



## METHODS

# A Bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions

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### Abstract

We develop a novel approach to analyse trophic metacommunities, which allows us to explore how progressive habitat loss affects food webs. Our method combines classic metapopulation models on fragmented landscapes with a Bayesian network representation of trophic interactions for calculating local extinction rates. This means that we can repurpose known results from classic metapopulation theory for trophic metacommunities, such as ranking the habitat patches of the landscape with respect to their importance to the persistence of the metacommunity as a whole. We use this to study the effects of habitat loss, both on model communities and the plant-mammal Serengeti food web dataset as a case study. Combining straightforward parameterisability with computational efficiency, our method permits the analysis of species-rich food webs over large landscapes, with hundreds or even thousands of species and habitat patches, while still retaining much of the flexibility of explicit dynamical models.

### Keywords

Bayesian network, habitat loss, metacommunity, spatial food web.

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## INTRODUCTION

Global biodiversity loss progresses at a rapid pace, with human-induced landscape changes such as habitat fragmentation and habitat loss being important drivers (Tylianakis *et al.*, 2008; Haddad *et al.*, 2015). To accurately forecast species extinction rates and develop efficient conservation strategies, ecologists must understand how species respond to these changes in habitat. Changes in the spatial configuration of a landscape drive species extinctions both directly but also through their effect on the interactions among species (Tylianakis *et al.*, 2008; Valiente-Banuet *et al.*, 2015). Their direction and extent is difficult to predict however, especially when considering complex ecological communities such as food webs.

Species in the same food web are inextricably linked, both directly and indirectly. Therefore, the extinction of one species can lead to a cascade of secondary extinctions which might affect the entire network (Ebenman and Jonsson, 2005; Dunne & Williams, 2009). This can have unpredictable consequences for the community as it might drastically change its structure and, at worst, lead to a highly impoverished community (Eklöf and Ebenman, 2006; Dunne and Williams, 2009).

Theoretical studies typically consider secondary extinctions in food webs without taking their spatial extent into account (Eklöf and Ebenman, 2006; Dunne and Williams, 2009; Staniczenko *et al.*, 2010; Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011; Brose *et al.*, 2017). In non-spatial webs, the main approaches to model secondary extinctions are purely topological models, solely based on food web structure (Dunne and Williams, 2009), and dynamical models, which explicitly simulate population dynamics using a system of differential equations (Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011). A

middle-ground approach between them are Bayesian networks (Eklöf *et al.*, 2013; Box 1).

Predictions derived from non-spatial studies are crucial for understanding how species extinctions reverberate through food webs and how this affects their persistence and stability. Yet, by neglecting the spatial context, they also neglect the potentially strong impact spatial aspects can have on (local) communities (Gibert and Yeakel, 2019). Therefore, non-spatial food web models might miss important ecological patterns and processes that play out at the landscape level such as spatial rescue effects, the co-distribution of predators and their prey, species range limits and the restructuring of food webs considering different spatial scales (Guzman *et al.*, 2018). Using a spatially implicit model, Gravel *et al.* (2011a) for example showed that regional dynamics could promote the persistence of species in complex food webs that were locally prone to extinctions.

More recently, several advances in food web ecology address the effect of spatial change on food webs (Pillai *et al.*, 2011; Eklöf *et al.*, 2012), mostly however in small food webs and/or landscapes. For example, Liao *et al.* (2016, 2017a, 2016) studied how the loss of habitat patches and landscape fragmentation affect food chains and simple food web motifs. An explicit population dynamical approach was taken by Ryser *et al.* (2019), who theoretically studied complex food webs in fragmented landscapes and found that habitat isolation drives top species extinctions due to bottom-up energy limitation. Using a system of differential equations, Ryser *et al.* (2019) explicitly simulate feeding and dispersal dynamics which allows for greater biological realism but also restricts the network sizes that are computationally feasible (Box 1).

### Box 1. Secondary extinctions in non-spatial food web models

*Topological models* provide the simplest approach to understanding secondary extinctions in food webs: a species undergoes secondary extinction once all its resources go extinct, otherwise it is extant. This method only requires the network structure as input, so it can be used to model very large networks (Dunne and Williams, 2009). However, the assumption that species' extinction risks do not respond at all to either the identity or the number of resource species lost until the last of them is gone (at which point the extinction probability suddenly jumps to certainty) is rather crude.

*Dynamical models* are on the other end of the spectrum and offer a highly detailed description of trophic communities. They explicitly model population dynamics using a system of coupled ordinary differential equations (Berlow *et al.*, 2009; Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011; Riede *et al.*, 2011). They depend on a large number of parameters and specific model assumptions, and are computationally expensive. Furthermore, while these models have the potential to be the most realistic of all, this potential is only realised if all model parameters are realistically represented. Although the rise in computational power promoted their use, the explicit modelling of population dynamics limits the food web size (and, in a spatial context, landscape size; Ryser *et al.*, 2019) that they can be applied to.

*Bayesian network models* (Eklöf *et al.*, 2013) provide a middle-ground between the two methods above. Bayesian networks permit extinction probabilities to increase gradually with resource loss, and allow them to be non-zero even when species have full access to their resources (quantifying the probability of species going extinct for causes other than those represented by the network). The numerical evaluation of Bayesian networks is highly efficient. This greatly reduces computation times and permits analysis of large food webs with hundreds or even thousands of species (and, in a spatial context, habitat patches).

In a Bayesian network, if a consumer species  $C$  has two prey items  $A$  and  $B$  whose extinction probabilities  $P(\neg A)$  and  $P(\neg B)$  are known, then one can obtain the marginal extinction probability  $P(\neg C)$  of the consumer using the law of total probability:

$$P(\neg C) = P(\neg C|AB)P(A)P(B) + P(\neg C|\neg AB)P(\neg A)P(B) + P(\neg C|A\neg B)P(A)P(\neg B) + P(\neg C|\neg A\neg B)P(\neg A)P(\neg B) \quad (\text{B1})$$

(this generalises straightforwardly to more than two prey items). Here  $P(A) = 1 - P(\neg A)$  (and similarly for species  $B$ ), and the conditional probabilities are determined from some set of model assumptions. One such assumption is that the probability  $P(\neg C|f)$  of a species  $C$  going extinct is a function of just the fraction  $f$ , and not the identity, of its resources that are absent (see the Supporting Information, Section S7 for a generalisation, where each prey contributes a different amount to the consumer's diet):

$$P(\neg C|f) = \pi_C + (1 - \pi_C)w(f) \quad (\text{B2})$$

where  $\pi_C$  is species  $C$ 's baseline extinction probability (the likelihood of extinction despite all its resources being present), and the weighting function  $w(f)$  is monotonically increasing in  $f$  such that  $w(0) = 0$  and  $w(1) = 1$ . For a basal species  $A$ , we assume its abiotic resources are always available ( $f = 0$ ), so  $P(\neg A) = \pi_A + (1 - \pi_A)w(0) = \pi_A$ . For a non-basal species  $C$ , one obtains  $P(\neg C)$  by using the already calculated extinction probabilities of its prey, and then applying eqn B1. Thus, determining the extinction probabilities of all species in a food web is a bottom-up calculation process: we start with basal species, then move on to species only consuming those basal species, and so on.

