was often attributed to the double pressures of competition and predation imposed by intraguild (IG) predator on IG prey. However, follow-up studies revealed that these empirical studies underestimated the frequency of omnivorous interactions, due to insufficient resolution and omission of weak trophic interactions (Martinez 1991, Polis 1991, McCann 2000). Omnivory structures are now considered to be ubiquitous across ecosystems and taxa (Kratina et al. 2012).

Recent theoretical and experimental studies suggest that effects of habitat structure may provide an explanation for the stabilizing mechanisms of food webs with omnivory (Diehl 1992, Fagan 1997, Morin 1999, Diehl and Feissel 2001, Melián and Bascompte 2002, Denno and Fagan 2003, Janssen et al. 2007, Gonzalez et al. 2011, Pillai et al. 2011, Kratina et al. 2012). In particular, physical barriers within a habitat (i.e., spatial refuges) can allow IG prey to avoid omnivores, permitting species coexistence that does not occur in a more connected habitat (Diehl 1992, Persson and Eklöv 1995, Holyoak and Sachdev 1998, Morin 1999, Diehl and Feissel 2001, Hillerislambers et al. 2006, Liess and Diehl 2006, Staddon et al. 2010, Martinson et al. 2012). However, this explanation presupposes that the omnivore is less able to cope with such barriers than its prey species. As it is more commonly observed that species at higher trophic levels display longer-range dispersal than their prey (e.g., Peters 1983, McCann et al. 2005, Greenleaf et al. 2007, Stevens et al. 2014), an additional mechanism may be required to explain the prevalence of omnivorous species. Liao et al. (2017a,b) proposed such an alternative mechanism, showing that

omnivory allows higher trophic level species (with dispersal superiority) to persist by feeding on different trophic levels despite habitat destruction. More specifically, the trophic rank hypothesis predicts that the top predator in a food web is most vulnerable to habitat destruction (Kruess and Tscharntke 1994) and thus will be the first species lost via a trophic cascade (Liao et al. 2016, 2017c). However, when the top predator is an omnivore, this vulnerability can be mitigated by switching to feeding on the more abundant prey species at lower trophic levels (Liao et al. 2017a,b). The greater dispersal range typical of such species can further reinforce this strategy by allowing them to access more prey species within the habitat (cf. Melián and Bascompte 2002, Pillai et al. 2011).

While they differ in their specifics, these mechanisms are both mediated primarily by the interaction between dispersal range and habitat heterogeneity. Variation in extinction rates arising from trophic interactions (e.g., feeding preference or predation pressure) also modifies species responses to habitat isolation and thus system robustness (Holt and Hoopes 2005, Chase et al.2010, Liao et al. 2017a,b). Here system robustness is defined as the degree of patch loss and fragmentation that can be tolerated without one or more species going extinct (Liao et al. 2017a). However, most relevant studies have focused on comparing a simple intraguild predation (IGP) system with a food chain, while ignoring more complex omnivory structures. In nature, many omnivorous predators can feed on two or more trophic levels without a direct competition link with their prey (i.e., without IGP) (Vadas 1990, O'Donoghue et al. 1995, Welch et al. 1997, Cooper and Vitt 2002, Persson et al. 2007). As such, we might reasonably anticipate that these more complex trophic interactions would modify, or even create new, responses to habitat heterogeneity with concomitant effects on community robustness (Amarasekare 2008). To gain insight into the effects of more complex omnivory structures on community robustness in fragmented landscapes, we make use of a spatially extended patch-dynamic framework (see Liao et al. 2017a,b) incorporating the factors mentioned above (Fig. 1): omnivory structure (e.g., the number of omnivorous links and their trophic positions), feeding traits, trophic-dependent

dispersal, patch loss and fragmentation. With this model, we attempt to answer the following urgent questions: (i) How do omnivorous trophic links affect the communities formed in spatially heterogeneous landscapes? (ii) Does the trophic position of prey species relative to the omnivore affect community response to habitat destruction? (iii) Can adding more omnivorous links promote metacommunity robustness to habitat loss and fragmentation? Finally, we analyze existing empirical data from real food webs to determine the relative frequency at which particular omnivory modules occur in order to validate our modelling predictions. Based on both theoretical predictions and statistical analysis, we hypothesize that there is a significant association between the frequencies of various modules observed in empirical food webs and their robustness to habitat destruction, i.e., more robust modules should occur more frequently in nature. More specifically, we can reasonably expect to observe more omnivory modules than the simple food chain in empirical food webs due to their higher robustness (Liao et al. 2017a). If so, we can further expect that adding more omnivorous links in the food chain should promote system robustness.

Methodology

Model overview

We model metacommunities on a broad landscape scale. In particular, we divide the landscape into patches of a characteristic size, representing an area which can support a self-sustaining subcommunity. We consider two patch types, suitable (*S*) and unsuitable (*U*) for colonization, and thus characterize the landscape with two parameters, patch availability (*S*) and patch connectivity ($q_{S/S}$), where $q_{S/S}$ measures the clustering degree of suitable patches (i.e., the aggregation of *S*-patches based on von Neumann neighbourship with four neighbours for each patch), representing the conditional probability that the neighbour of a randomly chosen *S*-patch is also an *S*-patch (Lloyd 1967, Matsuda et al. 1992, Harada and Iwasa 1994, Hiebeler 2000). Thus, patch availability is a direct representation of the habitat available within the landscape. The clustering degree is proportional to the size of connected regions of suitable habitat (*habitat fragments*) and thus captures one aspect of habitat fragmentation. As such, the fraction of unsuitable patches, i.e.,

patch loss $U = 1 - S$, and the fragmentation degree of suitable patches is inversely related to patch connectivity, i.e., patch fragmentation $1 - q_{S/S}$. Following the orthogonal neighbour correlation algorithm (Hiebeler 2000), we have

$$q_{S/S} > 2 - 1/S. \quad (1)$$

Model assumptions

In this study, we make several assumptions for model simplicity. Firstly, following existing models (With and King 1999, Hiebeler 2000, North and Ovaskainen 2007, Liao et al. 2013a), we assume that the landscape structure can be characterized in terms of the two parameters defined above. This allows us to consider the effects of habitat loss and habitat fragmentation separately without requiring us to use an explicitly spatial representation of the landscape. Secondly, we only consider trophic modules with four species at different trophic levels (Fig. 1a), as it is not feasible to model the full diversity of possible food web structures. These modules are a small system whose robustness to habitat destruction is easy to study and understand. Doing so can help identify the mechanisms on which complex network dynamics rely, avoiding confusion arising from the complexity of larger food webs. Thirdly, in accordance with natural observations (Peters 1983, McCann et al. 2005, Brose et al. 2006, Greenleaf et al. 2007, Stevens et al. 2014), we allow species dispersal range to increase with trophic level (trophic-dependent dispersal). Additionally, we make use of a categorical set of dispersal ranges (Fig. 1b-d), all of which can be described in terms of the landscape characteristics defined above, rather than a continuum of dispersal, which would require a more complex landscape representation. Fourthly, following Pillai et al. (2010, 2011), we assume that the omnivore prefers to consume the species at higher trophic level when prey species of different trophic levels are present in the same patch (i.e., feeding preference). Additionally, we assume that the predation pressure imposed on a prey species increases with the difference in trophic level between prey and predator. These assumptions are justified by the increase in body size and hence nutrient requirements, commonly observed as trophic level increases (Peters 1983, McCann et al. 2005, Brose et al. 2006, Greenleaf et al. 2007, Stevens et al.

