

# How do corridors connecting two separated landscapes affect the ability of trophic metacommunities to survive habitat loss?

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## **1 Abstract**

With an increasing worldwide infrastructure more habitats are fragmented by roads and buildings, which can cause a reduction in biodiversity up to 75%. One way to counteract this is by predicting the outcome, with the help of theoretical models, before it happens. In this study I used a Bayesian network model on a fragmented landscape, to test how well trophic metacommunities are able to persist habitat loss, when increasing dispersal between the fragments in the landscapes by implementing corridors. By implementing just three corridors, the species with the highest trophic level went extinct at a considerable later stage, and by just implementing 10 corridors, the metapopulation capacity for all species in all trophic levels increased. Similar results were obtained when changing the way the species extinction probabilities react to their resources being extinct, which further strengthen the efficacy of corridors. The results from this study suggests that increasing connectivity between landscape fragments, and therefore promoting dispersal of organisms, would help the conservation of biodiversity.

**Keywords:** Bayesian network, corridors, habitat loss, metacommunity.

## **2 Introduction**

With an increasing worldwide infrastructure more habitats are being fragmented by roads and buildings. Haddad et al. (2015) demonstrated through an extensive analysis (five continents and 35 years) that the biodiversity in a fragmented habitat is reduced with 13% to 75%, compared to a non-fragmented habitat. Projections of expected climate change and species-level extinction also revealed that species that are unable to migrate (e.g., due to habitat fragmentation) have almost double the estimated expected percentage of becoming extinct (34-52%) compared to species that are able to migrate (22-33%) (Thomas et al., 2004). Therefore, to preserve biodiversity, it is imperative that models and methods that are able to estimate the effect of habitat fragmentation are established and refined. However, there is one more consideration to be made: a food web with interacting- and interdependent species is sensitive to certain species going extinct (e.g. highly interactive species or basal species) (Soulé et al., 2003, Eklöf & Ebenman, 2006). Therefore, when a species in that community is lost, for example by extinction, it can cause the extinction of other species within that community, a so-called secondary extinction (Ebenman & Jonsson, 2005). Thus, models that aim to protect and preserve biodiversity, by studying the effect of habitat fragmentation, need to incorporate secondary extinctions.

Three common approaches to analysing secondary extinctions in ecological networks are topological models which originate from studies of complex networks, dynamical models which focus on the dynamics of abundances or biomasses over time for all species in the network, and lastly, the Bayesian network model (Albert et al., 2000; Eklöf & Ebenman, 2006; Eklöf et al., 2013). Usually, in studies using the topological models, the robustness of the network is analysed using simple properties such as connectivity and number of species (Solé & Montoya, 2001). The networks' robustness is measured based on the number of secondary extinction the network can be subjected to (Solé & Montoya, 2001). Because topological models typically only use those network structures as input, it is possible to analyse larger networks (Eklöf et al., 2013). However, there are some limitations to this approach. Topological models do not account for the dynamics of ecological communities, for example, all species are assumed to have the same extinction probability, which does not reflect natural systems, where some species are more prone to going extinct than others (Eklöf & Ebenman, 2006; Eklöf et al., 2013). Also, in the topological approach, secondary extinction of a species only occurs when all its resources are lost (Eklöf et al., 2013). This is a crude assumption since other causes of secondary extinctions, such as loss of predators and secondary extinctions of basal species, cannot be revealed (Eklöf & Ebenman, 2006).

With dynamical models other types of extinctions can be analysed, such as the secondary extinction of a predator's resources when the predator goes extinct (Eklöf et al., 2013). Dynamical models also take extinction thresholds into account, where lower density of resources might not be sufficient to support the consumer (Eklöf & Ebenman, 2006; Eklöf et al., 2013). Although dynamical models are the most realistic of the two presented models, they require a considerable number of parameters and are computationally expensive, which makes analysing larger food webs impractical (Eklöf et al., 2013; Häussler et al., 2020).

The third approach was created by Eklöf & co-workers in 2013. It uses a Bayesian network model that combines the simplicity of the topological model with some important features from the dynamical model, reducing the set of parameters to track population dynamics (Eklöf et al., 2013). The Bayesian network model consists of a set of variables with each having a finite set of states, such as on/off, yes/no (Jensen, 1996). The variables form a directed acyclic graph and attached to each variable is a probability table that calculates the probability that, for example, A goes to B or C (Jensen, 1996). So when the Bayesian network is provided with a structure

and a baseline probability of extinction for each species, the exact probability of secondary extinctions can be calculated (Eklöf et al., 2013).