This also means that the Bayesian network approach has two important limitations. First, the food webs must be acyclic, otherwise this bottom-up approach would not work. Second, since predators are influenced by their prey but prey dynamics do not depend on the presence of their predators at all, the method cannot capture any top-down effects (a property shared with topological models).

To be able to explore much larger systems, here we develop a novel approach to study trophic metacommunities which is rooted in single-species metapopulation models on fragmented landscapes (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001; Hanski and Ovaskainen, 2003; Grilli *et al.*, 2015). The essence of our method is that species' extinction rates are calculated from a Bayesian network representation of the food web (Eklöf *et al.*, 2013), which allows us to model food webs with hundreds of species and patches. Our approach can also be used for obtaining analytical solutions for simple community modules (Supporting Information, Section S4). The method retains many known properties of metapopulation theory, such as being able to rank the habitat

patches of the landscape with respect to their importance to the persistence of the metacommunity (Ovaskainen and Hanski, 2001). We make use of this ranking to study how progressive habitat loss affects species extinctions, depending on whether one prioritises the removal of valuable vs. non-valuable patches.

The article is structured as follows. After briefly presenting our modelling framework and its parameterisation (Section 2), we use it to study the effect of habitat loss on community persistence—first on model food webs (Section 3), then in a case study on an empirical example (Section 4). We finish by reflecting on the advantages and limitations of our approach, and its place in the wider context of trophic metacommunity theory (Section 5).

## METHODS

### Model summary

Our starting point is a spatially explicit, Levins-type metapopulation model over a fragmented landscape consisting of  $N$  habitat patches connected by dispersal (Hanski and Ovaskainen, 2000, 2003; Ovaskainen and Hanski, 2001; Grilli *et al.*, 2015). Each of  $S$  species has a metapopulation over this landscape. Colonisation depends on species' current patch occupancies and dispersal abilities, and is unaffected by interspecific interactions. Extinctions, on the other hand, happen both due to local patch conditions and the fact that the species form a trophic network: extinction risk in a given patch increases when more prey items of a species are locally absent. We do not consider non-trophic interactions here.

More formally, we model the probability  $p_i^k$  that species  $i$  is found in patch  $k$ . (Here and elsewhere, subscripts refer to species and superscripts to patches.) Colonisation rates of patch  $k$  by species  $i$ ,  $C_i^k = \sum_{l=1}^N M_i^{kl} p_i^l$ , are modelled using a species-dependent landscape matrix whose  $(k, l)$  th entry  $M_i^{kl}$  gives the dispersal rate of species  $i$  from patch  $l$  to  $k$ . In turn, extinction rates are obtained from the probability  $\delta_i^k$  that species  $i$  disappears from patch  $k$ . As metapopulation models assume that migration operates on a slower time scale than local population dynamics (Hanski, 1994), we assume that within-patch extinction rates are not affected by the occupancy rates of other patches, so that within-patch extinction can be modelled as a Poisson process with rate  $E_i^k$ . So the probability of extinction occurring within one unit of time is  $\delta_i^k = 1 - \exp(-E_i^k)$ , from which  $E_i^k = -\log(1 - \delta_i^k)$ . With these colonisation and extinction rates, the model reads (Supporting Information, Section S2):

$$\frac{dp_i^k}{dt} = (1 - p_i^k) \sum_{l=1}^N M_i^{kl} p_i^l + p_i^k \log(1 - \delta_i^k) \quad (i = 1, \dots, S; k = 1, \dots, N) \quad (1)$$

The central idea of our approach is to couple these independent metapopulation equations by making the extinction probabilities  $\delta_i^k$  depend on the local persistence probabilities of species  $i$ 's prey items via a Bayesian network representation of the food web (Eklöf *et al.*, 2013). When modelling species extinctions using Bayesian networks, each species  $i$  in patch  $k$  has a baseline probability of extinction  $\pi_i^k$ ; the species goes extinct with this probability even if it has full access to its resources. Second, the conditional probability of a species to go extinct in a patch depends on the fraction  $f$  of its resources that are locally absent. This conditional probability increases monotonically with  $f$ , from the baseline probability  $\pi_i^k$  to certainty as  $f$  increases from 0 to 1. The marginal probability  $\delta_i^k$  is then obtained by substituting all conditional probabilities into the law of total probability (Box 1; Supporting Information, Section S1).

The model retains many known results from the classic metapopulation theory on which it is based. We can determine the persistence of any species  $i$  by its metapopulation capacity  $\lambda_i$ : if this quantity exceeds 1 it means that the metapopulation persists at equilibrium, otherwise all  $p_i^k$  are zero. For eqn 1,  $\lambda_i$  is given by the leading eigenvalue of the

matrix  $A_i^{kl} = -M_i^{kl} / \log(1 - \delta_i^k)$  (Supporting Information, Section S3). Also, the relative patch value  $V_i^k = (\lambda_i - \lambda_i^{-k}) / \lambda_i$  (where  $\lambda_i^{-k}$  is species  $i$ 's metapopulation capacity after patch  $k$  is removed) can be obtained as the normalised product of the dominant left and right eigenvectors of  $A_i^{kl}$  (Ovaskainen and Hanski, 2001). This quantity measures how important a patch is for the persistence of a species. We use it to rank the patches of a landscape with respect to their importance to the persistence of the metacommunity.

### Model parameterisation

We first constructed four model food webs via the allometric method of Schneider *et al.* (2016) (Supporting Information, Section S5.1). Each web has 400 species, but with a varying fraction of consumer to basal species (200:200, 250:150, 300:100, and 350:50). To study how progressive habitat loss affects these webs, we generated five landscapes, each with 300 uniformly distributed patches in the unit square. The landscape matrices were constructed by making their entries decline exponentially with the distance  $d^{kl}$  between patches  $k$  and  $l$ :  $M_i^{kl} = \exp(-d^{kl} / \xi_i)$ , where  $\xi_i$  is the characteristic dispersal distance of species  $i$ .

We assume homogeneous landscapes where all patches have the same abiotic conditions and each patch can potentially harbour the full food web. This means that both the baseline extinction probabilities  $\pi_i$  and dispersal distances  $\xi_i$  are patch-independent. Their species-dependence may take one of two forms. First, they can be constant across all species, with  $\pi_i = 0.2$  and  $\xi_i = 0.055$ . Second, they may be trophic level-based. We calculated the trophic level  $T_i$  of each species  $i$  as a prey-averaged trophic level (Williams and Martinez, 2004; Supporting Information, Section S5.2). Denoting their arithmetic average by  $\bar{T}$ , we set  $\pi_i = 0.2 T_i / \bar{T}$  and  $\xi_i = 0.055 T_i / \bar{T}$ . The numerical factors adjust the arithmetic average  $\bar{\pi}$  and  $\bar{\xi}$  to be equal to 0.2 and 0.055 respectively, for a better comparison with the constant case. Additionally, to explore the role of habitat connectivity in general, we gradually increased  $\xi_i$  from 0.01 to 0.1 (keeping it equal across species), and let  $\pi_i$  be trophic level-based (Supporting Information, Section S6).