2014). Finally, we assume that high trophic level species cannot survive in a local patch if none of its prey species are present (bottom-up control), following the patch-dynamic framework of food webs (e.g., Melián and Bascompte 2002, Fortuna and Bascompte 2006, Pillai et al. 2010, 2011).

Model system

We model a community consisting of four species at distinct trophic levels. Thus, there are eight possible trophic configurations (modules) for this community (see Fig. 1a). These configurations are distinguished by the 'rank of omnivory', that is, the number of prey-predator interactions in excess of those without omnivory structure, and by the trophic position of these interactions (Pimm and Lawton 1978).

The systematic framework introduced by Pillai et al. (2010) is used to describe the effects of trophic interactions on the patch occupancy of each species. As this framework is non-spatial, we follow Liao et al. (2017a,b) by assigning each species one of three categorical dispersal ranges, which determines its colonization rate with reference to the degree of habitat fragmentation in the landscape (Fig. 1b-d). The lowest trophic level species uses *neighbour dispersal*, which restricts it to colonizing adjacent *S*-patches (Fig. 1b). As such, the availability of colonizable patches for such species is given by the clustering degree of their colonies with unoccupied *S*-patches, and the patch-occupancy dynamics can be described using a pair approximation method (Liao et al. 2017a,b). The second species uses *within-fragment dispersal*, which allows it to colonize *S*-patches within a habitat fragment. Unsuitable patches can block dispersal between habitat fragments (Fig. 1c). Thus, the colonization rate for this species is determined by the average size of habitat fragments which we describe using the habitat connectivity $q_{S/S}$ (Lloyd 1967, Matsuda et al. 1992, Harada and Iwasa 1994, Hiebeler 2000, Liao et al. 2016). The third and fourth species use *global dispersal*, which allows them to colonize any *S*-patch in the landscape (Fig. 1d). Species using such dispersal mode are described in our model in exactly the same way as in existing patch-dynamic models (Pillai et al. 2010).

To provide an example of how this description translates to a mathematical representation of the module dynamics, we take the four species food chain 1→2→3→4 (Fig. 1a) as a reference structure. Similar to Liao et al. (2017a,b), the patch dynamics of this module are given by

$$\frac{dP_1}{dt} = \underbrace{c_1(P_1 - \rho_{11} - \rho_{1U})}_{\text{Neighbour dispersal}} \underbrace{- e_1 P_1}_{\text{Intrinsic extinction}} \underbrace{- \mu_{21} F_{1,2}}_{\text{Predation}}, \quad (2)$$

$$\frac{dF_{1,2}}{dt} = \underbrace{c_{21} F_{1,2}(P_1 - F_{1,2}) q_{S/S}}_{\text{Within - fragment dispersal}} \underbrace{- (e_1 + e_2) F_{1,2}}_{\text{Intrinsic extinction}} \underbrace{- \mu_{21} F_{1,2} - \mu_{32} F_{2,3}}_{\text{Predation}}, \quad (3)$$

$$\frac{dF_{2,3}}{dt} = \underbrace{c_{32} F_{2,3}(F_{1,2} - F_{2,3})}_{\text{Global dispersal}} \underbrace{- (e_1 + e_2 + e_3) F_{2,3}}_{\text{Intrinsic extinction}} \underbrace{- (\mu_{21} + \mu_{32}) F_{2,3} - \mu_{43} F_{3,4}}_{\text{Predation}}, \quad (4)$$

$$\frac{dF_{3,4}}{dt} = \underbrace{c_{43} F_{3,4}(F_{2,3} - F_{3,4})}_{\text{Global dispersal}} - \underbrace{(e_1 + e_2 + e_3 + e_4) F_{3,4}}_{\text{Intrinsic extinction}} - \underbrace{(\mu_{21} + \mu_{32} + \mu_{43}) F_{3,4}}_{\text{Predation}}, \quad (5)$$

in which all parameters are defined in Table 1. Note that this modelling framework characterizes the patch dynamics of the possible trophic links instead of individual species subject to the colonization-extinction-predation processes.

To represent neighbour dispersal, species 1 can only colonize empty suitable patches adjacent to itself, i.e., the clustering of suitable sites with its colonized sites $q_{s/1} = (1 - q_{1/1} - q_{U/1})$. This follows from the fact that there are three possible states for a neighbor of species 1: unoccupied suitable patch (*s*), occupied suitable patch (1), and unsuitable patch (*U*). To obtain the rate at which new colonies of this species are created, we multiply by the colonization rate c_1 and the size of the population P_1, with $c_1 P_1(1 - q_{1/1} - q_{U/1}) = c_1(P_1 - \rho_{11} - \rho_{1U})$ due to $q_{1/1} = \rho_{11}/P_1$ and $q_{U/1} = \rho_{1U}/P_1$ (see Eq. 2 and Table 1; defined by Matsuda et al. 1992, Hiebeler 2000). In order to construct a closed dynamical system, we further derive the dynamics of ρ_{11} and ρ_{1U} (as shown in Appendix S1: Eqs S9 & S10), which involve both patch availability (*S*) and connectivity ($q_{S/S}$). As such, we are able to investigate the effects of patch loss ($U = 1 - S$) and fragmentation ($1 - q_{S/S}$) on the persistence of species 1, and these effects can be transmitted to other species via trophic cascading effect.

Similarly, the term involving colonization by species 2, found in Eq. 3, is multiplied by the clustering degree $q_{S/S}$ to estimate the limited dispersal within habitat fragments for species 2, thus the dispersal range of species 2 is determined by patch connectivity (cf. Liao et al. 2016, 2017a,b). Finally, since we assume that species 3 & 4 disperse globally, we do not modify the colonization terms used by Liao et al. (2017a,b) for these two species in Eqs 4 & 5. The patch-dynamics for other omnivory structures listed in Fig. 1a can be found in Appendix S1.

