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Diverse responses of species to landscape fragmentation in a simple food chain

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Running headline: Habitat fragmentation and food chain

Summary

1. Habitat destruction, characterized by habitat loss and fragmentation, is a key driver of species extinction in spatial extended communities. Recently, there has been some progress in the theory of spatial food webs, however to date practically little is known about how habitat configurational fragmentation influences multi-trophic food web dynamics.

2. To explore how habitat fragmentation affects species persistence in food webs, we introduce a modelling framework that describes the site occupancy of species in a tri-trophic system. We assume that species dispersal range increases with trophic level, exploiting pair-approximation techniques to describe the effect of habitat clustering.

3. In accordance with the trophic rank hypothesis, both habitat loss and fragmentation generally cause species extinction, with stronger effects occurring at higher trophic levels. However, species display diverse responses (negative, neutral or positive) to habitat loss and fragmentation separately, depending on their dispersal range and trophic position.

4. Counter-intuitively, prey species may benefit from habitat loss due to a release in top-down control. Similarly, habitat fragmentation has almost no influence on the site occupancy of the

intermediate consumer in the tri-trophic system, though it decreases those of both basal species and top predator. Consequently, species' responses to habitat destruction vary as other species become extinct.

5. Our results reiterate the importance of the interplay between bottom-up and top-down control in trophically linked communities, and highlight the complex responses occurring in even a simple food chain.

Key-words: food web, habitat fragmentation, habitat loss, species dispersal.

Introduction

Ongoing habitat destruction is the primary cause of species loss in human-modified landscapes (Fahrig 2001; Ewers & Didham 2006). Understanding its effects has consequently become a central issue in ecology and conservation (Tilman & Kareiva 1997; Dieckmann, Law & Metz 2000). According to Fahrig (2002, 2003, 2017), habitat destruction can be characterized by two main processes: habitat loss and habitat fragmentation. The former is the reduction in habitat availability, while the latter refers to changes in the spatial arrangement of the remaining habitat. Many studies, including both empirical (Kruess & Tscharnkte 1994; Dobson *et al.* 2006; Feeley & Terborgh 2006; González-Gómez, Estades & Simonetti 2006; Gotelli & Ellison 2006; Cagnolo *et al.* 2009; Fenoglio *et al.* 2010; Valladares, Cagnolo & Salvo 2012; Morante-Filho *et al.* 2016) and theoretical work (Holt 1993, 1997; Bascompte & Solé 1998; Melián & Bascompte 2002; Kondoh 2003; Pillai, Loreau & Gonzalez 2010), have examined the effects of habitat loss on food web dynamics, and significant advances have been made in our understanding of how simple food webs

respond to it. For instance, habitat loss can reduce population sizes and trophic links, ultimately leading to species loss (Kruess & Tscharnkte 1994; Bascompte & Solé 1998; Kondoh 2003; Pillai, Loreau & Gonzalez 2010). However, how populations respond to habitat fragmentation (that is the spatial configuration of the habitat) in trophically linked communities has been largely overlooked (Holt 2002; Amarasekare 2008; McCann & Rooney 2009; Gonzalez, Rayfield & Lindo 2011; Hagen *et al.* 2012). Mathematical analysis of complex trophic interactions in heterogeneous landscapes remains difficult and consequently there exists little theory concerning spatial food webs (Pimm & Raven 2000; Amarasekare 2008; Calcagno *et al.* 2011).

Drivers of habitat fragmentation include natural barriers (e.g. rivers and deserts) and anthropogenic barriers (e.g. roads, dams and fences), which block the dispersal of species between habitat fragments (Andrews 1990; Jaeger & Fahrig 2004; Di Giulio, Holderegger & Tobia 2009). According to Fahrig (2002, 2003) and Ewers & Didham (2006), habitat fragmentation can induce at least three consequences: (a) increase of edge density; (b) loss of habitat connectivity; (c) reduction in mean fragment sizes. In addition, Liao *et al.* (2013a, b) found that species with different dispersal capabilities can respond differently to habitat fragmentation, with longer-range dispersers displaying lower sensitivity to fragmentation. As species at lower trophic levels typically exhibit shorter range dispersal in nature (McCann, Rasmussen & Umbanhowar 2005; Greenleaf *et al.* 2007), they may suffer more from habitat fragmentation (e.g. impeding dispersal between fragments). A bottom-up trophic cascade may subsequently induce a decline in the predator populations (Eklöf & Ebenman 2006), even though the predators are less directly affected by habitat fragmentation due to their longer range dispersal. Thus, habitat fragmentation can reduce food chain length by disrupting trophic interactions, thereby leading to cascading secondary extinctions in food webs (confirmed by empirical studies by Bolger *et al.* 2000; Tscharntke & Brandl 2004; Solé