We also looked at how the functional form of a consumer's response to the loss of resources affects the response of a food web to habitat loss, by implementing four different forms of the response function. All are described by regularised beta functions of the fraction  $f$  of resource species lost, with different shape parameters  $\alpha$  and  $\beta$ :

- (1)  $\alpha = \beta = 1$  (linear function; see inset in top right corner of Fig. 3a). Here a consumer's probability of extinction is simply proportional to the fraction of resources lost.
- (2)  $\alpha = 5, \beta = 1$  (Fig. 3b). This is a convex function, meaning that consumer extinction probabilities only start appreciably increasing after some fixed fraction of the resources have already been lost.
- (3)  $\alpha = 1, \beta = 5$  (Fig. 3c). A concave function: consumer extinction probabilities attain high values even after the removal of a small fraction of their prey.
- (4)  $\alpha = \beta = 5$  (Fig. 3d). A sigmoidal function, combining properties of the convex and concave cases.

### Implementing habitat loss

First, we obtain the equilibrium patch occupancies for each food web on each landscape. We do so beginning with the basal species (for whom  $\delta_i^k = \pi_i^k$ ), by solving for their equilibrium state in eqn 1 (Supporting Information, Section S3). We use these occupancy data and the Bayesian network representation of the food web (Box 1) to obtain their  $\delta_i^k$ . With these parameters, we then solve eqn 1 for all those species consuming only basal ones. We then obtain their  $\delta_i^k$  in turn, and go on to solve for the patch occupancies of species consuming only basal and primary consumer species—and so on, until top predators are reached (Supporting Information, Section S1–S2).

We start implementing habitat loss if at least one consumer species persists. We do this by gradually removing patches from each landscape, always 10 at a time. The order of removal differs between three habitat loss scenarios:

- (1) Best-case scenario: patches are removed in increasing order of patch value (least valuable patches first). Since species at different trophic positions may differ in which patches are most valuable to them, we rank the patches based on the patch values of basal species.
- (2) Worst-case scenario: as above, but removing patches in decreasing order of patch value (most valuable first).
- (3) Random scenario: patches are removed at random.

The patch ranking formula only applies for small perturbations of the landscape. Therefore, after each patch loss step (simultaneous removal of 10 patches), we recalculate the patch values to re-rank the order in which we will remove patches next. We repeat this process until either all but basal species have gone extinct, or less than two patches remain in a landscape. Figure 1 illustrates the habitat loss scenarios by displaying the patch occupancies for a basal species and a top predator over a landscape.

For the linear functional form of predator response to prey loss ( $\alpha = \beta = 1$ ), we additionally looked at removing patches based on the patch value rankings of top species, instead of basal ones (Supporting Information, Section S6.2). This means that patch removal was stopped whenever the top species have gone extinct.

Finally, we have also implemented a numerical experiment where we remove the links connecting the patches, instead of the patches themselves. This was also done in a random, best-case, and worst-case sequence (Supporting Information, Section S9). Link removal expresses the assumption that individuals have more difficulty travelling across patches due to the deterioration of the habitat matrix, even though the patches themselves are intact.

### RESULTS

Our approach can be used to obtain analytical approximations for the metapopulation capacities in simple food web structures (Supporting Information, Section S4). One such structure is a linear food chain (species 1 is the basal species eaten by species 2, which is in turn eaten by species 3, and so on, until the top species) over a homogeneous landscape (baseline extinction probabilities are patch-independent,

$\pi_i^k = \pi_i$ ). In this case the following recursion equation approximates the metapopulation capacities  $\lambda_i$ :

$$\lambda_{i+1} \approx \frac{\lambda_{M_{i+1}}}{\lambda_{M_i}/\lambda_i - \log[(1 - \pi_{i+1})(1 - 1/\lambda_i)]} \quad (2)$$

for all  $i > 1$ , and  $\lambda_1 = -\lambda_{M_1}/\log(1 - \pi_1)$  for the basal species.  $\lambda_{M_i}$  is the dominant eigenvalue of species  $i$ 's landscape matrix  $M_i^{kl}$ , which we do not assume to be generated by any particular kernel form here. We can simplify this expression further by assuming  $\pi_i = \pi$  and  $\lambda_{M_i} = \lambda_M$  are constant across species:

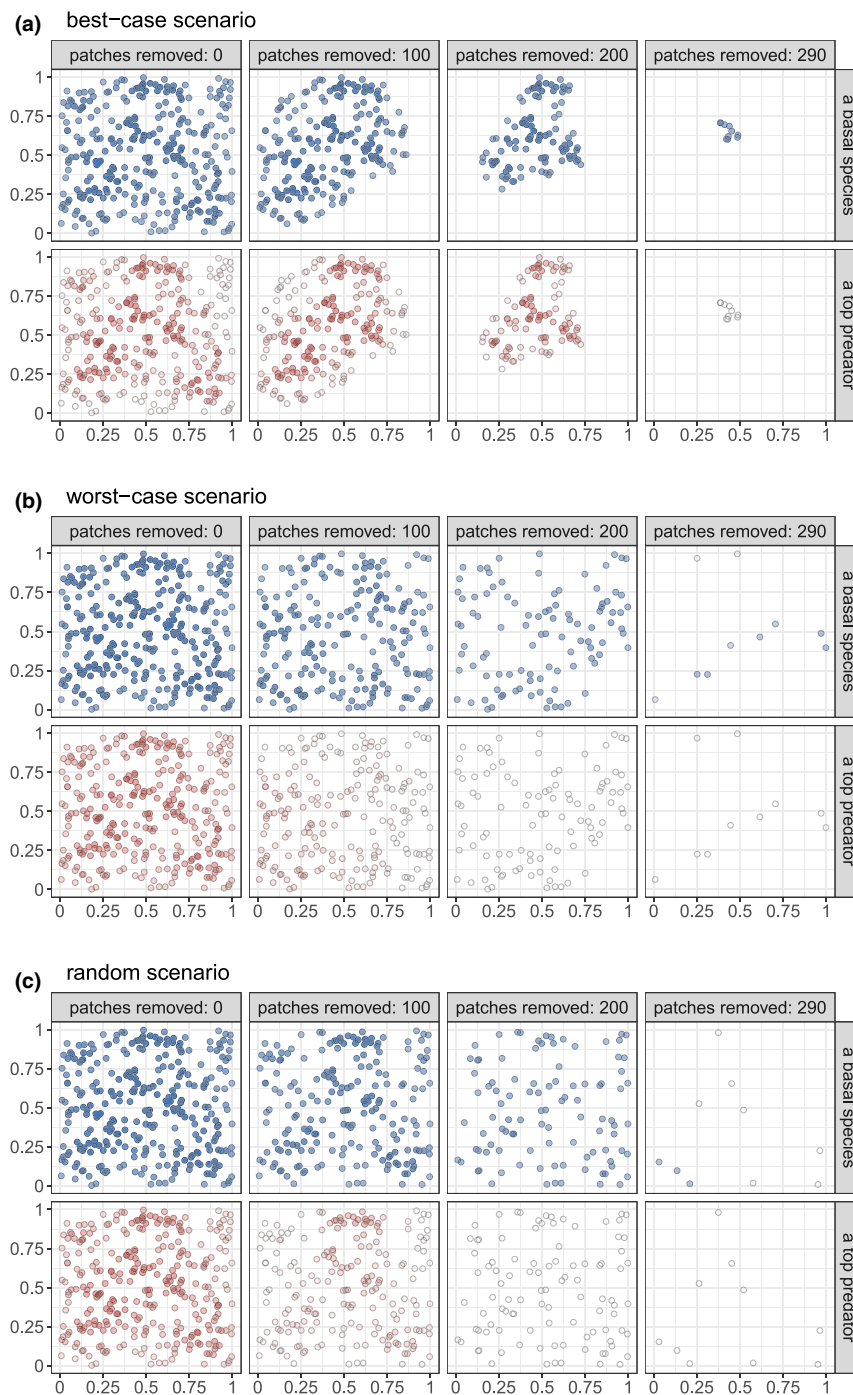
$$\lambda_{i+1} \approx \frac{\lambda_M}{\lambda_M/\lambda_i - \log[(1 - \pi)(1 - 1/\lambda_i)]} \quad (3)$$