In this study, we primarily use numerical methods to derive the non-trivial stable equilibrium states for system simulations, thereby determining which species survive or go extinct. To our knowledge, spatial food webs at the regional scale have not been parameterized using realistic biological estimates yet, thus we choose a single set of parameter ranges (similar to previous models of Liao et al. 2017a,b) for all modules. Parameter values (relative extinction rate e_i/c_i at fixed c_i=1 and top-down extinction rate μ_{ji}) are varied within the defined ranges (see Table 1) to assess the robustness of our results. Meanwhile, changes in these parameter values allow us to further explore how feeding preference (φ) or/and predation pressure (ω) modify the effect of habitat destruction on spatial food web persistence (i.e., coexistence of all species at ecological regime). For example, we represent species feeding preference by altering the extinction rate of the omnivore when preying on different trophic levels. In particular, we assume that the omnivore has a lower extinction rate when feeding on its preferred prey ($\varphi=e_{jk}/e_{ji}$). We represent predation pressure by including predation-induced extinction rates (i.e., top-down control) which increase with the trophic level of the predator ($\omega=\mu_{ki}/\mu_{ji}$). Our results are qualitatively robust for a broad range of parameter combinations (Appendix S2: Figs S1-S24), for example, assigning different dispersal ranges to different trophic-level species (Appendix S2: Figs S10-S14), and varying feeding preference (φ) or/and predation pressure (ω) (Appendix S2: Figs S15-S24). As such, we use symmetrical parameter combinations as a representative reference parameter set throughout.

Module composition of empirical food webs

To test our model predictions, we analyze the module composition of a set of 113 empirical food webs across terrestrial, freshwater, marine and soil ecosystems (compiled by Cohen et al. 1990). Within each food web, we begin by determining the number of modules which contain 4 species linked in a food chain. Then, we categorize these modules according to how many additional omnivorous links they contain.

The frequency with which such modules occur depends on the number of species and links within the food web (Appendix S3: Fig. S1). To correct for this, we fit a linear model relating link density (links/species$^{1.25}$) to number of modules, allowing the intercepts to vary for each module type, and use this model to adjust module numbers for each community to a common link density (Appendix S3). We also calculate the relative frequency of each module type (number of modules of given type/total number of modules) in each food web as an alternative correction for this issue.

Results

Overview of community formation patterns

We begin with a general overview of the effects of patch availability and connectivity on the communities formed for each of the food web modules considered (Fig. 2). In all modules, as both patch availability and connectivity increase continuously, the community formed transits from the case containing only the basal species to another case containing all possible species. However, the order in which species are added to the community during this transition is determined by the omnivorous links included in the food web module and the strength of interactions between the species. As the effects of the interaction strength are relatively straightforward (Appendix S2: Figs S18-S24), we focus on the effects of food web structure.

In a simple food chain, community formation follows the trophic rank hypothesis; as habitat availability and connectivity decrease, species become extinct in order of decreasing trophic level (Fig. 2a). Omnivorous links modify this, with lower-level consumers going extinct sooner than the omnivores in more destructive habitats (Fig. 2b & 2d provide clear examples). This occurs when

the shared prey is present in the community and the omnivore is able to outcompete lower-level consumers due to its dispersal superiority. This mechanism can be clearly seen by comparing Fig. 2b (where species 3 is an omnivore capable of consuming species 1) with Fig. 2a (the simple food chain). Figure 2a shows that species 2 (the direct consumer of the basal species) can tolerate much more patch loss and fragmentation than species 3, in contrast to Fig. 2b where species 3 as the omnivore can survive at much lower thresholds of habitat availability and connectivity due to its greater dispersal range. This pattern is evident for those modules where the omnivore is able to feed on the basal species (e.g., Fig. 2b, d-h). Note that when species 3 and 4 are able to consume this species (Fig. 2c, e & h), they display the same extinction thresholds of habitat metrics (although with different patch occupancies, see Appendix S2: Figs S1-S8). This occurs because both species 3 & 4 display the same dispersal range, and species 4 is able to offset species 3's superior feeding efficiency (lower resource requirements) by feeding on species 3 in addition to the basal species in such communities.

Additionally, for reasonable assumptions about the interaction parameters, we observe more complex community formation patterns (see Fig. 2b, d & g), mediated by habitat connectivity (inversely related to fragmentation). In particular, if species 2 has lower resource requirements than the larger omnivores, it outcompetes them in highly connected habitats but is excluded in less connected habitats. In the former habitat type, there is little difference between within-fragment dispersal and global dispersal, so community formation is dominated by the interactions between species. However, in the latter habitat type, increased dispersal range allows the large omnivore to find more prey offsetting the competitive disadvantage of higher resource requirements, while species 2's dispersal range is greatly restricted.

The effect of omnivory structure on community robustness

We observe that the number of, and species involved in, omnivorous links alters the robustness of the full community to habitat destruction (Fig. 3). Food webs with a single omnivorous link (Fig. 3a) are most robust when the omnivore is species 3, and least robust when species 4 can feed on

the basal species. However, when a second omnivorous link is included (Fig. 3b), the most robust community is obtained when both omnivores 3 & 4 can feed on the basal species. This demonstrates that the effect of a given trophic link depends on the structure of the rest of the food web.

Furthermore, increasing the number of omnivorous links does not always increase community robustness (Fig. 3c & 3d). We see that the community is most robust with two specific omnivorous links (species 3 and 4 consuming the basal species) although including all possible omnivorous links is only slightly less robust (Appendix S2: Fig. S9). Furthermore, a single omnivorous link, species 3 feeding on species 1, produces similar robustness to habitat loss to that observed in these cases but not to habitat fragmentation (Fig. 3d). In relatively low levels of patch connectivity ($q_{S/S} < 0.7$ in Fig. 3c), we also observe that the community with a single 1-4 omnivorous link can tolerate much more habitat destruction than the module containing 1-4 & 2-4 links. In extreme cases, adding omnivorous links even makes the community less robust to habitat destruction than the simple food chain in relatively fragmented landscapes by increasing predation pressure (Appendix S2: Fig. S16c).

Combining these observations, we suggest that the primary factor determining how omnivory influences community robustness is the degree to which it truncates maximum food chain length. In particular, the most robust communities occur when all species are able to feed directly on the basal species. Competition between species, mediated by resource requirements, dispersal range and feeding traits (by varying feeding preference or/and predation pressure in Appendix S2: Figs S15-S24), plays a secondary role as evidenced by the differences in robustness between the single omnivory link cases (species 3 or 4 feeding on species 1) and the fact that system robustness decreases when all omnivorous links are present.