Häussler et al. (2020) created a model that combines Eklöf et al.'s (2013) approach to analysing secondary extinctions with classic metapopulation models on fragmented landscapes, to be able to study the effects of habitat loss on food webs in a metacommunity. A metacommunity can be defined as a number of local communities linked by dispersal of multiple interacting species (Gilpin & Hanski, 1991; Leibold et al., 2004; Leibold & Chase, 2018). By using Eklöf & co-workers approach, local extinction rates can be calculated using a Bayesian network model which allows for modelling of food webs with hundreds of patches and species (Eklöf et al., 2013; Häussler et al., 2020). By using the classic metapopulation models on fragmented landscapes, patches can be ranked based on their long-term persistence which enables us to analyse how habitat loss affects species extinctions, depending on whether valuable or non-valuable patches are removed (Hanski, 1994; Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2001; Häussler et al., 2020). Through this model, approximations such as how habitat loss affects the ability of metacommunities to survive can be obtained (Häussler et al., 2020).

By modifying the model, such as number of species and trophic levels in food webs and number of patches in a landscape, different scenarios are created, and therefore different outcomes can be obtained. For example, Häussler et al. (2020) tested this by removing certain patches, either the least/most valuable patches were removed or patches were removed at random. The results showed that there was almost no difference between removing the most valuable patches and removing patches at random. In both scenarios, all species had a high risk of extinction after moderate amounts of patch removal. By contrast, removing the least valuable patches first caused species to have a higher chance to persist a larger number of patch removals. Häussler et al. (2020) also deduced that an increased habitat connectivity counteracts species extinction during habitat loss, until habitat loss is too extreme, which falls in line with previous studies (Dunne et al., 2002).

Due to the impact habitat fragmentation has on biodiversity, I expand the current knowledge by studying if and how an increased connectivity between two landscapes, as opposed to within one landscape, affect species extinctions probabilities. In this way, we can identify under what circumstances increased connectivity can counteract the effect of habitat fragmentation, and therefore help the preservation of biodiversity. This scenario is possible to simulate and analyse

thanks to Häussler et al.'s (2020) model, which allows us to create a fragmented landscape, increase connectivity between those landscapes, calculate species extinction probabilities during habitat loss, and compare those results with a fragmented landscape without connectivity. Thus, I will study how the implementation of corridors between two separated landscapes affect trophic metacommunities ability to survive habitat loss.

### 3 Materials and methods

The model created by Häussler et al. (2020) is based on a Levins-type metapopulation model over a fragmented landscape, where  $N$  habitat patches are connected by dispersal (Levins, 1969; Hanski & Ovaskainen, 2000). In this landscape, each species has a metapopulation and their colonisation of habitat patches depends on two factors; which patches are currently occupied by species and how the species can migrate (Häussler et al., 2020). The colonisation rate of patch  $k$  by species  $i$  can be modelled as

$$C_i^k = \sum_{l=1}^N M_i^{kl} p_i^l,$$

where the probability that species  $i$  is found in patch  $k$  is  $p_i^k$  and where  $M_i^{kl}$  gives the dispersal rate of species  $i$  from patch  $l$  to  $k$  in a species-dependent landscape matrix.

Species can also go extinct, which occurs through both local patch conditions and through an increased extinction risk in a patch caused by the absence of local prey items for a species (Häussler et al., 2020). The extinction rates are acquired from the probability  $\delta_i^k$  that species  $i$  disappears from patch  $k$  and with that the probability of extinction per unit of time is

$$\delta_i^k = 1 - \exp(-E_i^k).$$

By combining these equations with a food web constituted of a Bayesian network, the following equation is acquired:

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

#### 3.1 Bayesian networks

To use this model, some parameters must be defined/determined. First, the baseline probability  $\pi_i^k$  for species  $i$  to go extinct in patch  $k$  that is,

$$\delta_i^k = 1 - \exp(\pi_i^k),$$

even when we assume that all resources of species  $i$  are present. Second, the dispersal distance is determined as  $\xi_i$  of species  $i$ . Through these parameters we can obtain the conditional probability for species  $C$  to go extinct,  $P(\neg C|f)$ , as a function of the fraction  $f$  of its resources that are absent in its patch. The shape of the function determines how the species extinction

probabilities react to a fraction  $f$  of its resources that are absent. The shape the function can take on is determined by regularized beta functions, with the shape parameters  $\alpha$  and  $\beta$  (Figure 1). The first one is when  $\alpha$  and  $\beta$  are both equal to 1, which creates a linear function and therefore makes a consumer's extinction probability proportional to the fraction of resources lost. The second one is when  $\alpha$  is 5 and  $\beta$  is 1, which creates a convex function, and makes the consumer's extinction probability increase only after a larger fraction of its resources have already been lost. The third one is when  $\alpha$  is 1 and  $\beta$  is 5, which creates a concave function, and makes the consumer's extinction probability high only after a small amount of its resources have been lost. And finally, the fourth case is when both  $\alpha$  and  $\beta$  are 5, which creates a sigmoidal function, with properties from both case 2 and 3 (Häussler et al., 2020).

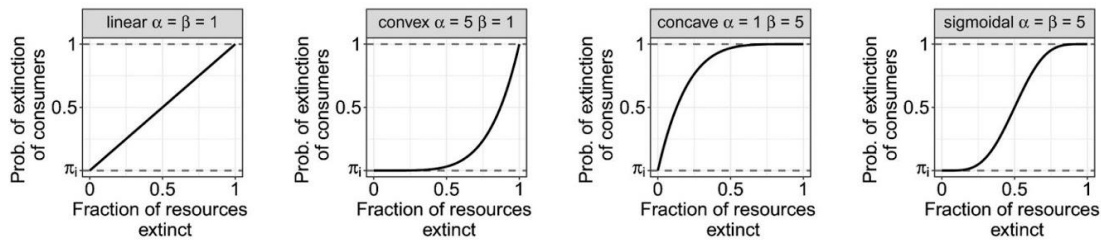


Figure 1. Forms of response function. Consumer's extinction probability on y-axis. On the x-axis, the fraction of resources extinct. Created by Häussler et al. (2020).

The conditional probability also increases with  $f$ , from  $\pi_i^k$ , when  $f=0$ , to certain extinction, when  $f=1$ :

$$P(\neg C|f) = \pi_c + (1 - \pi_c)w(f),$$

where  $\pi_c$  is species C baseline extinction probability, and  $w(f)$  is a weighting function, so that  $w(0)=0$  and  $w(1)=1$ . For all basal species whose resources are always available,  $f=0$ , so that

$$P(\neg A) = \pi_A + (1 - \pi_A)w(0) = \pi_A.$$

For a non-basal species C, the probability of extinction  $P(\neg C)$  is obtained by combining the extinction probabilities of its prey with the law of total probability:

$$P(\neg C) = P(\neg C|AB)P(A)P(B) + P(\neg C|\neg AB)P(\neg A)P(B) + \\ P(\neg C|A\neg B)P(A)P(\neg B) + P(\neg C|\neg A\neg B)P(\neg A)P(\neg B).$$

When we have specified the probability for each species to go extinct based on the state of its resources, we have a Bayesian network (Eklöf et al., 2013). But because the resources depend on other species in this metacommunity we need to calculate the probability of extinction of species  $i$  for all the possible states of all species. One way of doing so is by randomly simulate, based on the species probability of extinction, an outcome for species  $i$ , so it becomes either

extinct or extant. If this is done for all species, over many iterations, we would get the marginal probability of extinction. In this study, the number of iterations for the Bayesian network was 1000.

We can also obtain the persistence of any species  $i$ , which can be determined based on the metapopulation capacity  $\lambda_i$ , a relative value that indicates how well a fragmented landscape can support a species' metapopulation (Hanski & Ovaskainen, 2000). The metapopulation capacity of species  $i$  can be computed as the dominant eigenvalue of the landscape matrix  $M_i^{kl}$  (Ovaskainen & Hanski, 2001). If  $\lambda_i$  is more than 1, the metapopulation will persist and if  $\lambda_i$  falls below 1, all  $p_i^k$  are zero and therefore the species goes extinct. The relative patch value can also be obtained, which measures how vital that patch is for the survival of a species and/or metacommunity (Eklöf et al., 2013, Häussler et al., 2020).