One can show that eqn 3 implies strictly decreasing metapopulation capacities with increasing trophic level, eventually dropping them below 1 (Supporting Information, Section S4.2). This imposes a limit on the maximum length of the trophic chain, because species persistence requires  $\lambda_i > 1$ . The following simple approximation can be derived for the maximum number of trophic levels  $T$ :

$$T = -\lambda_M \log(\pi) \quad (4)$$

Empirical estimates of  $\lambda_M$  from three different butterfly metapopulations (Hanski, 1994) gave 3.9, 0.97, and 0.74 (Supporting Information, Section S4.2). If these are indeed typical values, then eqn 4 reveals that trophic chain length is quite restricted unless  $\pi$  is quite low (Fig. 2). For instance, with  $\lambda_M = 2$  and  $\pi = 0.1$ , the number of trophic levels is already limited to 5 at most. The upshot is that, quite apart from energetic or other constraints, the simple realities of metacommunity structure alone can restrict the maximum possible number of trophic levels to a handful—a conclusion consistent with an earlier study employing a slightly different modelling approach (Calcagno *et al.*, 2011).

Beyond such simple food web structures, one can rely on numerical solutions to eqn 1, which we have done to explore our four large model food webs. Since they produce similar trends, we present results for the one with 300 consumer and 100 basal species (Fig. 3; see Supporting Information, Section S6 for the others). The extent to which habitat loss threatens species persistence differs significantly between patch removal scenarios. In the best-case scenario, unless consumer response to prey absence is described by a strongly concave function (Fig. 3c), species have a high chance to persist even if a large fraction of habitat patches are lost. This applies to species at all trophic levels, though metapopulation capacities are generally higher at lower levels. By contrast, in the random and worst-case scenarios, species across all trophic levels have a much higher risk of extinction even after moderate levels of habitat removal. Interestingly, it makes almost no difference whether habitat loss starts with the most valuable patches or occurs randomly. This means that random patch removal is practically as harmful to a metacommunity as if one intentionally tried to cause the greatest damage. This pattern was observed for all food webs, landscapes, and parameterisations, and highlights the importance of planned landscape alterations whereby only patches of low value are removed. Note however that when removing links between patches instead of the patches themselves, random removal

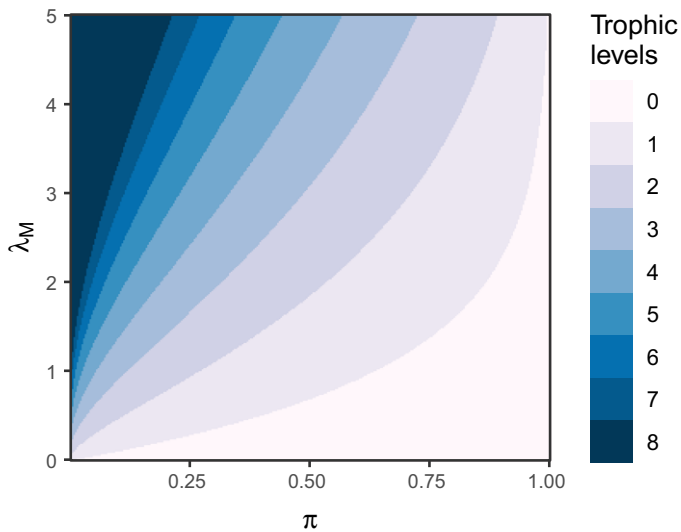


**Figure 1** Patch occupancies along a habitat loss gradient, for a basal species (blue) and a top predator (red) in a model food web with 300 consumer and 100 basal species. Axes are coordinates of the landscape, circles are patches and their shading is proportional to local persistence probabilities (dark blue/red: 100% persistence; empty circle: 0%). In the best-case scenario (a), we first remove patches that contribute the least to the metapopulation capacity of the basal species; in the worst-case scenario (b), we start with patches that contribute the most; and in (c) we remove patches randomly. The dispersal distance  $\xi_i$  is 0.055 for all species, and baseline extinction probabilities  $\pi_i$  increase linearly with trophic level.

falls more in-between the best- and worst-case link removal scenarios, even though all other aspects of the results are qualitatively identical (Supporting Information, Section S9).

Both the baseline extinction probability  $\pi_i$  and dispersal distance  $\xi_i$  affect the described outcomes, but in most cases do not change the overall trends (Fig. 3). If  $\pi_i$  (but not  $\xi_i$ )

increases with trophic level, differences in metapopulation capacity across trophic levels are elevated compared to the constant case, with higher values for lower trophic levels. When both  $\pi_i$  and  $\xi_i$  increase with trophic level (a likely scenario if trophic level and body mass are correlated, since larger-bodied organisms disperse faster and also tend to have



**Figure 2** The maximum number of trophic levels in trophic chain metacommunities, as a function of a common baseline extinction probability  $\pi$  and the leading eigenvalue of a common landscape matrix  $\lambda_M$ . Unless  $\pi$  is low and  $\lambda_M$  simultaneously high, the metacommunity structure itself puts a cap on the number of possible trophic levels. This colour map was generated by iterating eqn 3 until metapopulation capacities dropped below the persistence threshold of 1. However, the same result is obtained by approximating the maximum number of trophic levels simply with  $-\lambda_M \log(\pi)$  (eqn 4; see also Supporting Information, Fig. S3).

lower population sizes, increasing extinction risk), these differences are reduced, and metapopulation capacities start decreasing even after moderate habitat loss. Finally, when  $\xi_i$  but not  $\pi_i$  increases with trophic level, we find a reversed relationship between metapopulation capacity and trophic level for low to moderate habitat loss, with higher trophic levels now also having higher metapopulation capacities. In line with our Bayesian network approach which neglects top-down effects, species at the top of the food web generally have lower metapopulation capacities and are more likely to go extinct than species at lower levels. The reason we do not see this here is that the stronger landscape connectivity gained by faster dispersal at higher trophic levels offsets the increased risk of extinction due to local prey absence.

Note that, while we have assumed that dispersal ability is either constant or increases with trophic level, this need not be the case. In some systems, dispersal rates may actually decrease (Pedersen *et al.*, 2016). Beisner *et al.* (2006) show evidence that zooplankton and fish (species at higher trophic levels) disperse more rarely than smaller organisms in lakes. Villarino *et al.* (2018) show the same phenomenon for plankton, based on body sizes. In such systems, one can implement dispersal rates that decrease with trophic level. All other things equal, this will further hinder the persistence of higher trophic levels.