& Montova 2006; <u>Woodward *et al.* 2012</u>). However, very few theoretical models systematically investigate how habitat fragmentation influences the dynamics of species with varying dispersal capabilities in a trophic system (<u>McCann, Rasmussen & Umbanhowar 2005;</u> <u>Amarasekare 2008</u>). To address this problem, we develop a modelling framework that can characterize the site occupancy of species whose dispersal range increases with trophic level, in order to explore how habitat loss and fragmentation act and interact to alter species persistence in a tri-trophic community.

Methods

System description and underlying assumptions

On the landscape scale, variation in environmental conditions and human driven land-use change creates a complex mosaic of functionally distinct habitat types, i.e. patches of varying suitability for the native species (<u>Forman 1995;</u> <u>Guisan & Zimmermann 2000;</u> <u>Jeganathan *et al.* 2004;</u> <u>Johnson, Seip & Boyce 2004;</u> <u>Mortelliti, Amori & Boitani 2010</u>). For model simplicity and mathematical tractability, we assume an idealized landscape composed of two habitat types: *natural habitat*, which can be colonized by any species; and *unnatural habitat*, which is not suitable for colonization. This simplification allows us to focus on the effects of habitat destruction, which produces unnatural habitat in this sense, and in particular on the global structure of the habitat as measured by habitat fragmentation.

We assume further that habitat destruction has a characteristic spatial scale, corresponding to the minimum size of a region of one habitat type (cf. land unit; <u>Zonneveld 1989</u>). This might be, for example, the minimum amount of space that can be farmed economically. With this assumption, we can describe a landscape using the framework of a two-dimensional square lattice with cells of this characteristic size representing regions with a single habitat type, e.g. natural habitat (*S-sites*) and unnatural habitat (*U-sites*).

We model the dynamics of three species which can colonize the *S*-sites in the landscape. Since *S*-sites have a constant size, it is reasonable to assume that they can support the same maximum population of a given species (although these maximum populations may vary between species). Thus, the number of *S*-sites colonized by a species, or *site occupancy*, can be regarded as a measure of its total population.

The three species interact in a simple food chain with a basal species, an intermediate consumer and a top predator. In addition to these trophic interactions, individuals from these species are able to disperse in order to find new colony sites or, in the case of the predators, to hunt for prey. This means a predator does not require its prey to be present at a site before it can colonize it, in contrast to existing metapopulation models (Bascompte & Solé 1998; Pillai, Loreau & Gonzalez 2010).

In accordance with experimental observations (Peters 1983; McCann, Rasmussen & Umbanhowar 2005; Greenleaf *et al.* 2007), we assume that dispersal range increases with trophic level. With this in mind, we assign each species a different dispersal range in terms of the landscape structure described as follows. Individuals from the basal species are only able to access *S*-sites adjacent to their colony sites (nearest neighbour dispersal). Intermediate consumers are able to access *S*-sites within a habitat fragment that consists of a number of connected *S*-sites (dispersal within fragments), i.e. they cannot disperse through *U*-sites. Finally, top predators can access any *S*-site across the landscape (global dispersal), i.e. they can disperse through *U*-sites although they cannot colonize them.

Characterization of landscape structure

In order to study the effects of habitat loss and habitat fragmentation on the site occupancy dynamics of the three species, we first need to characterize the landscape in these terms. Matsuda *et al.* (1992) and Hiebeler (2000) provide an approach to describe a landscape using

the *total density of S-sites* in the landscape (S), and the *clumping degree* of such sites ($q_{S/S}$). It is immediately clear that S is a measure of the amount of available habitat and is directly related to the degree of habitat loss $U = 1 - S$ (i.e. total density of U-sites).