Prevalence of omnivory modules in empirical food webs

There is considerable variation in the number of each type of module occurring in the empirical food webs considered (Fig. 4). Nonetheless, we can see that modules containing omnivorous links occur, on average, more frequently than the simple 4-species food chain (Fig. 4a & c), with 57% of omnivory modules compared with 43% simple food chains. Note that the median values reflect a similar ratio as do the adjusted absolute numbers of modules (Fig. 4a).

Considering types of omnivory module individually (Fig. 4b & d), we find that the most common types are the 1-3, 2-4 and 1-3 & 2-4 modules, all of which are predicted to increase food web robustness to habitat destruction substantially relative to a simple food chain. The median percentages of modules, 1-4 and 1-4 & 2-4, which increase robustness much less, are close to zero, though the mean values are higher due to the relatively high prevalence (up to 25%) in some food webs. The 1-3 & 1-4 and 'All' modules (All – including all possible omnivorous links), which in theory maximize food web robustness, occur relatively infrequently but still more frequently than those that decrease robustness.

Discussion

The relationship between omnivory structure and system stability is a longstanding focus of attention in ecology (Diehl 1992, Morin 1999, McCann 2000, Diehl and Feissel 2001, Arim and Marquet 2004, Kratina et al. 2012). The present model supports the theoretical prediction that omnivory structures can be of paramount importance for the stability of ecological communities. Communities form according to complex mechanisms involving trophic structure, landscape characteristics (patch loss and fragmentation), and species dispersal ranges.

When omnivorous links are added to a food chain, the trophic distance between omnivores and basal resources decreases. This allows omnivores to reduce their vulnerability to the trophic cascade underlying the trophic rank hypothesis (Kruess and Tscharntke 1994). If species at lower trophic levels are able to coexist with the omnivore due to decreased predation, this increases the robustness of the community to habitat destruction. However, the precise outcome is sensitive to

the relative competitiveness of the omnivore and these lower trophic level species, as demonstrated in Figs 3 and Appendix S2: Figs S15-S17. A particular example of this, which can be supported with empirical evidence, is the relative robustness of the 1-3 module (Fig. 2a *vs.* 2b). Without the fourth species, the second species faces the dual pressure of competition and predation from the omnivore and thus is very vulnerable to extinction. In a whole lake invasion study, Persson et al. (2007) found that long-term coexistence of species could only occur when an intraguild (IG) predator was consumed preferentially by another predator. Essentially, adding a predator of the IG predator would reduce its feeding pressure on the IG prey, thereby stabilizing the trophic system (the mechanism of predator interference; see Amarasekare 2008). Similarly, adding 1-4 links to the system with 2-4 links, where omnivorous feeding can offset the superiority of species 3 competing for prey species 2, leads to the lowest system robustness to habitat destruction among configurations with two omnivorous links. In this system, species 3 becomes highly vulnerable due to predation and competitive pressure from species 4 (Figs 2 & 3).

Another potential mechanism by which omnivory can increase community robustness to habitat destruction is adaptive feeding behavior (Holt and Polis 1997, Kratina et al. 2012). This is captured by our model (Appendix S2: Figs S2-S8). In high quality landscapes, the patch occupancy of links between the omnivore and its direct prey species is high. However, as habitat deterioration increases, there is a gradual increase in patch occupancy of links where it feeds on its other prey, reaching a maximum where its direct prey becomes extinct (Appendix S2: Figs S2c, S4e, S5d & g, S6d, S7d & S8c & f). This suggests that the omnivore at high trophic level can switch its feeding on different prey species by adjusting the proportion of each in a mixed diet in response to habitat destruction, thereby reducing trophic cascading effect and offering more opportunities for its survival (Liao et al. 2017a,b). Furthermore, in our model, when an IG predator is placed in competition for the shared prey with its IG prey, these species can co-occur regionally. This should be due to the tradeoff between the competitive superiority of IG prey and the dispersal advantage of IG predator. Therefore, adaptive feeding behavior in addition to the

dispersal-competition tradeoff allows the full community to persist at higher levels of habitat destruction, as observed in empirical studies (Scheirs and De Bruyn 2002, Shochat et al. 2004).

It should be emphasized that increasing omnivory within a community does not always enhance food web persistence in fragmented landscapes (Fig. 3; Appendix S2: Figs S15-S17), since the omnivorous links have different effects dependent on their trophic position. Additionally, changing omnivory degree by increasing feeding preference or predation pressure can largely alter system robustness to habitat destruction (Appendix S2: Figs S15-S17). If the predation pressure introduced by the omnivore is too strong, the presence of the omnivore can even make the community more vulnerable to particular forms of habitat destruction (Appendix S2: Fig. S16c). In such cases the increase in predation pressure leads to an increased extinction rate of prey, thereby lowering the robustness of the overall system.

Our analysis of empirical food webs shows that the four-species modules containing an omnivore occur more frequently than simple food chains in nature (Fig. 4). This observation is in good agreement with our model prediction that these modules generally display greater robustness to habitat destruction than the simple food chain. The similarity of the results for isolated modules and entire food webs suggests that increasing the presence of omnivorous modules may result in more robust food webs. However, it does not mean that there is a direct, one-to-one, relationship between the relative persistence of modules in isolation and their effects on persistence of the whole food web, as the persistence of these modules can be altered by other species or other trophic and/or non-trophic interactions (e.g., indirect competition) (Stouffer and Bascompte 2010). Thus, caution is required when assuming that one can directly scale up from the module, microcosm or mesocosm scale to that of entire food webs. Furthermore, at least for modules with a single omnivorous link, there is a clear correlation between the theoretical effect of that link on community robustness and the frequency with which it occurs. In particular, the 1-3 and 2-4 links, which result in relatively high robustness (Fig. 2), are observed more frequently than the 1-4 link which results in relatively low robustness. Given that we can expect more robust communities to

occur more frequently in nature (McCann et al. 1998), these observations provide indirect support for our modelling predictions. Nonetheless, we must emphasize that there may be additional factors influencing the frequency with which these modules occur. In particular, modules with more than one omnivorous link all occur relatively infrequently (Fig. 4), regardless of their predicted effects on community robustness. One explanation for the rarity of these modules could be constraints on biologically viable feeding behaviors. In three of these modules, the top predator is able productively consume the basal species, in practice the size differentials that develop across trophic levels, and the specialization required to hunt prey, make this unlikely. Additionally, we cannot directly analyze how habitat availability and connectivity varies across this data set, since these metrics were not recorded. Consequently, given the variability present in the data available, it is not possible to conclusively assert that these patterns arise from the effects that our model predicts.