Changing the functional form of a consumer's response to the loss of its resources alters the overall, absolute scaling of the metapopulation capacities, with little effect on their relative values (compare Fig. 3a–d). For functional forms leading to reduced metapopulation capacities, this means extinctions happen at lower numbers of removed patches. In the case of a

concave response function for instance, we find that the highest trophic levels are often unable to persist even on a fully intact landscape. This is because their persistence probabilities are disproportionately reduced by the absence of even a few of their prey items.

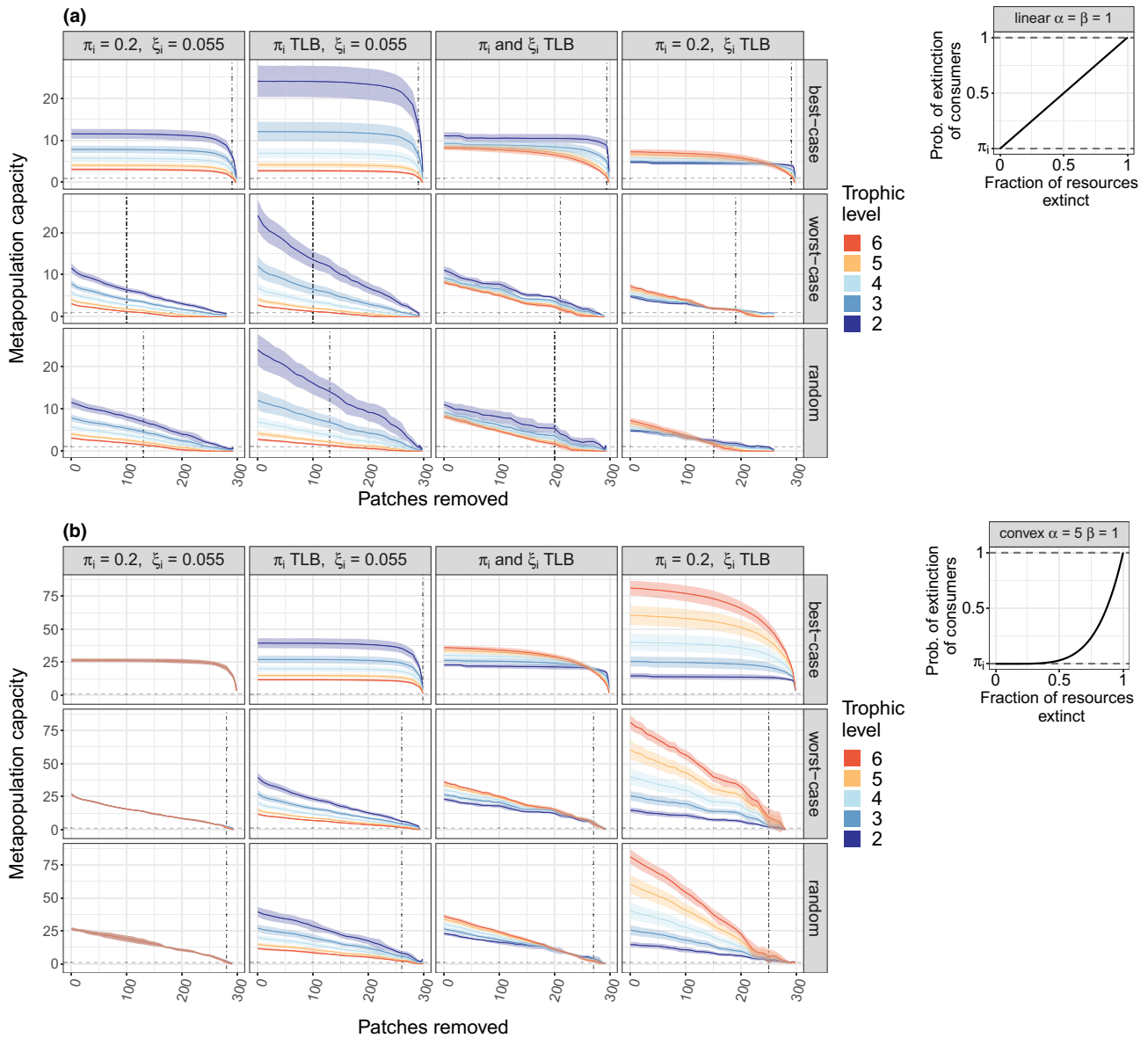
Predictably, an overall increase in habitat connectivity, emulated by gradually increasing  $\xi_i$  from 0.01 to 0.1 (keeping it equal across species, and letting  $\pi_i$  be trophic level-based), acts as a general buffer against species extinctions up until habitat loss becomes too severe (Supporting Information, Section S6). Also, removing patches based on the patch value rankings of top species instead of basal ones does not alter the general patterns we observed, at least for the linear consumer response to prey loss we tested ( $\alpha = \beta = 1$ ). The only difference is that, since patch removal is stopped whenever the top species go extinct, there is no information on metapopulation capacities beyond that point (Supporting Information, Section S6.2). Finally, we have also checked what happens over landscapes where patches are arranged in a more regular, grid-like manner than expected by chance (Supporting Information, Section S10). It turns out that more regular landscapes behave much like random ones; however, they lead to reduced metapopulation capacities overall, hindering metacommunity persistence.

### A case study

We demonstrate that our framework can be readily applied to empirical systems using, as a case study, the plant-mammal Serengeti food web dataset (Baskerville *et al.*, 2011). This is a species-rich web with the plant species mostly associated with particular habitats and mammals often tightly associated with well-defined plant groups (Baskerville *et al.*, 2011). Although the Serengeti ecosystem is a protected area, there are nevertheless threats towards the habitat types within the system. First, the rapidly growing human population outside the park borders increase livestock grazing within the park, resulting in habitat degradation that is particularly severe near the borders (Veldhuis *et al.*, 2019). Second, climate change has recently caused warmer and longer dry season as well as more powerful rains, resulting in soil erosion and washouts (Ritchie, 2008). As such, assessing the effects of habitat loss is relevant for the system. This, together with the data set's species richness and organisation into well-defined trophic levels, make it a good case study for demonstrating our method.

The Serengeti food web data set (Baskerville *et al.*, 2011) contains a total of 161 species and 592 feeding links across three distinct trophic levels, with nine carnivore species feeding on 23 herbivore species feeding on 129 plant species. Apart from a single cannibalistic link (belonging to *Panthera leo*, the lion), the web is completely acyclic. Since the Bayesian network approach requires acyclic networks, we removed this self-link from the data.