The clumping degree of S-sites is defined as the probability that the neighbour of an S-site is also an S-site, i.e. $q_{S/S} = \rho_{SS}/S$, where the pair density ρ_{SS} is the probability that a randomly chosen pair of neighbouring sites are both S-sites. We use the von Neumann neighbourhood with 4-nearest neighbours per site throughout this work. Thus, the clumping degree is a measure of the aggregation of S-sites and thus the average fragment size (Lloyd 1967; Matsuda *et al.* 1992; Harada & Iwasa 1994). Naturally, this can be used to describe the fragmentation (F) of the habitat as $F = 1 - q_{S/S}$. The maximum possible degree of habitat fragmentation is constrained by habitat loss (Hiebeler 2000, 2007)

$$F \leq U/(1 - U). \tag{1}$$

Further details can be found in Appendix S1 (see *Supporting Information*).

To visualize these effects, we show several typical landscape configurations of varying habitat fragmentation (F) at a fixed habitat loss (U) in Fig. 1a-c. In the special case of $F=U$, the two habitat sites (S and U) are randomly distributed (Fig. 1b). Over-dispersed ($F>U$) and clumped ($F<U$) patterns are shown in Fig. 1a and 1c respectively.

Modelling the effect of landscape structure on site occupancy dynamics

The population dynamics of species in a food chain can be modelled as a series of predator-prey systems (Freedman & Waltman 1977; Kuznetsov & Rinaldi 1996). Such models can typically be separated into two terms: a *growth term*, which takes into account species reproduction rate, and prey encounter rate for predators; and a *death term*, which takes into account intrinsic mortality rate and increased mortality rate for prey due to predation. We

develop a model for the site occupancy dynamics (which are directly proportional to population of a species in this system) following this basic structure, noting that the landscape structure and dispersal range of species affect their ability to find new colony sites and the encounter rate between prey and predator. This model is given below:

$$\frac{dP}{dt} = b_3 PC(1 - U - P) - e_3 P, \tag{2a}$$

$$\frac{dC}{dt} = b_2 CR q_{s/s}^2 (1 - U - C) - (\mu_2 P + e_2)C, \tag{2b}$$

$$\frac{dR}{dt} = b_1 R (1 - q_{U/R} - q_{R/R}) - (\mu_1 C q_{S/S} + e_1)R, \tag{2c}$$

where P, C, and R denote the site occupancy of the top predator, intermediate consumer, and basal species respectively (all other parameters are summarized in Table 1). In each equation the first term describes colonization of new sites (i.e. population growth), while the second term describes extinction of the species at colony sites (i.e. population death).

To explain how these equations were derived, we first consider the extinction terms. Each species has an intrinsic extinction rate (e_1, e_2 or e_3), analogous to the intrinsic mortality rate in population models. Additionally, the intermediate consumer and basal species may also become extinct due to predation by the top predator or intermediate consumer respectively. This is determined by the impact of predation on extinction rate (μ_1 and μ_2) and the encounter rate between prey and predator. The latter depends on the effective predator site occupancy (i.e. population), ultimately determined by its dispersal range. Since the top predator can hunt globally, a given consumer can encounter a top predator from any colony site, and hence the total site occupancy of the top predator P is used in eqn 2b. By contrast, as the intermediate consumer hunts only within habitat fragments, a given basal species individual can only encounter intermediate consumers from a colony site within such a

fragment. This limits the effective intermediate consumer population to the total population multiplied by the average fragment size, e.g. $Cq_{S/S}$ in eqn 2c (Liao *et al.* 2016).

Similarly, the colonization terms for each species is controlled by its colonization rate $(b_1, b_2$ and $b_3)$, the availability of colony sites which it can access, and the prey encounter rate for predators. Thus, for the globally dispersing top predator we simply use the total density of colony sites which have not been colonized by the top predator $(1 - U - P)$, and the total site occupancy of the intermediate consumer C in eqn 2a. By contrast, since the intermediate consumer is limited to habitat fragments, it can only access prey and colony sites within such a fragment. Thus, these availabilities are, again, limited by the average fragment size and are given by $Rq_{S/S}$ and $q_{S/S}(1 - U - C)$ respectively in eqn 2b. Note that, if $q_{S/S} \approx 1$, the colonization terms for top predator and intermediate consumer become identical. This corresponds to the case where all S-sites are connected together and thus both species have equal access to all colony sites. If instead $q_{S/S} \approx 0$, corresponding to the case where S-sites are highly fragmented, the colonization rate of the intermediate consumer is close to zero, since the dispersal of the intermediate consumer is extremely restricted by U-sites.