### 3.2 Landscape

To be able to study how different food webs are affected by habitat loss, both food webs and landscapes must be generated. Häussler et al (2020) created 4 food webs, each containing 400 species and different ratios of consumer to basal species, and five landscapes, each containing 300 patches. The landscape was created so that species' ability to move between two patches (the dispersal distance) decreased exponentially with the distance  $d^{kl}$  between the patches, according to this equation

$$M_i^{kl} = \exp\left(-\frac{d^{kl}}{\xi_i}\right),$$

where  $\xi_i$  is species  $i$ 's dispersal distance (Häussler et al., 2020). Additionally, each patch can theoretically house a full food web. Habitat loss is then implemented into these landscapes. Habitat loss can be implemented by three scenarios, which is determined as “best”, “worst” and “random”. In the best-case scenario, the patches are removed in order of the basal species patch value, where the least valuable patches are removed first. In the worst-case scenario, the patches are removed in order of the basal species patch value, but instead the most valuable patch is removed first. In the random scenario, patches are not removed depending on any patch value, they are simply removed at random. Patch values can be calculated based on the outer product of the dominant left and right eigenvectors of  $M_i^{kl}$  (Ovaskainen & Hanski, 2001), where  $i$  is the species for which the patch values are evaluated. After each set of patch removal, the patch values are recalculated to obtain new ranks for the patches.



The starting point to be able to create my scenario and answer my research question was to use the model created by Häussler et al. (2020). To be able to use their model I downloaded all their available codes and scripts that were used in their study. Throughout the study, I used R, version R-4.0.5 and the Sigma computing cluster at the National Supercomputer Centre (NSC) in Linköping, Sweden. After that, I had to modify the existing scripts so that they were able to simulate my scenario.

### **3.3 Modifications to the landscape matrix**

The main modification to the script was done to be able to create a landscape, where one half of the landscape was disconnected from the other. To do this, I divided the landscape into two matrices, with one matrix having all the x-coordinates below 0.5 and the other matrix with x-coordinates above 0.5 (the side lengths of the landscape were scaled to be equal to 1). This was done so that when each patch in the landscape was assigned a dispersal distance  $\xi_i$ , instead of creating dispersal distances between all patches, only the patches in their own matrix were connected. They were then put back together into one big matrix, so that the patches on the left half of the matrix did not have a dispersal value (value 0) to the patches on the right side, creating a barrier between them. This made sure that both the halves were fully independent from each other, which was necessary for my research question. After that, I created corridors between these two landscapes, allowing the species to move between them.

### **3.4 Implementation of corridors**

To create the corridors between these separated landscapes, I chose a number of pairs of patches from the landscape, with each pair containing one patch from the left half and one from the right half of the landscape, where one corridor is equal to one pair of patches. These patches were then given a dispersal value of 1, which allowed migration within each pair from one side of the landscape to the other. I also protected these patches from being removed when stimulating habitat loss, to receive the highest possible effect. I intend to simulate multiple scenarios with different numbers of corridors, to generate a clearer picture of whether corridors do indeed make a difference. In this study, I chose to add 3, 10, 20 and 30 pairs of patches.

### **3.5 Parameters for the simulations**

For the simulations, I chose a pre-existing landscape generated by Häussler et al. (2020) in their study. The landscape I chose contained 300 patches, with x and y coordinates ranging between

0.0 and 1.0. The food web I chose was also generated by Häussler et al. (2020) and it contained 400 species, with 50 basal species and 350 consumers (herbivores, omnivores, and carnivores). In this particular food web, the baseline extinction probability is trophic level based,  $\pi_i = \text{TLB}$ , which was calculated as  $\pi_i = 0.2T_i/\bar{T}$ , where  $T_i$  is the trophic level for species  $i$  and  $\bar{T}$  is the average trophic level for the whole web and the dispersal distance between the patches are constant,  $i = 0.055$ . For both simulations, the number of patches removed for each habitat loss phase was 10.