In their work, Baskerville *et al.* (2011) used a modified version of the group model (Allesina and Pascual, 2009) and showed that the web contains functionally distinct groups of plants strongly associated with habitat types, connected to distinct groups of primary consumers that in turn are connected to distinct groups of secondary consumers. The nested



**Figure 3** Effect of habitat loss on species persistence in a model food web with 300 consumer and 100 basal species. (a–d) are for different functional forms of a consumer’s response to the loss of resources (top right insets). Species are grouped into trophic levels (colour legends); lines show the mean and the bands around them the one standard deviation range of the metapopulation capacities of species in the corresponding trophic level. Rows indicate patch removal scenario (best-case, worst-case and random); columns the parameterisation method: baseline extinction probabilities  $\pi_i$  and dispersal distances  $\xi_i$  can either take on one value across all species, or increase with trophic level (trophic level-based, TLB). Horizontal dashed lines highlight a metapopulation capacity of 1, the threshold for long-term species persistence. Vertical dashed lines show when the metapopulation capacity of the top species in the food web drops below this threshold.

network structure coupled to a spatial component, together with a high species richness, make the Serengeti food web a good case study to apply our method to. However, since there are only three distinct trophic levels in this system (with a strong bias towards basal species), we use the groups to parameterise our model in addition to the constant and trophic level-based parameterisations we relied on earlier (Supporting Information, Section S6). We follow the group labelling in Baskerville *et al.* (2011) and assign carnivores to groups 1-2, herbivores to groups 3-6, and basal species to groups 7-14. Since group labels decrease with trophic level but

we would like both the baseline extinction probabilities  $\pi_i$  and dispersal distances  $\xi_i$  to increase with them, we define  $\pi_i = 0.2(15 - G_i)/\bar{G}$  and  $\xi_i = 0.055(15 - G_i)/\bar{G}$ , where  $G_i$  is the group index and  $\bar{G}$  their arithmetic average. While this particular parameterisation of groups within a trophic level does not have any specific ecological relevance, it demonstrates how parameter values can be assigned if, for example, ecological information on dispersal properties for certain groups of species is available.

The original dataset does not contain any explicit spatial arrangement of the food web in a landscape. Therefore we use

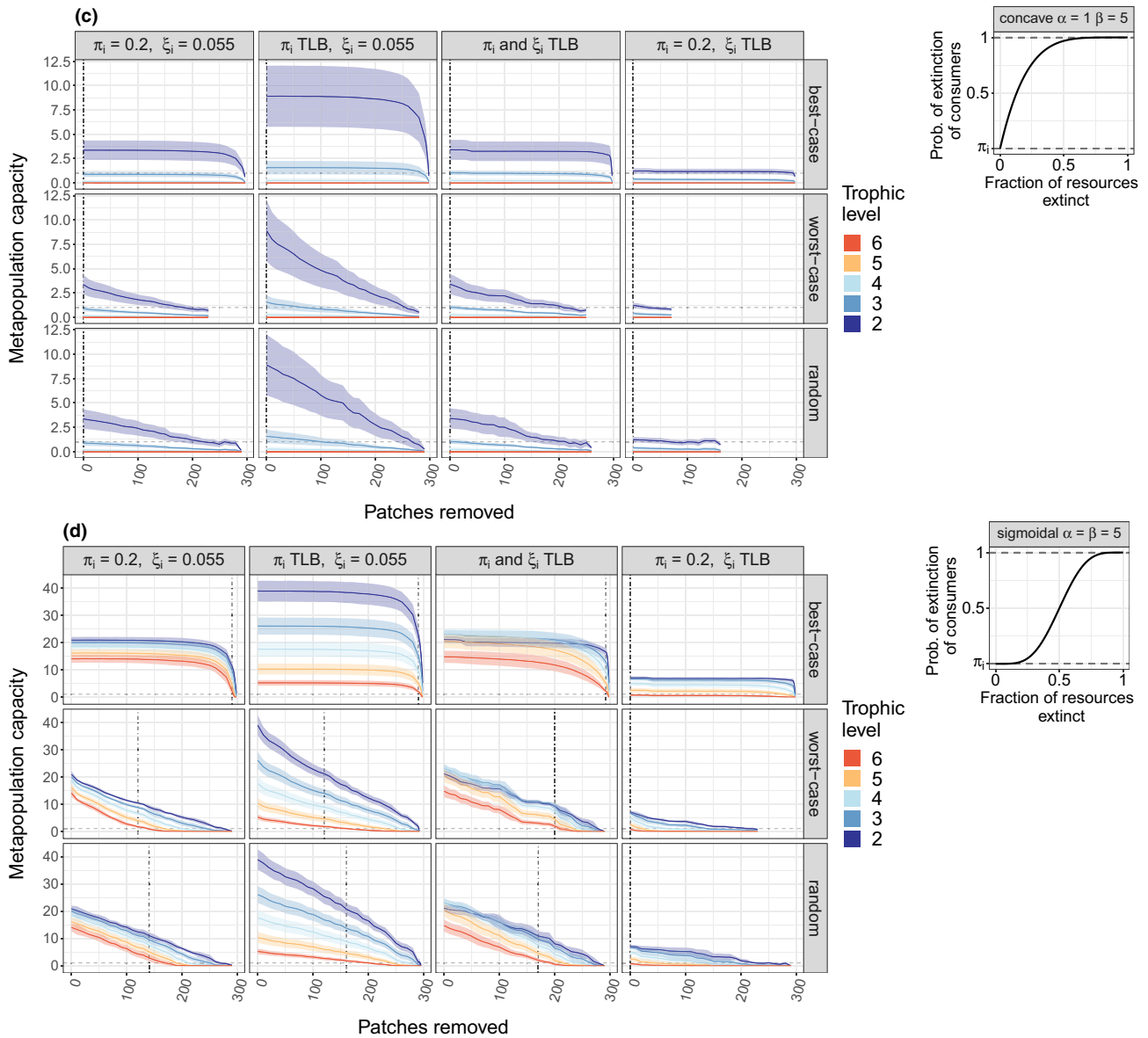


Figure 3 Continued.

the same approach here as for our model food webs and construct a landscape of 300 patches uniformly placed in the unit square. In the best- and worst-case habitat loss scenarios, we ranked patches for removal based on their contribution to the metapopulation capacity of a basal species. This species was chosen to be the Gum arabic tree (*Acacia senegal*), because it is a basal species that is also the sole member of spatial group 12.