Previous studies have demonstrated that habitat isolation can promote species coexistence by providing spatial refugia for prey species, thereby increasing community robustness (Diehl 1992, Persson and Eklöv1995, Morin 1999, Diehl and Feissel 2001, Finke and Denno 2006, Janssen et al. 2007). This type of behavior is not captured in our model, as we explicitly assume that the IG predator with global dispersal can access to any prey colony sites freely. Essentially, this is a natural consequence of the scale chosen for our model; we consider large-scale habitat structure, the arrangement of patches which can support a population. In contrast, the mechanism of spatial refugia is based on small scale variation within a patch (Diehl 1992, Morin 1999, Diehl and Feissel 2001), for example, terrain features which are inaccessible to the predator. Nonetheless, we suggest that the effects of this mechanism may not be straightforward if an omnivore is present in the food web. In particular, Peckarsky and McIntosh (1998) and Janssen et al. (2007) observed that intraguild (IG) and shared prey often use similar habitat structures as refuges to escape from the omnivore. This has the potential to increase predation by the IG prey on the shared prey, thereby increasing the vulnerability of the latter to extinction.

In order to formulate this relatively simple mathematical model, we have had to make a number of assumptions. While some of these assumptions (e.g., trophic-dependent dispersal, trophic modules with four species, and feeding preference/pressure) can be justified from empirical observations, there are three that require further comment. Firstly, real landscapes rarely consist of neatly divided patches of 'habitat' and 'non-habitat' as we have assumed. Instead habitat degradation coincides with reduction in habitat quality, so that most landscapes show at least some levels of habitat variegation (varying species suitability; Liao et al. 2013b). This could be modelled directly by assigning each patch (in a spatially explicit landscape) a habitat quality that would determine colonization (or extinction) rates. Our model can be regarded as an approximation of this more complex description, with the colonization and extinction rates used being the averages that would be obtained over this landscape. With this in mind, we might expect that our simpler formulation will slightly overestimate community robustness for a given set of parameters, as on this scale, variability in these rates tends to depress populations (i.e., increasing interspecific difference). Secondly, our use of categorical dispersal ranges is a strong restriction on the types of dispersal behavior that we consider. We do obtain qualitatively similar results (Appendix S2: Figs S12-S14) when we assign alternative dispersal ranges within the community, suggesting that the effect of this limitation is not too great. Nonetheless, it would clearly be beneficial to develop a larger set of possible dispersal ranges based on the existing landscape characterization. Finally, the strict rules for feeding behavior, i.e., predators require a prey in the same patch and predators always consume their highest trophic level prey (Pillai et al. 2010), constrain the types of community that can emerge. The former assumption is reasonable if habitat patches are relatively large, but would breakdown at smaller scales. Thus, this assumption places a lower limit on the size of habitat patches (the hunting range of the largest predator), i.e., it defined a characteristic scale of our model. The latter assumption means that predation pressure from omnivores is not spread between all possible prey species within a module, instead being focused on the shared prey species. As such, it may result in underestimating community robustness

relative to a model which allows the omnivore to consume all possible prey species present (Melián and Bascompte 2002).

We investigate how different omnivory structures affect system robustness to habitat loss and fragmentation using a mathematical model. Species within a food web module exhibit varying sensitivities to the differing forms of habitat destruction, yielding diverse patterns of species survival. Furthermore, adding more omnivory links does not always promote food web persistence, instead it may increase vulnerability to habitat destruction. While observed patterns of occurrence of modules containing omnivores are consistent with our modelling predictions, conclusive tests of these predictions would require measurement of the degree of habitat destruction to which a community was subject. This could be achieved either through field observations (by estimating habitat loss and fragmentation within a landscape) or laboratory-based microcosms (where these properties could be manipulated directly) (Persson et al. 2007, Chase et al. 2010, Chisholm et al. 2011, Carrara et al. 2012). Overall, our findings enrich our knowledge of the omnivory-stability relationship in a spatial context, suggesting that further study should focus on identifying conditions under which omnivory structure is a stabilizing feature of more complex natural systems.

Acknowledgments

This study was supported by the National Science Foundation of China (No. 31760172 & 31901175), the Thousand Young Talents Plan of China, the Key Joint Youth Project of Jiangxi Province (No. 20192ACBL21029), the Jiangxi Provincial Education Department (No. GJJ160274), and the Doctoral Scientific Research Foundation of Jiangxi Normal University (No. 12017778). J.L. designed this study, performed numerical simulations and wrote the manuscript; J.L. and D.B. analyzed the results; all authors contributed substantially to revisions.

Literature cited

Amarasekare, P. 2008. Coexistence of intraguild predators and prey in resource-rich environments. Ecology 89:2786-2797.

Arim, M., and P. A. Marquet. 2004. Intraguild predation: A widespread interaction related to species biology. Ecology Letters 7:557-564.

Brose, U. et al. 2006. Consumer-resource body-size relationships in natural food webs. Ecology 87:2411-2417.

Carrara, F., F. Altermatt, I. Rodriguez-Iturbe, and A. Rinaldo. 2012. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. Proceedings of the National Academy of Sciences USA 109:5761-5766.

Chase, J. M., A. A. Burgett, and E. G. Biro. 2010. Habitat isolation moderates the strength of top-down control in experimental pond food webs. Ecology 91:637-643.

Chisholm, C., Z. Lindo, and A. Gonzalez. 2011. Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. Ecography 34:415-424.

Cohen, J. E., F. Briand, and C. M. Newman. 1990. Community food webs: Data and theory. Springer-Verlag, New York, New York, USA.

Cooper, W. E., and L. J. Vitt. 2002. Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology 257:487-517.

Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology 84:2522-2531.

Diehl, S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73:1646-1661.

Diehl, S., and M. Feissel. 2001. Intraguild prey suffer from enrichment of their resources: A microcosm experiment with ciliates. Ecology 82:2977-2983.

Fagan, W.F. 1997. Omnivory as a stabilizing feature of natural communities. American Naturalist 150:554-567.

Finke, D. L., and R. F. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia 149:265-275.

Fortuna, M. A., and J. Bascompte. 2006. Habitat loss and the structure of plant-animal mutualistic networks. Ecology Letters 9:281-286.

Gonzalez, A., B. Rayfield, and Z. Lindo. 2011. The disentangled bank: How loss of habitat fragments and disassembles ecological networks. American Journal of Botany 98:503-516.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589-596.

Harada, Y., and Y. Iwasa. 1994. Lattice population dynamics for plants with dispersing seeds and vegetative propagation. Research on Population Ecology 36:237-249.

Hiebeler, D. 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. Ecology 81:1629-1641.