For the simulation without the corridors, I replicated the scenario and parameters from the simulation with corridors, with a few exceptions. In this simulation, there were no pairs of patches given dispersal value and no patches were protected. I also filtered out all the x-coordinates which were  $< 0.5$ , in the landscape. I did this because both halves of the landscape contained approximately the same number of patches and they are completely independent from each other, which would have created a similar outcome for both halves. One can simulate with both halves, but it is more time efficient to only include one half. I tested for each simulation, with and without corridors, how the metacommunity reacted to the “best”, “worst” and “random” habitat loss scenarios previously described. After that I tested how these results might differ if the  $\alpha$  and  $\beta$ -parameters of the Bayesian network were changed between  $\alpha=\beta=1$ ,  $\alpha=5$  &  $\beta=1$ ,  $\alpha=1$  &  $\beta=5$ ,  $\alpha=\beta=5$  (*Figure 1*).

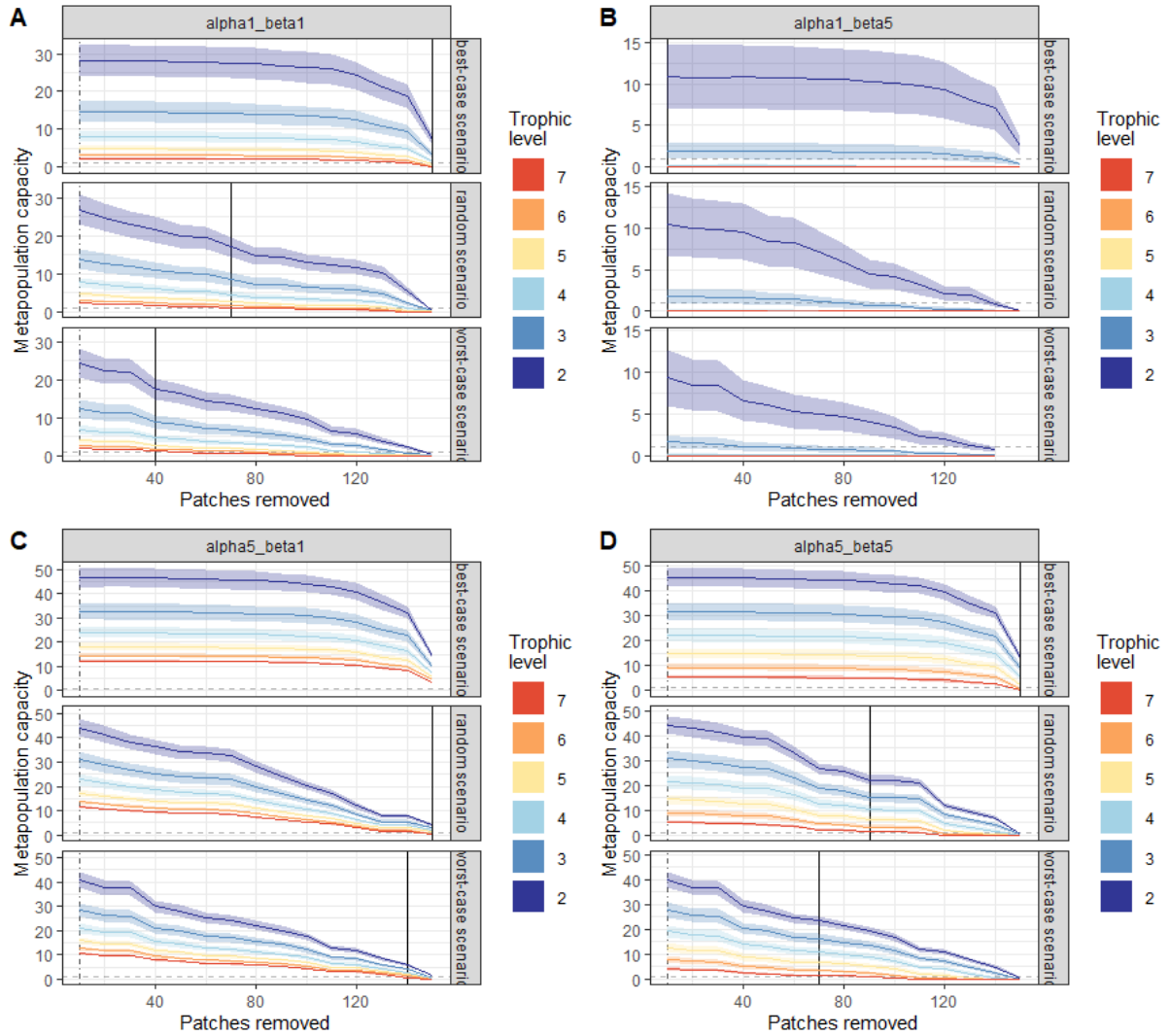
## 4 Results

For all simulations, fragmented landscapes were better at supporting the metapopulation of lower trophic levels (high metapopulation capacity) than that of higher trophic levels (lower metapopulation capacity).