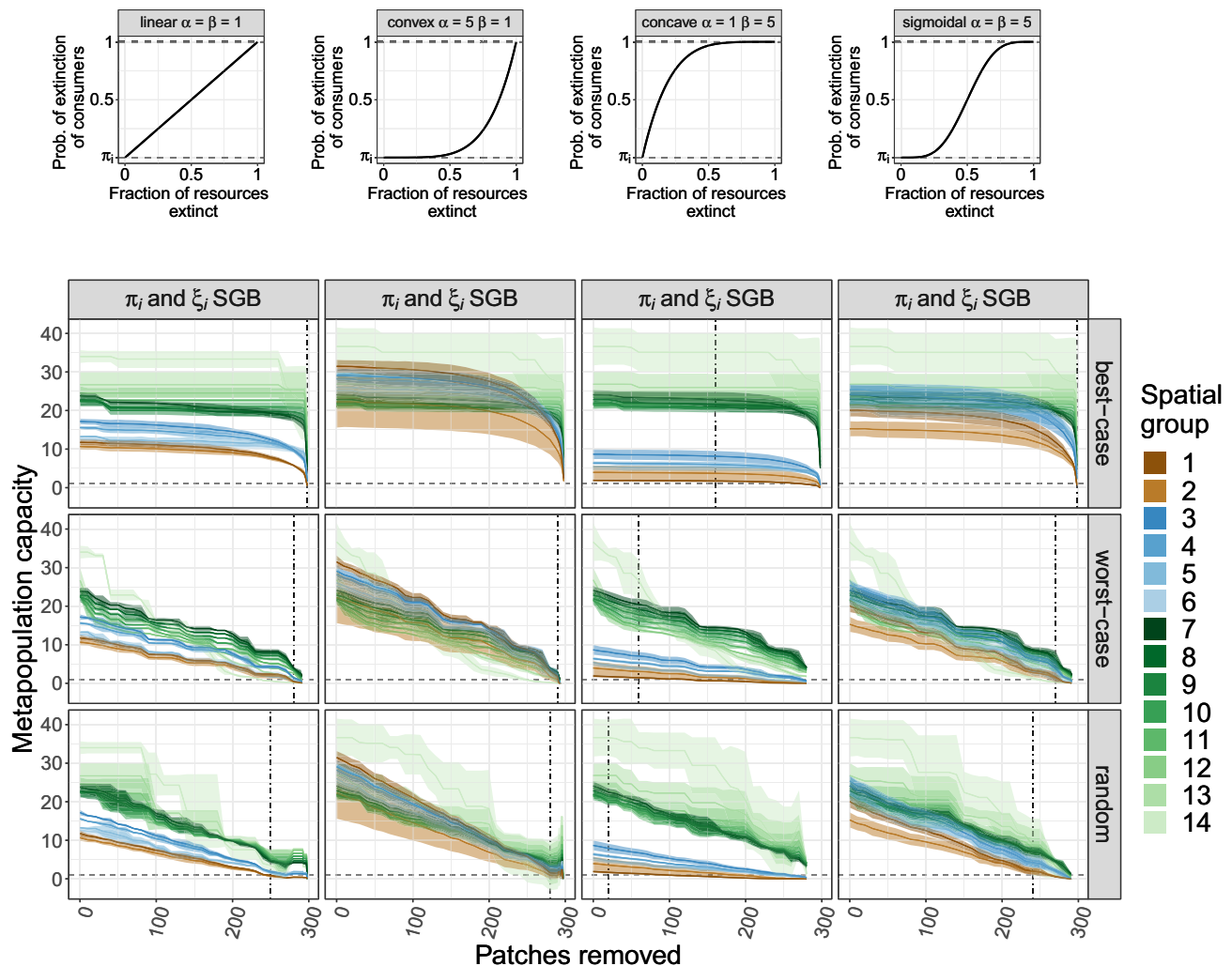
The patterns we obtain for the Serengeti food web when  $\pi_i$  and  $\xi_i$  are constant or trophic level-based are consistent with the results found for the model food webs (Supporting Information, Section S6), with one exception. We find that the negative effect of a concave predator response on metacommunity persistence is strongly mitigated, with the metacommunity persisting even under severe habitat loss and a worst-case patch removal scenario. This is in contrast to the

pattern seen in the model food webs, where the concave form immediately leads to the loss of the topmost trophic levels. However, this result is an artefact of the overabundance of basal species in the Serengeti dataset, and the low baseline extinction probability they all receive under a strictly trophic level-based parameterisation. When parameters are spatial group-based (Figure 4), the better resolution of the parameterisation leads to an outcome in line with those seen in the model food webs when both  $\pi_i$  and  $\xi_i$  are trophic level-based.

## DISCUSSION

Understanding how habitat loss affects complex communities such as food webs remains a major challenge in ecology (Guzman *et al.*, 2018; Leibold and Chase, 2018). Due to indirect effects present in ecological networks, the extinction of one





**Figure 4** Effect of habitat loss on species persistence in the Serengeti food web. Layout as in Fig. 3, except colour legends show spatial group instead of trophic level, and columns show different functional forms of a consumer's response to the loss of resources (top insets). We show the results for the spatial group-based parameterisation (SGB), whereby both the baseline extinction probabilities  $\pi_i$  and dispersal distances  $\xi_j$  decrease with spatial group. In the colour scheme, green colours are groups whose species are primary producers, blue colours are groups with secondary consumers and brown colours are groups with top predators.

species can set in motion an entire cascade of secondary extinctions (Ebenman and Jonsson, 2005; Dunne and Williams, 2009). Here we have studied the effect of habitat loss on food webs by developing a novel approach to trophic metacommunities, combining the methods of classic metapopulation models on fragmented landscapes (Hanski and Ovaskainen, 2000, 2003; Ovaskainen and Hanski, 2001; Grilli *et al.*, 2015) with a Bayesian network representation of trophic interactions (Eklöf *et al.*, 2013) for calculating local extinction rates. The approach has much of the flexibility of explicit dynamical models (Ryser *et al.*, 2019), but is close in tractability and computational efficiency to simple topological methods (Dunne and Williams, 2009). This allows one to apply it to much larger food webs and landscapes than would be feasible with fully fledged dynamical models, while still retaining the ability to make predator extinction a smooth function of prey absence (as in Cazelles *et al.*, 2015). It thus provides an

alternative, complementary way of analysing spatial food webs.

Thanks to its origin in well-studied metapopulation models, the method inherits many of their useful analytical properties, such as the ability to rank habitat patches with respect to their value to the community as a whole (Ovaskainen and Hanski, 2001). We demonstrated the importance of this ranking by simulating the patch removal process, taking away patches in sequence based on their value. This has revealed that trophic metacommunities can tolerate substantial habitat loss if the least valuable patches are removed first. However, starting with the most important ones greatly accelerates collapse. Surprisingly, random removal of patches is almost indistinguishable in its effects from the worst-case scenario of removing patches in decreasing order of importance, leading to similar landscapes in which habitat is scattered randomly (Fig. 1). In contrast to this, removing less valuable patches

first in the best-case scenario preserved habitat islands in which species were able to persist even under severe habitat loss. This highlights the need to estimate patch rankings in real-life conservation efforts, and to either prioritise conserving high-value patches, or else to improve the value of others—e.g. by increasing habitat connectivity. Land use strategies which take these considerations into account can then substantially promote food web persistence, and especially prevent top species extinctions.

Our metacommunity approach is similar to some trophic models of island biogeography (Holt, 2009; Gravel *et al.*, 2011a,b). In fact, our work can be seen as an extension and a change of focus from these works. It is an extension in two ways. First, our model is spatially explicit. Second, it replaces the strict dichotomy of a predator either being able to colonise a patch or not at all (depending on whether at least one of its prey items are locally present) with a more gradual approach using Bayesian networks, in which the presence of a predator is a smoothly increasing function of the likelihood of its prey items being present. It is a change of focus in that we have concentrated on the effects of habitat loss in closed metacommunities, instead of species-area relationships and the effect of network metrics on regional persistence in an island-mainland setting.