HilleRisLambers, R., J. van de Koppel, and P. M. J. Herman. 2006. Persistence despite omnivory: Benthic communities and the discrepancy between theory and observation. Oikos 113:23-32.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist 149:745-764.

Holt, R. D., and M. F. Hoopes. 2005. Food web dynamics in a metacommunity context. In: Metacommunities: Spatial Dynamics and Ecological Communities (eds. Holyoak M., M. A. Leibold, and R.D. Holt). University of Chicago Press, Chicago and London, pp.68-93.

Holyoak, M., and S. Sachdev. 1998. Omnivory and the stability of simple food webs. Oecologia 117:413-419.

Janssen, A., M. W. Sabelis, S. Magalhaes, M. Montserrat, and T. Van der Hammen. 2007. Habitat structure affects intraguild predation. Ecology 88:2713-2719.

Kratina, P., R. M. Lecraw, T. Ingram, and B. R. Anholt. 2012. Stability and persistence of food webs with omnivory: is there a general pattern? Ecosphere 3:50.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. Science 264:1581-1584.

Landi, P., H. O. Minoarivelo, Å. Brännström, C. Hui, and U. Dieckmann. 2018. Complexity and stability of ecological networks: a review of the theory. Population Ecology 60:319-345.

Liao, J., Z. Li, D. E. Hiebeler, M. El-Bana, G. Deckmyn, and I Nijs. 2013a. Modelling plant population size and extinction thresholds from habitat loss and habitat fragmentation: effects of neighbouring competition and dispersal strategy. Ecological Modelling 268:9-17.

Liao, J., Z. Li, D. E. Hiebeler, Y. Iwasa, J. Bogaert, and I. Nijs. 2013b. Species persistence in landscapes with spatial variation in habitat quality: a pair approximation model. Journal of Theoretical Biology 335:22-30.

Liao, J., J. Chen, Z. Ying, D. E. Hiebeler, and I. Nijs. 2016. An extended patch-dynamic framework for food chains in fragmented landscapes. Scientific Reports 6(6):33100.

Liao, J. et al. 2017a. Robustness of metacommunities with omnivory to habitat destruction: disentangling patch fragmentation from patch loss. Ecology 98:1631-1639.

Liao, J., D. Bearup, and B. Blasius. 2017b. Food web persistence in fragmented landscapes. Proceedings of the Royal Society B 284:20170350.

Liao, J., D. Bearup, and B. Blasius. 2017c. Diverse responses of species to landscape fragmentation in a simple food chain. Journal of Animal Ecology 86:1169-1178.

Liess, A., and S. Diehl. 2006. Effects of enrichment on protist abundances and bacterial composition in simple microbial communities. Oikos 114:15-26.

Lloyd, M. 1967. Mean crowding. Journal of Animal Ecology 36:1-30.

Martinez, N. D. 1991. Artifacts or attributes: effects of resolution on the little-rock lake food web. Ecological Monographs 61:367-392.

Martinson, H. M., W. F. Fagan, and R. F. Denno. 2012. Critical patch sizes for food-web modules. Ecology 93:1779-1786.

Matsuda, H., N. Ogita, A. Sasaki, and K. Sato. 1992. Statistical mechanics of population: the lattice Lotka-Volterra model. Progress in Theoretical Physics 88:1035-1049.

McCann, K. S., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794-798.

McCann, K. S. 2000. The diversity-stability debate. Nature 405:228-233.

McCann, K. S., J. R. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. Ecology Letters 8:513-523.

Melián, C. J., and J. Bascompte. 2002. Food web structure and habitat loss. Ecology Letters 5:37-46.

Morin, P. 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology 80:752-760.

North, A., and O. Ovaskainen. 2007. Interactions between dispersal, competition, and landscape heterogeneity. Oikos 116:1106-1119.

O'Donoghue, M., E. Hofer, and F. I. Doyle. 1995. Predator versus predator. Natural History 104:6-9.

Peckarsky, B.L., and A. R. Mcintosh. 1998. Fitness and community consequences of avoiding multiple predators. Oecologia 113(4):565-576.

Persson, L., and P. Eklöv. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. Ecology 76:70-81.

Persson, L., A. M. De Roos, and P. Bystrōm. 2007. State dependent invasion windows for prey in size structured predator-prey systems: whole lake experiments. Journal of Animal Ecology 76:94-104.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Pillai, P., M. Loreau, and A. Gonzalez. 2010. A patch-dynamic framework for food web metacommunities. Theoretical Ecology 3:223-237.

Pillai, P., A. Gonzalez, and M. Loreau. 2011. Metacommunity theory explains the emergence of food web complexity. Proceedings of the National Academy of Sciences USA 108:19293-19298.

Pimm, S. L., and J. H. Lawton. 1978. Feeding on more than one trophic level. Nature 275:542-544.

Pimm, S. L. 1980. Properties of food webs. Ecology 61:219-225.

Pimm, S. L. 1982. Food webs. Chapman & Hall. London, UK.

Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. American Naturalist 138:123-155.

Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biological Control 5:303-335.

Scheirs, J., and L. De Bruyn. 2002. Integrating optimal foraging and optimal oviposition theory in plant-insect research. Oikos 96:187-191.

Shochat, E., S. Lerman, M. Katti, and D. Lewis. 2004. Linking optimal foraging behavior to bird community structure in an urban-desert landscape: field experiments with artificial food patches. American Naturalist 164:232-243.

Staddon, P., Z. Lindo, P. D. Crittenden, F. Gilbert, and A. Gonzalez. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. Ecology Letters 13:543-552.

Stevens, V. M. et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semiterrestrial animals. Ecology Letters 17:1039-1052.

Stouffer, D. B., and J. Bascompte. 2010. Understanding food-web persistence from local to global scales. Ecology Letters 13:154-161.

Vadas, R. L. 1990. The importance of omnivory and predator regulation of prey in fresh-water fish assemblages of North-America. Environmental Biology of Fishes 27:285-302.

Welch, C. A., J. Keay, K. C. Kendall, and C. T. Robbins. 1997. Constraints on frugivory by bears. Ecology 78:1105-1119.

With, K. A., and A. W. King. 1999. Extinction thresholds for species in fractal landscapes. Conservation Biology 13:314-326.