The site colonization processes of top predator and intermediate consumer are effectively mean field. By contrast, to model the nearest neighbour dispersal of the basal species we make use of a pair approximation model (Matsuda *et al.* 1992; Harada & Iwasa 1994; Boots & Sasaki 2000; Hiebeler 2000; Liao *et al.* 2013a, 2016; Ying *et al.* 2014). The growth term for this species in eqn 2c can still be understood in terms of a colonization rate b_3, and the clumping degree of unoccupied S-sites surrounding occupied R-sites $q_{S/R} = (1 - q_{U/R} - q_{R/R})$. Note that there are only three possible neighbour states for a given R-site: R, U or S, meaning that $q_{S/R}$ is determined by the clumping degrees of R-sites with U-sites ($q_{U/R}$) and

other R-sites ($q_{R/R}$). Since $q_{U/R}$ and $q_{R/R}$ change as the basal species spreads, the dynamics of these two variables are characterized by moment closure in eqns S6-S7 (see derivation in Appendix S1, *Supporting Information*).

Approach to system analysis

We primarily make use of numerical methods to derive non-trivial solutions for this system in order to investigate how habitat loss and habitat fragmentation affect the community state which arises on a given landscape (A formal mathematical analysis of the steady states of a simplified mean-field system can be found in Appendix S2, *Supporting Information*). We obtain similar qualitative results regardless of the other system parameters, however for some parameter combinations the interval between community states is small. Consequently we choose a parameter combination for which all community states can be easily distinguished as our reference case for this study (see Figs 2 and 3). We stress that using other parameter combinations does not alter our general results and conclusions (see Figs S1-S3 in *Supporting Information*).

Modelling validation

Appropriate datasets combining landscape fragmentation (varying habitat loss and configurational fragmentation separately) and dispersal-dependent trophic relationships remain scarce. As part of a meta-analysis of 419 studies, Martinson & Fagan (2014) compiled a large dataset summarizing the effects of habitat loss and fragmentation on resource consumption in terrestrial arthropod food webs. This dataset does not include the dispersal ranges of the species considered, or the structures of the communities in which they are

embedded, but it does include their trophic rank. Consequently, while this dataset does not allow us to test our model predictions directly, it does permit us to illustrate general trends in the effect of trophic level on species responses to habitat destruction.

Martinson & Fagan (2014) provide six classes of spatial variable which we can reclassify as habitat loss ("patch size", "proportion habitat") or habitat fragmentation ("connectivity", "edge", "fragmentation *per se*", "matrix"), and a seventh class "other" is discarded. Additionally non-integer trophic ranks were rounded to the nearest integer. Species responses to these variables were evaluated using a standardized measure, the log response ratio *LRR* (see further details in Martinson & Fagan 2014). A negative *LRR* indicates fewer resources consumed after habitat destruction, while a positive *LRR* indicates the reverse.

Results

We begin by testing the individual effects of habitat loss and fragmentation on species persistence (Fig. 2). Generally, species at different trophic levels show different responses to habitat loss (Fig. 2a-c). As habitat loss increases, the site occupancy of basal species initially decreases, then increases (with a peak value occurring where the consumer goes extinct; see Fig. 2b) due to a rapid decline in site occupancy of the intermediate consumer, and finally declines to zero (Fig. 2a). The intermediate consumer exhibits a completely different response to habitat loss (Fig. 2b). Consumer site occupancy initially increases (with a maximum occupancy occurring at the point where the top predator becomes extinct) but then decreases sharply with habitat loss (Fig. 2b). The top predator displays the simplest response to habitat loss, and its site occupancy monotonically decreases to zero as habitat loss increases (Fig. 2c). As expected, habitat loss increases species extinction rate, with higher trophic level species exhibiting more sensitivity to habitat loss. Additionally we observe that

the degree of habitat fragmentation modifies species extinction thresholds (defined as the maximum habitat loss above which a species goes extinct), with higher fragmentation leading to greater extinction risk especially for consumers and top predators (see Fig. 2a-c). In other words, species can tolerate more habitat loss in less fragmented landscapes.

Habitat loss has a significant effect on the impact of habitat fragmentation on species persistence (Fig. 2d-f). At higher levels of habitat loss, consumers and top predators can only persist in highly clumped habitats, and species at higher trophic level show more vulnerability to habitat fragmentation. Additionally, the length of the food chain (i.e. how many species persist in the steady state) affects each species' response to habitat fragmentation (Fig. 2d-f). In a mono-trophic system (i.e. only basal species persist), habitat fragmentation decreases the site occupancy of basal species, while for a bi-trophic system (without the top predator), basal species abundance increases due to decreasing abundance of the intermediate consumer. In a tri-trophic system, habitat fragmentation decreases the site occupancy of both the basal species and the top predator, but interestingly the abundance of the intermediate consumer is relatively unaffected (Fig. 2e). While the responses of the basal and consumer species to habitat fragmentation are relatively complex, the top predator abundance simply decreases monotonously (Fig. 2f).