Our framework characterises each species by (1) their position in the food web; (2) their patch-specific baseline extinction probabilities  $\pi_i^k$ ; and (3) their dispersal kernel (which, in our case, was always chosen to be exponential with a species-specific dispersal distance  $\xi_i$ ). In the literature, an increased risk of extinction has been related to various indicators such as high trophic level, large body size, and low abundance (Gaston and Blackburn, 1995; Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Davidson *et al.*, 2009; Lee and Jetz, 2011). In agreement with several previous studies (Kondoh, 2003; van Nouhuys, 2005; Eklöf and Ebenman, 2006; Curtsdotter *et al.*, 2011; Liao *et al.*, 2017b; Ryser *et al.*, 2019), we found that species at higher trophic levels indeed tend to suffer elevated extinction risks. Differences in other indicators can be accounted for through their effects on the species-level parameters  $\pi_i^k$  and  $\xi_i$ . For instance, if a patch can only support a small number of individuals of a given species, it has a higher chance of disappearing due to demographic stochasticity even when all its resources are present. Such a situation can be represented by increasing the species' patch-specific baseline extinction probability. While this can and should be done whenever adequate data are available to characterise each patch on the landscape, here we deliberately assumed all habitat patches to share the same abiotic conditions (Leibold *et al.*, 2004) and thus baseline extinction probabilities to be independent of patch identity. This allowed us to focus on the general effects of habitat loss.

Similarly, dispersal ability is crucial for persistence in fragmented landscapes; all other things equal, species that are good dispersers are at an advantage. In our model, we can integrate different assumptions for the dispersal abilities of species by assigning species-specific dispersal distances and dispersal kernel forms. We have looked at constant dispersal distances across species, and also ones that increase with trophic level (and, in case of the Serengeti food web, scale

with the spatial guild of a species). Ideally, detailed information on species-specific dispersal would be used to construct realistic dispersal kernel functions in conjunction with realistic habitat structures, as the combination have profound consequences for species persistence (Årevall *et al.*, 2018). This may include possibilities such as multiplying the dispersal kernel of each species by an overall size-dependent scaling factor. While data are scarce, it is conceivable that this factor is in fact inversely related to size, due to smaller organisms having more offspring that disperse, as well as having faster population dynamics. The interplay of such a scaling relationship with the direct size dependence of dispersal distances may alter the interpretation of Fig. 3.

However, regardless of such details, it follows from the structure of our model that habitat destruction likely affects species at the highest trophic levels the most, since apart from having fewer available patches for colonisation in the landscape, they must also cope with the problem of reduced prey availability. In line with this expectation, we found that habitat isolation deconstructed food webs from top to bottom, with species at higher trophic levels going extinct first (Ryser *et al.*, 2019; McWilliams *et al.*, 2019). Dispersal ability can also be seen as a measure of habitat connectivity, i.e. how well species can access habitat patches in general. This is particularly important as human land use practices causing habitat loss often also decrease the quality of the habitat matrix in which the patches are embedded (Bonte *et al.*, 2012). A decrease in matrix quality manifests itself in overall reduced dispersal likelihoods, whereby the kernel yields a lower dispersal rate for all distances, reducing the chance of successful colonisation between habitats (Eklöf *et al.*, 2012).

Despite its tractability, computational efficiency, and straightforward parameterisability, our metacommunity approach also has idiosyncrasies and important limitations. First, it should be noted that only extinction rates depend on species interactions, not colonisation rates. This may look strange, implying that a predator  $i$  may establish in a patch  $k$  that is devoid of any prey. That, however, turns out to be irrelevant, because the extinction probability  $\delta_i^k$  of the predator in such a patch is equal to one. Thus, the extinction rate  $E_i^k = -\log(1 - \delta_i^k)$  is infinitely large, immediately negating the effect of the colonisation process (eqn 1). While incorporating interaction-dependent colonisation in the model is definitely a promising avenue for future development, the lack of this dependence does not undermine the model's results or applicability.

Second, throughout this work, we have made conditional predator extinction probabilities either a function of the fraction, or weighted fraction (Supporting Information, Section S7), of prey species lost. There may be cases when it is better to make them some absolute function of the available prey in a given location—such as for opportunistic feeders which consume anything within a certain size range. Fortunately, our model is extensible to deal with such scenarios (Supporting Information, Section S1), though at the cost of replacing eqn B2 with something more complicated.

Third, the calculation of extinction rates depends heavily on the assumption of the separation of time scales between extinction and colonisation: the Bayesian network method of calculating extinction probabilities assumes that there is no

chance of an extinction cascade within a patch being stopped by a colonist of a prey species arriving midway through. This essentially means that mass effects are assumed not to influence extinction dynamics. It also explicitly assumes that everything is in (quasi-)equilibrium when calculating local extinction rates, so our method might not be suited for calculating extinction debts or patch occupancy dynamics far from equilibrium.

Fourth, the food web structure must be acyclic (no “A eats B eats C eats A” scenarios), because the Bayesian network formalism can only be used for such webs. Fortunately, while real food webs are not perfectly acyclic, they are generally close, and there are ways of removing cyclic links from food webs in a robust way that has minimal effect on the rest of the web (Allesina *et al.*, 2009; Eklöf *et al.*, 2013).

Finally, an important limitation is that species’ dynamics depend only on the persistence probabilities of their prey, not their predators. In real food webs, secondary extinctions can emerge bottom-up (if consumers lose their resources), and top-down, by resources responding to the loss of their consumers. Species may, for example, be locally predated to extinction (Huffaker, 1958; Schoener *et al.*, 2001), and the loss of a predator can release a prey species which then grows to the point of eliminating other species in the web (Paine, 1966, 1974; Lafferty and Suchanek, 2016). However, since Bayesian networks operate on a strict bottom-up principle whereby prey influence their predators but not vice versa (from the perspective of prey, their predators might as well not even be present), extinctions resulting from top-down effects are not implemented in our framework. This is a severe limitation; moreover, there is no immediate, straightforward remedy that would unambiguously extend the model to take top-down effects into account. This has to be considered when interpreting its results and applying the method to empirical systems: if, in a given system, top-down effects are deemed important, other methods should be used instead.

The current consensus within community ecology is that new ways of thinking about trophic metacommunities are needed to move the field forward (Leibold and Chase, 2018; Guzman *et al.*, 2018; Hirt *et al.*, 2018). Here we offered one possible approach to this problem, rooted in classic metapopulation theory and the method of Bayesian networks. Due to its flexibility and ability to handle large systems, we see our approach as a stepping-stone along the way to a fuller understanding. Our numerical experiments demonstrate that preserving high-value patches increases the likelihood of community persistence, even under severe habitat loss. Increasingly isolated landscapes, on the other hand, accelerate species extinctions and particularly drive top species towards extinction, reducing trophic complexity. Using a different methodology, similar trends have been observed by Ryser *et al.* (2019); in fact, our model qualitatively reproduces their results (Supporting Information, Section S8). Our findings reinforce that trophic interactions, dispersal ability and the spatial configuration of patches are crucial when assessing the extinction risk of species in fragmented landscapes. We hope that our method will be of use to ecologists interested in metacommunity processes and to provide useful insights for real-life conservation efforts to preserve complex trophic communities.

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## AUTHORSHIP

JH and GB contributed equally to the project and are joint first authors. JH, GB and AE conceived of the study; JH and GB developed the modelling framework; JH and GB wrote the manuscript and performed numerical studies; GB wrote the supplement and derived analytical results. All authors contributed to the final form of the manuscript.

## PEER REVIEW

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## DATA ACCESSIBILITY STATEMENT

Data and code to reproduce our results can be found at: <https://doi.org/10.5281/zenodo.4028326>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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