### 4.1 Simulations without corridors

When simulating a landscape with 0 corridors (and a linear response function, i.e. the relationship between extinction probabilities and missing resources) (*Figure 2A*) the metapopulation capacity is generally low for all trophic levels, resulting in all trophic levels to go extinct, and the species at the highest trophic level not surviving for so long (*Table 1*). Changing the response function to sigmoidal (*Figure 2D*) the metapopulation capacity for all trophic levels and the point at which the species at the highest trophic levels went extinct increased, however, all trophic levels still went extinct. The convex shape causes all trophic

levels to persist (*Figure 2C*), while the concave shape caused all trophic levels (except trophic level 2) to go extinct at the first instance of patch removal (*Figure 2B*).



*Figure 2. Metapopulation response to habitat loss in landscape with **no** corridors and varying shape of response curve. (A) Linear, (B) Concave, (C) Convex and (D) Sigmoidal. The x-axis shows number of patches removed and the y-axis shows long term persistence (metapopulation capacity). Colors indicate species' trophic level, see legend. Line indicates the mean for that trophic level and the color around shows the standard deviation range for that trophic level. Horizontal dashed line indicates where the threshold for long-term species persistence is, a metapopulation capacity of 1. Vertical line indicates when the metapopulation capacity for the top species drops below this threshold. Each row is one scenario; "best-case scenario", "random scenario", "worst-case scenario".*

## 4.2 Simulation with corridors

As expected, an increased presence of corridors increased the long-term persistence for all trophic levels. For ten corridors or more, even more trophic levels stayed above the threshold.

Implementing more corridors generally increased the amount of trophic levels above the threshold, and therefore decrease the amount of trophic levels extinct. The point at which the species at the highest trophic level went extinct increased when just implementing 3 corridors (*Table 1*).

*Table 1. Patches removed for species with highest trophic level to go extinct. Headings indicates shape of response function. Rows indicate number of corridors. Columns indicate scenario.*

	$\alpha=\beta=1$		$\alpha=\beta=5$	
	Worst-case	Random	Worst-case	Random
0 corridors	40	70	70	90
3 corridors	80	130	150	160
10 corridors	100	150	140	170
20 corridors	100	140	140	190
30 corridors	100	150	140	180