Next we investigate how the interactions between habitat loss and fragmentation influence tri-trophic community patterns (including species coexistence and site occupancy) (Fig. 3). While three species can coexist at low habitat loss and fragmentation, species of higher trophic level tend to go extinct sooner when both habitat loss and fragmentation are increased (Fig. 3a).

In addition, we plot global site occupancy for each species at steady state (Fig. 3b-d). Again, only the top predator occupancy displays a monotonous decline with habitat loss, the responses of basal species and intermediate consumer to habitat loss are more varied. In general, basal species occupancy decreases with increasing habitat loss, but increases in an intermediate range (Fig. 3b). In contrast, intermediate consumer occupancy initially increases as habitat loss increases, and then declines sharply to zero in the same range that basal species occupancy increases.

The effect of habitat fragmentation on species occupancies is dependent on the degree of habitat loss. At extremely low levels of habitat loss, fragmentation has minimal effect on the site occupancy for all species. At higher levels of habitat loss, reducing habitat fragmentation generally allows higher species occupancies to be maintained. Unintuitively, intermediate levels of landscape fragmentation can create optimal conditions for the basal species. The final observation is that habitat fragmentation has almost no impact on consumer site occupancy when all three species coexist.

Finally, using the dataset compiled by Martinson & Fagan (2014), we investigate how the effects of habitat loss and fragmentation vary with trophic level in empirical systems. Both forms of habitat destruction elicit a broad range of responses regardless of trophic level (Fig. 4). We emphasize that these ranges always include both positive and negative responses to habitat destruction, a phenomenon which is observed for both basal species and intermediate consumers in our tri-trophic system. This highlights a limitation of the dataset, i.e. that it records only the trophic rank of the species not its position in the food web.

The mean, rather than individual, responses at each trophic level display more definite trends. In particular, the response to habitat loss becomes less negative between the primary and secondary trophic levels and more negative between secondary and tertiary trophic levels

(Fig. 4a). This suggests that species in the tertiary trophic level are more likely to have a strong negative response to habitat loss, consistent with the behavior of top predators in our model (cf. Fig. 2c). Similarly, species in the secondary trophic level are more likely to have a positive response to habitat loss, corresponding to the behavior of species consumed by a top predator in our model (cf. Fig. 2b). Finally, species in the primary trophic level are more likely to have a negative response to habitat loss and thus behave like basal species in our model (cf. Fig. 2a).

The mean responses to habitat fragmentation decline monotonously from primary to tertiary trophic level (Fig. 4b). Since it becomes more likely that a species is the top predator in its food web as its trophic level increases, this is consistent with our model predictions (cf. Fig. 3a). The mean response in both primary and secondary trophic levels is close to zero, as individual responses are split almost equally between positive and negative. This suggests that species in these trophic levels may occupy a diverse range of positions relative to the top predator in their respective food webs (cf. Fig. 2d,e).

Discussion

Classical metacommunity theory for food webs considers only models of the relative occurrence of species within patches across a landscape (i.e. non-spatial patch-dynamic models), while ignoring spatial habitat arrangement and species limited dispersal (e.g. Holt 1993, 1997; Melián & Bascompte 2002; Kondoh 2003; Pillai, Loreau & Gonzalez 2010). Additionally, many existing studies of the effect of habitat fragmentation on communities focus on a single trophic level (e.g. Andren, 1994; Fahrig 1998; Trzcinski, Fahrig & Merriam 1999; Pardini *et al.* 2010; Tscharntke *et al.* 2012). By incorporating both trophic and

landscape structure in our modelling framework, we are able to demonstrate that these two factors interact to produce counter-intuitive effects on the resulting community structure.