Tables

Table 1. Definitions and the range of values of variables and parameters

Symbols	Definitions	Range values
U	Fraction of unsuitable patches (patch loss)	[0, 1]
S	Fraction of suitable patches (patch availability)	[0, 1]
s	Fraction of unoccupied suitable patches	[0, S]
$q_{S/S}$	Conditional probability that a randomly chosen neighbour for a S-patch is also suitable (patch connectivity)	[2-1/S, 1]
c_i	Colonization rate of species i	1
c_{ji}	Colonization rate of species j when feeding on species i	1
e_i	Intrinsic extinction rate of species i	[0.025, 0.225]
e_{ji}	Intrinsic extinction rate of species j when feeding on species i	[0.025, 0.225]
μ_{ji}	Top-down extinction rate of species i eaten by species j due to over-predation	[0.035, 0.315]
P_i	Patch occupancy of species i (=1,2,3,4)	[0, 1]
$F_{i,j}$	Patch occupancy of trophic link i→j, with "→" indicating species j feeding on species i in a local patch	[0, P_i]
ρ_{kl}	Probability of a randomly chosen pair of neighbours that one is k-patch and another is l-patch	[0, 1]
$q_{k/l}$	Conditional probability that a randomly chosen neighbour for a l-patch is a k-patch with $q_{k/l}=\rho_{kl}/P_l$	[0, 1]

Figure Legends

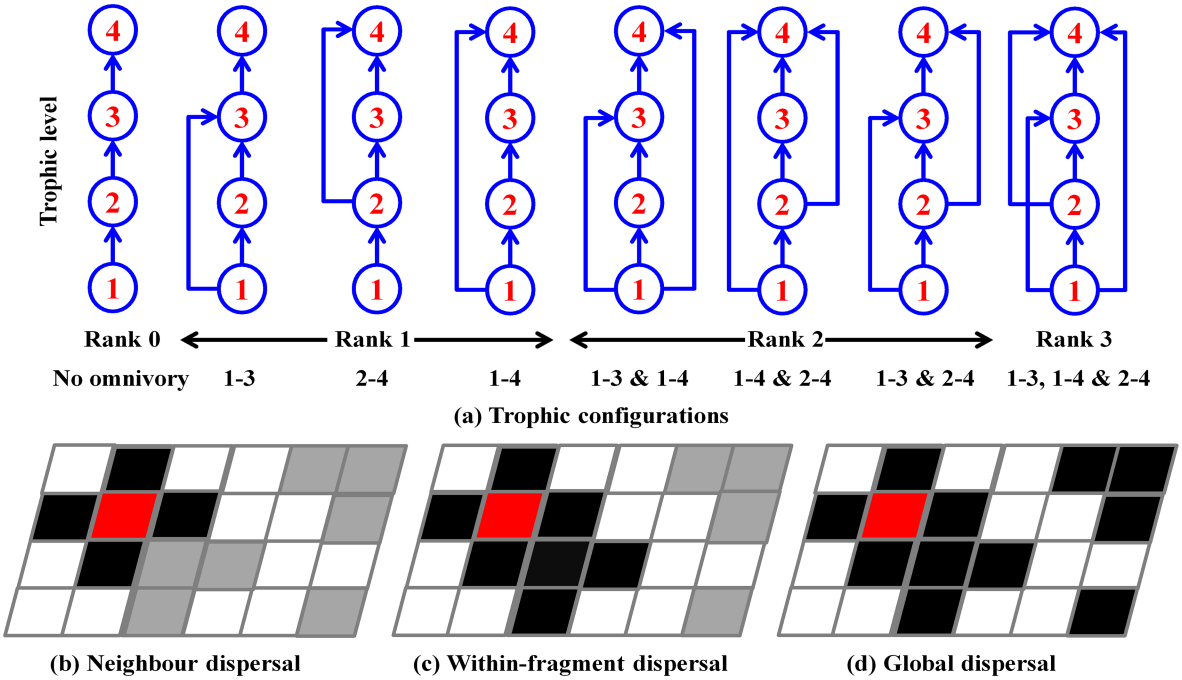
Figure 1. Schematic illustration of a community consisting of four species placed at four trophic levels respectively in fragmented landscapes. (a) Possible trophic configurations: a simple food chain with no omnivory structure, with one omnivorous link (i.e., 1-3, 2-4 or 1-4), with two omnivorous links (i.e., 1-3 & 1-4, 1-4 & 2-4, or 1-3 & 2-4), and with three omnivorous links (i.e., including all 1-3, 1-4 & 2-4 links); (b) species 1 (red) with *neighbour dispersal* can only access to its adjacent suitable patches (black); (c) species 2 (red) having *within-fragment dispersal* can colonize suitable patches (black) within a habitat fragment (defined as a number of connected suitable patches); (d) both species 3 & 4 (red) with *global dispersal* as the omnivore can colonize any suitable patches (black) across the landscape. Panels (b-d): white – unsuitable patches, grey – suitable patches but inaccessible due to dispersal range, and black – suitable patches and accessible within the dispersal range.

Figure 2. Species regional coexistence among different omnivory structures in fragmented landscapes (varying both patch availability and connectivity). Species dispersal range: 1 – neighbour dispersal, 2 – within-fragment dispersal, 3 & 4 – global dispersal. Invalid region: see Eq. 1 (different colors – different community patterns, None – all species extinction). Parameter values: species colonization rate c_i=c_{ji}=1, intrinsic extinction rate e_i=e_{ji}=0.025 and top-down extinction rate μ_{ji}=0.035 ($i,j\in\{1,2,3,4\}$ with $j>i$).

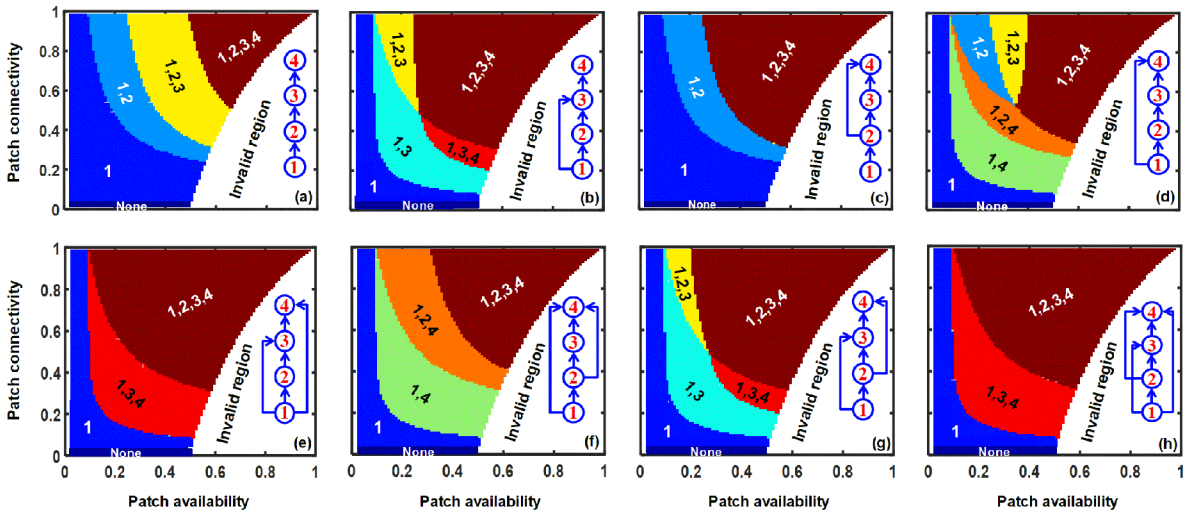
Figure 3. Interactive effects of patch availability and connectivity on food web persistence among different omnivorous configurations, simultaneously by considering species dispersal (1 – neighbour dispersal, 2 – within fragment dispersal, and 3 & 4 – global dispersal). The black, red and blue solid lines dividing the region of food web persistence (i.e., all species survive; upper-right region) and species exclusion (i.e., one or more species go extinct; lower-left region) varies with patch availability and connectivity. Invalid region: Eq. 1. Parameter values: see Fig. 2.