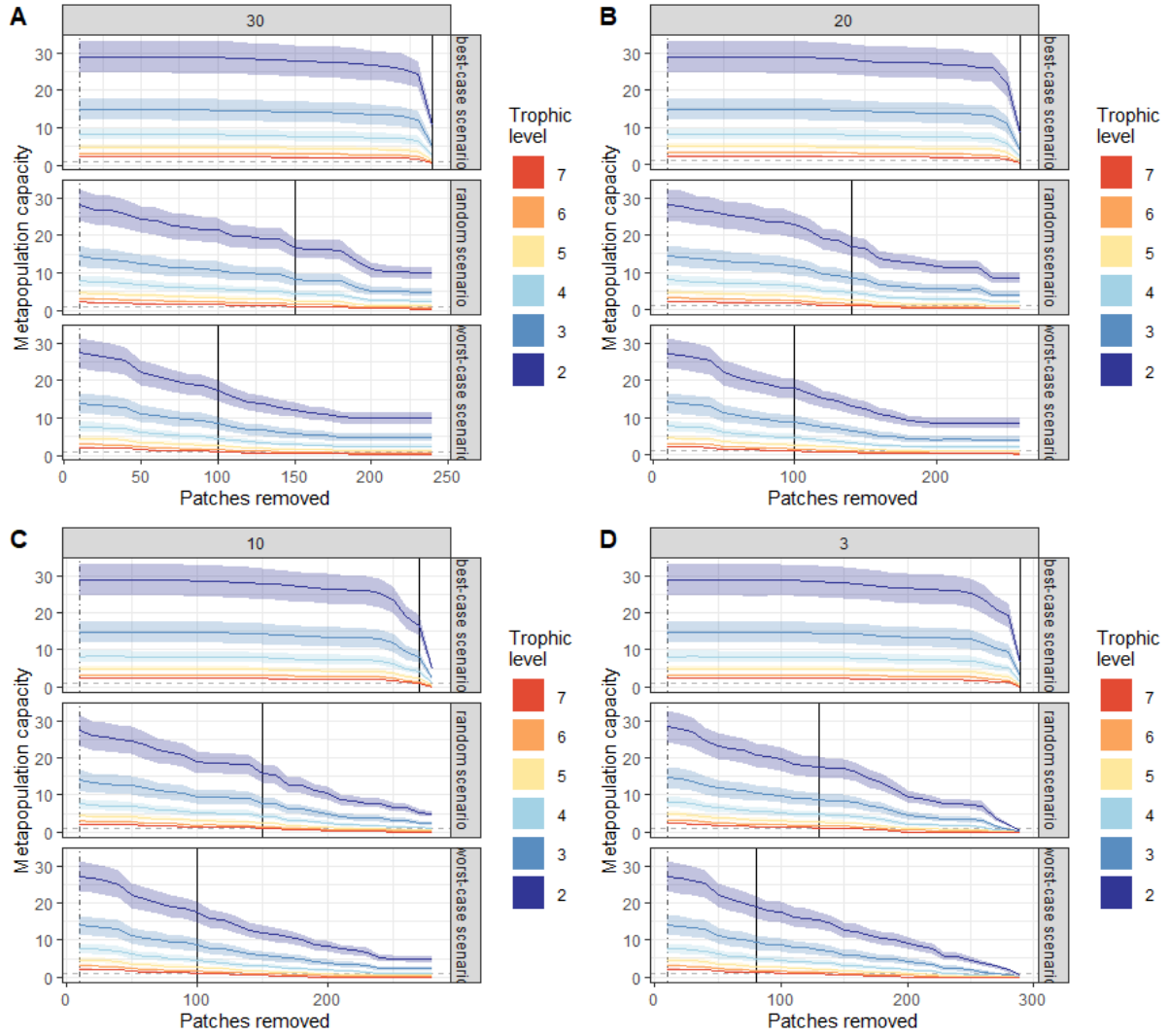


Figure 3. Metapopulation response to habitat loss with different number of corridors,  $\alpha=\beta=1$  (linear). With 30 (A), 20 (B), 10 (C) and 3 (D) corridors. The x-axis shows number of patches removed and the y-axis shows long-term persistence (metapopulation capacity). Colors indicate species' trophic level, see legend. Line indicates the mean for that trophic level and the color around shows the standard deviation range for that trophic level. Horizontal dashed line indicates where the threshold for long-term species persistence is, a metapopulation capacity of 1. Vertical line indicates when the metapopulation capacity for the top species drops below this threshold. Each row is one scenario; "best-case scenario", "random scenario", "worst-case scenario".

#### 4.3 Simulation with different response curves

Similar results were achieved when changing the Bayesian network to have a sigmoidal shape (Figure 4): the presence of corridors did increase the long-term persistence for all trophic levels, lower trophic levels stayed above extinction threshold, implementing at least 3 corridors increased the persistence for the species at the highest trophic level (Table 1).