For example, it has been demonstrated that species with longer-range dispersal are less influenced by habitat fragmentation (Liao *et al.* 2013a, b). However, this general conclusion does not hold when the species is embedded in a trophic community. Our results show that the population of top predator, which is not directly affected by habitat fragmentation due to its long-range dispersal, declines in fragmented habitats (Fig. 2f). By contrast, while the top predator is present, the intermediate consumer, which does have dispersal limitations, is almost unaffected by habitat fragmentation (Fig. 2e). This combination of responses arises as follows. Habitat fragmentation limits the maximum possible occupancy of the dispersal-limited prey species, thereby reducing the total occupancy of top predators that can be supported via a trophic cascade (Eklöf & Ebenman 2006). The decreased top-down control in turn allows the dispersal-limited species to more closely approach their maximum occupancy. This interplay of differing control effects (habitat availability - bottom-up control and predation - top-down control) and trophic structure also results in the counter-intuitive increase in intermediate consumer occupancy with increasing habitat loss (Figs 2b and 3c).

Similar effects have been observed in other modelling and empirical studies (Roland 1993; Kruess & Tscharnkte 1994; Kareiva & Wennergren 1995; Bascompte & Solé 1998; Cappuccino *et al.* 1998; Kondoh 2003; Martinson & Fagan 2014). Thus our model suggests that release from top-down control may explain the observation that some intermediate consumers respond positively to habitat loss (Fahrig 2002; Ewers & Didham 2006; Martinson & Fagan 2014). If this explanation is correct, it could have serious ecological or economic consequences, e.g. in agro-ecosystems where pest insect populations may go out of control as natural enemy populations decrease.

More fundamentally, we wish to highlight the fact that, at least in our model, the effects of habitat loss and habitat fragmentation on a given species depend on its trophic position relative to the top predator in the system. Examples of this can be seen in Fig. 2 where population responses to habitat destruction reverse when a species becomes extinct, thereby changing the relative positions of the surviving species. The generality of these results might be questioned on the grounds that real ecological communities can be significantly more complex than three species linked in a food chain. However, we argue that a complex community is, in fact, made up of these smaller modules. As such, we can expect these patterns in response to habitat destruction to be reproduced in natural communities.

The empirical dataset assembled by Martinson & Fagan (2014) exhibits a diverse range of responses to habitat destruction regardless of the trophic level of the species considered (Fig. 4). This is also supported by a recent review by Fahrig (2017), which found that a significant proportion of studies showed positive responses to habitat fragmentation. These observations could arise from variation in the structure of the community in which each study species is embedded, lending support to our conclusion above. Unfortunately, the community context is not currently consistently reported in studies of the effects of habitat destruction and thus it is not possible to provide more definitive support for this conclusion. We would recommend that future studies consider the responses of as many species as possible within a study community. Alternatively, where only a single species can be considered, a measure of its position relative to the top predator in the community should be included.

If it can be substantiated, this prediction, that the response to habitat fragmentation depends on a species position relative to the top predator in its food web, has the following important ecological consequence: increasing habitat connectivity as much as possible may not be the optimal strategy for maximizing crop yields in an ecosystem (e.g. grassland ecosystems) with

an even number of trophic levels, contradicting previous studies ignoring trophic interactions (Fahrig 2002; Ewers & Didham 2006; Fischer & Lindenmayer 2007; Mortelliti, Amori & Boitani 2010). This positive fragmentation effect on locally dispersing species has been observed empirically (Fahrig 2002, 2017), but has previously been ascribed to a positive edge effect rather than trophic interactions between species.

Andren (1994) proposed the existence of a sharp threshold in habitat fragmentation above which a species with given dispersal capabilities would become extinct (the threshold fragmentation hypothesis). Subsequent studies (Fahrig 1998; Trzcinski, Fahrig & Merriam 1999; Pardini *et al.* 2010; Tscharntke *et al.* 2012; Villard & Metzger 2014) have refined this hypothesis, suggesting that the effect of habitat fragmentation is greatest at intermediate levels of habitat loss. Our results broadly support this intermediate landscape-complexity hypothesis, with the strongest effects of habitat fragmentation being seen for habitat loss between 0.4 and 0.6 (Fig. 3). In this region, relatively minor changes in habitat configuration can substantially modify the robustness of the food chain by regulating population occupancy. We do not observe a step change in site occupancy at a particular level of fragmentation (as might be expected from the fragmentation threshold hypothesis), but rather a continuous decline as fragmentation increases (Fig. 2). However, as this decline is relatively rapid for the dispersal limited species (the basal species and the intermediate consumer), it may be observed as a sharp threshold in empirical studies. Finally, we again emphasize that the effect of habitat fragmentation is dependent on the community context of a species, which provides a possible explanation as to why Fahrig (2017) did not find evidence to support the threshold fragmentation hypothesis.