Figure 4. Frequency of the occurrence for four-species modules in empirical food webs. Panels (a) & (b): number of modules adjusted to a single link density (0.907); Panels (c) & (d): fraction of

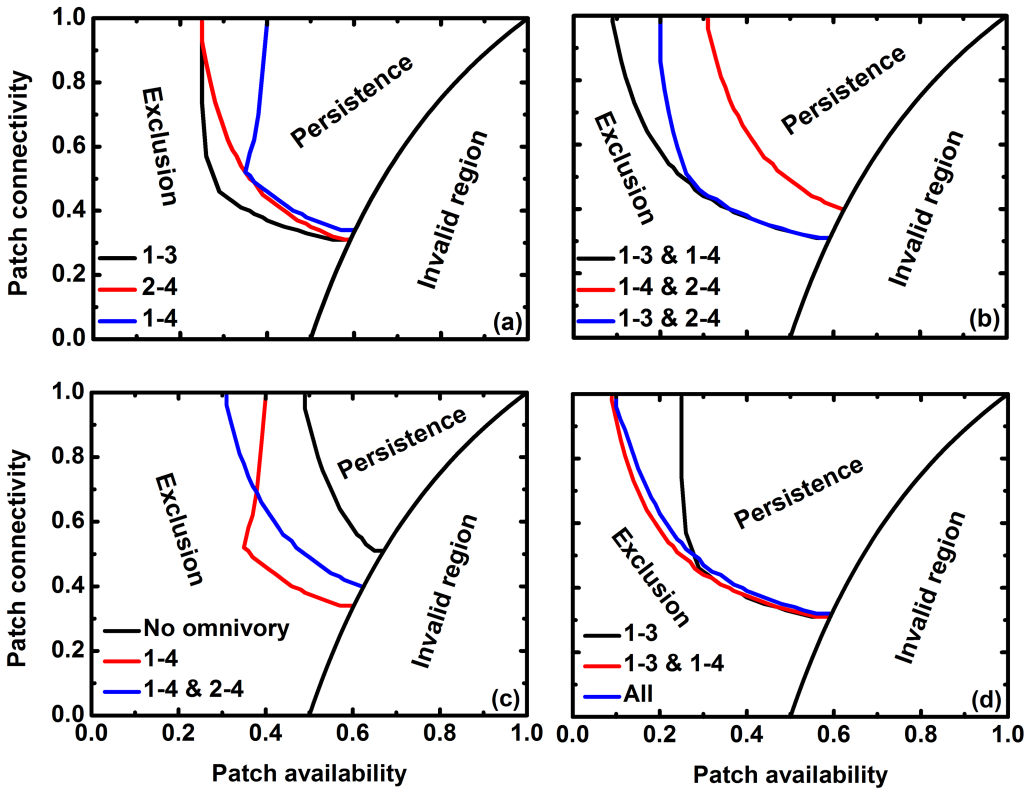
modules of a particular type. In (a) and (c) modules containing omnivorous links are compared to a simple food chain. In (b) and (d) each trophic configuration (see Fig. 1) is considered separately (All – including all possible omnivorous links).



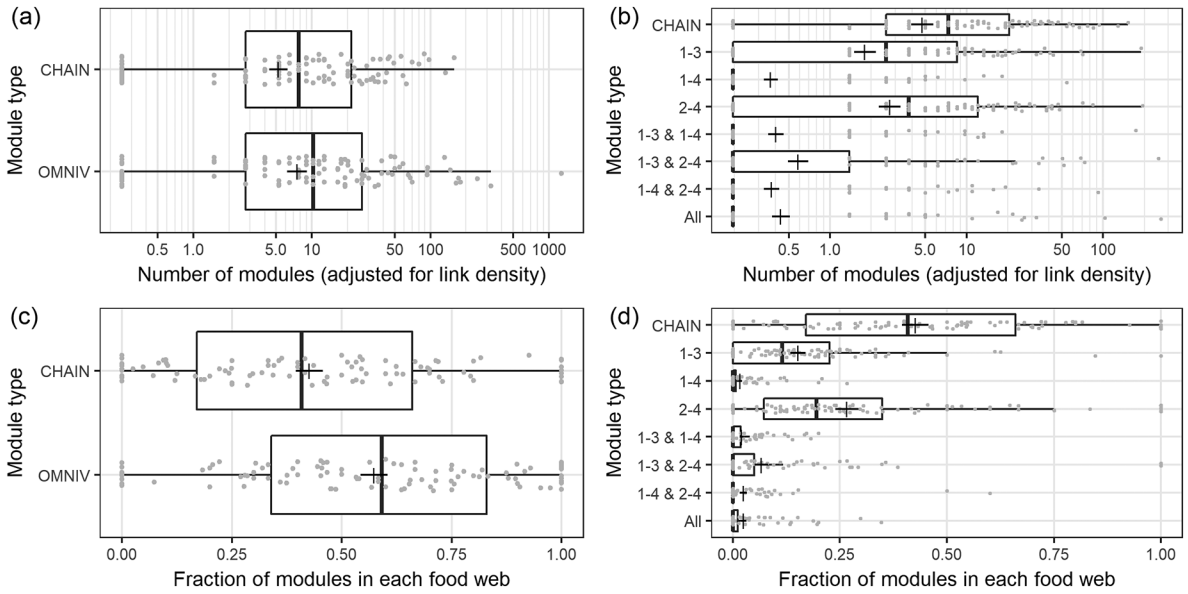
ecy_3026_f1.tif



ecy_3026_f2.tif



ecy_3026_f3.tif



ecy_3026_f4.tif