In formulating this model we have made several simplifying assumptions. Firstly, we consider only two habitat types (natural and unnatural). Real landscapes rarely consist of neatly divided patches of "habitat" and "non-habitat" (Mortelliti, Amori & Boitani 2010; Liao *et al.* 2013a; Melo *et al.* 2013) instead habitat degradation coincides with reduction in habitat quality, so that most landscapes exhibit at least some level of habitat variegation (i.e. varying suitability for species). To account for this, future study could expand the range of possible habitat types, with each being characterized by different colonization and/or extinction rates, and introduce more complex metrics to describe the overall spatial structure. Secondly, Huth *et al.* (2014) theoretically demonstrated that the (*U*, *F*) characterization by Hiebeler (2000) does not provide a unique description of landscape structure. However, it is appealing for ecologists dealing with spatial population dynamics in fragmented landscapes for its mathematical tractability (Matsuda *et al.* 1992; Harada & Iwasa 1994; Boots & Sasaki 2000; Hiebeler 2000; Liao *et al.* 2013a, 2016; Ying *et al.* 2014). The effects of more detailed landscape characterization techniques, e.g. Hurst exponent (Milne 1992) or spectral methods (Keitt 2000), could be considered in future work. Thirdly, our dispersal ranges are essentially categorical, whereas in reality we might expect them to be continuous variables, i.e. the physical distance from which an individual ranges from its home site. This categorical description can be naturally linked to the effects of fragment size and habitat connectivity, but it does eliminate the effect of distance between fragments (Fahrig 2002, 2003; Ewers & Didham 2006). The effect of this omission could be further investigated by comparing the results presented here to those models using more realistic dispersal ranges. Finally, the current model only simulates a simple food chain, while most ecological communities are more complex and may contain other food web modules, such as omnivory (Liao *et al.* 2017), apparent or/and exploitative competition. Therefore, areas for further study could include the effects of: alternative food web modules (e.g. using the patch-dynamic framework by Pillai,

Loreau & Gonzalez 2010); alternative combinations, or more complex, dispersal traits; and landscapes with more gradual variation in habitat quality.

Our theoretical model raises two specific predictions: (i) extinction thresholds for a given species in a simple food chain will vary as a function of habitat configuration especially at intermediate habitat loss, following the landscape fragmentation hypothesis (Villard & Metzger 2014). As such, we suggest that, in conservation efforts, the community structure to be preserved must be considered in combination with habitat configuration; (ii) species' diverse responses (negative, neutral and/or positive) to both habitat loss and fragmentation are closely related to their biotic traits (e.g. dispersal capacity and trophic position), thus identification of these traits from empirical data would contribute to the setting of conservation priorities in applied ecology. Experimental tests of these predictions could be performed in natural (e.g. field observations for the food chain of basal plant-insect-bird in multiple island ecosystems) or laboratory-based synthesized systems (e.g. microcosms) that allow the direct manipulation of habitat amount and configurational fragmentation (Fagan 1997; Diehl & Feissel 2000; Liess & Diehl 2006; Gravel *et al.* 2011; Chisholm, Lindo & Gonzalez 2011; Long, Bruno & Duffy 2011). For example, testing the hypothesis of significant effects of habitat configuration (e.g. more or less aggregated) at intermediate habitat loss will require true landscape-level or land-mosaic studies (sensu Bennett, Radford & Haslem 2006), with replication so that species responses can be compared across gradients in habitat amount and configuration (Oliveira-Filho & Metzger 2006; Villard & Metzger 2014). Specifically, assessing the potential interaction effects of habitat loss and fragmentation are particularly relevant to improve management strategies. For example, based on the intermediate landscape-complexity hypothesis (sensu Tscharntke *et al.* 2012), the landscape-scale effectiveness of local management actions can be highest in landscapes with intermediate landscape complexity, than in extremely simplified (i.e. with very high

habitat loss) or in complex landscapes (i.e. with very low habitat loss). On the other hand, the common recommendation to mitigate negative impacts of landscape fragmentation on biodiversity is to increase habitat availability and/or connectivity (Fischer & Lindenmayer 2007; Heller & Zavaleta 2009). Yet, in our model, increasing habitat amount and configurational connectivity might be detrimental to some populations (Figs 2 and 3). In addition, Fahrig (2017) reviewed numerous empirical studies, finding that most significant fragmentation effects on species diversity are positive. Thus, this calls for particular caution when designing conservation strategies for biodiversity maintenance in multi-trophic systems, as species loss resulting from habitat management will simultaneously influence multiple species across trophic levels via a trophic cascade.

In conclusion, we show that habitat fragmentation can have significant, and indeed unintuitive, effects on the persistence of species in trophically linked communities (reviews in Fahrig 2002, 2017). Consequently, we strongly recommend considering the effects of habitat fragmentation separated from habitat loss, when planning conservation and other ecological or economic activities. Finally, our findings reiterate the importance of the interplay between bottom-up and top-down control in trophically linked communities (Walker & Jones 2001; Morante-Filho *et al.* 2016) and highlight the complex responses occurring in even a simple food chain (as empirically confirmed in Fig. 4). Overall, our model provides an important new framework to investigate how landscape fragmentation affects food web dynamics.

Acknowledgements

Authors' contributions

J.L. and B.B. designed this study; J.L. and D.B. performed numerical simulations and analyzed the results; J.L. wrote the first draft of the manuscript and all authors contributed substantially to revisions.

Data Accessibility

We have not any empirical data in this theoretical modelling study.

Supporting Information

Supporting information accompanying this manuscript is also supplied below.

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Figure legends

Fig. 1. Three artificial fragmented landscapes with a two-dimensional square lattice of size $L \times L = 100 \times 100$ cells (L is the length of the lattice) consisting of two habitat types (white – suitable habitat, gray – unsuitable habitat) at a fixed habitat loss $U=0.5$, differentiated by the degree of habitat fragmentation F (a-c). Each image shows a typical configuration for the given fragmentation: (a) an over-dispersed habitat pattern with $F=0.9>U$, (b) a random habitat distribution at $F=U=0.5$, and (c) an aggregated pattern, consisting of large connected habitat patches (white), with $F=0.1<U$. Calculations are based on the orthogonal neighbouring correlation algorithm.

Fig. 2. Individual effects of habitat loss (U) and habitat fragmentation (F) on species persistence in a food chain of R (basal species)$\rightarrow C$ (intermediate consumer)$\rightarrow P$ (top predator). Note that the range of habitat fragmentation shrinks with reducing habitat loss (see eqn 1). Parameter values: species colonization rate (b_1, b_2, b_3)=(0.3, 0.2, 0.08), intrinsic extinction rate (e_1, e_2, e_3)=(0.01, 0.01, 0.01) and added extinction rate due to predation (μ_1, μ_2)=(0.5, 0.5).

Fig. 3. Interactive effects of habitat loss (U) and habitat fragmentation (F) on the tri-trophic community patterns at steady state (species are assumed to be extinct when their site occupancy is lower than 0.0001), including: (a) species coexistence pattern (R – basal species, C – intermediate consumer, P – top predator, and None – extinction of all species), and (b-d) global site occupancy respectively of species R, C and P. Other parameter values are the same as in Fig. 2. Invalid region: see eqn 1.

Fig. 4. The effects of habitat loss (a) and fragmentation (b) on resource consumption (blue – mean log response ratio (LRR) ± standard deviation (SD), gray circle – distribution of effect sizes from different empirical studies, and dash line – LRR=0) in trophic systems by using a meta-analysis on a dataset compiled by Martinson & Fagan (2014 and more details therein; n - number of empirical studies for each trophic level). Negative effect sizes indicate decreased resource consumption in more fragmented habitats.

Tables

Table 1. Parameter definitions

Parameter	Description
U	Fraction of the unsuitable sites in the entire landscape
$q_{U/U}$	Clumping degree of unsuitable habitat sites
$q_{S/S}$	Clumping degree of suitable habitat sites before introducing species (related to mean habitat fragment size and fragmentation)
F	Habitat fragmentation ($F=1-q_{S/S}$)
$q_{i/j}$	Conditional probability that the neighbour of a j-site is an i-site (i.e. local density)
ρ_{ij}	Probability of a randomly chosen pair of neighbouring sites that one is i-site and another is j-site (i.e. pair density)
μ_i	Increased extinction rate due to predation
b_i	Species colonization rate
e_i	Species intrinsic extinction rate

$U=0.5, F=0.9$ $U=0.5, F=0.5$ $U=0.5, F=0.1$

(a) Overdispersion   (b) Randomness   (c) Clustering

(a) Coexistence pattern

(b) Basal species

(c) Intermediate consumer

(d) Top predator

(a) Habitat loss

(b) Habitat fragmentation