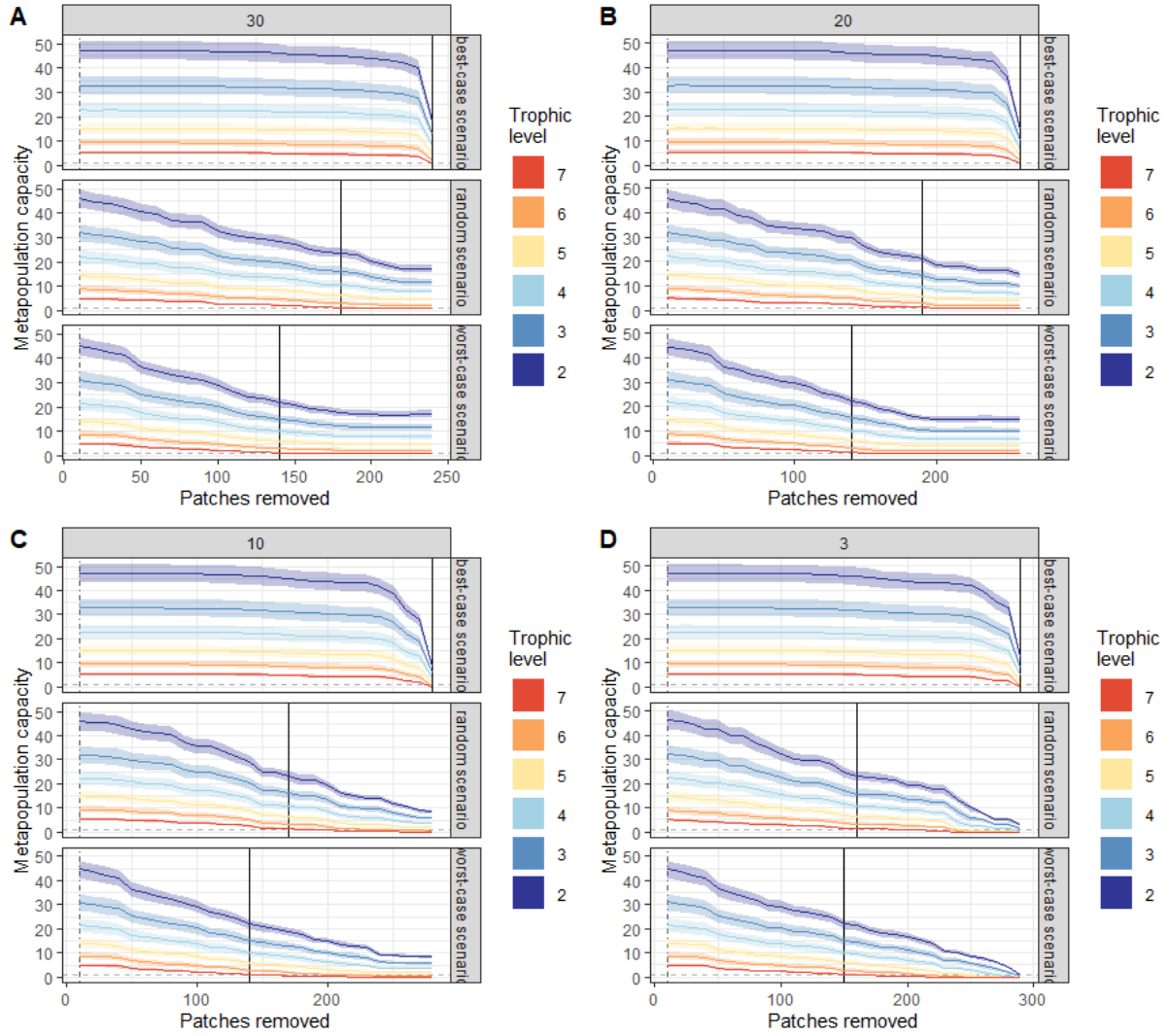


Figure 4. Metapopulation response to habitat loss with different number of corridors,  $\alpha=\beta=5$  (Sigmoidal). With 30 (A), 20 (B), 10 (C) and 3 (D) corridors. The x-axis shows number of patches removed and the y-axis shows long-term persistence (metapopulation capacity). Colors indicate species' trophic level, see legend. Line indicates the mean for that trophic level and the color around shows the standard deviation range for that trophic level. Horizontal dashed line indicates where the threshold for long-term species persistence is, a metapopulation capacity of 1. Vertical line indicates when the metapopulation capacity for the top species drops below this threshold. Each row is one scenario; "best-case scenario", "random scenario", "worst-case scenario".

When the Bayesian network took on a concave form, every trophic levels metapopulation capacity was drastically reduced to the point that only trophic level 2 was over the threshold for long-term species persistence (Figure 5). Still, increasing the amount of corridors did increase metapopulation capacity for trophic level 2, and when implementing 10 or more corridors, that trophic level survived extinction. The species with the highest trophic levels went extinct at the first patch removal instance, for all scenarios and iterations of corridors.

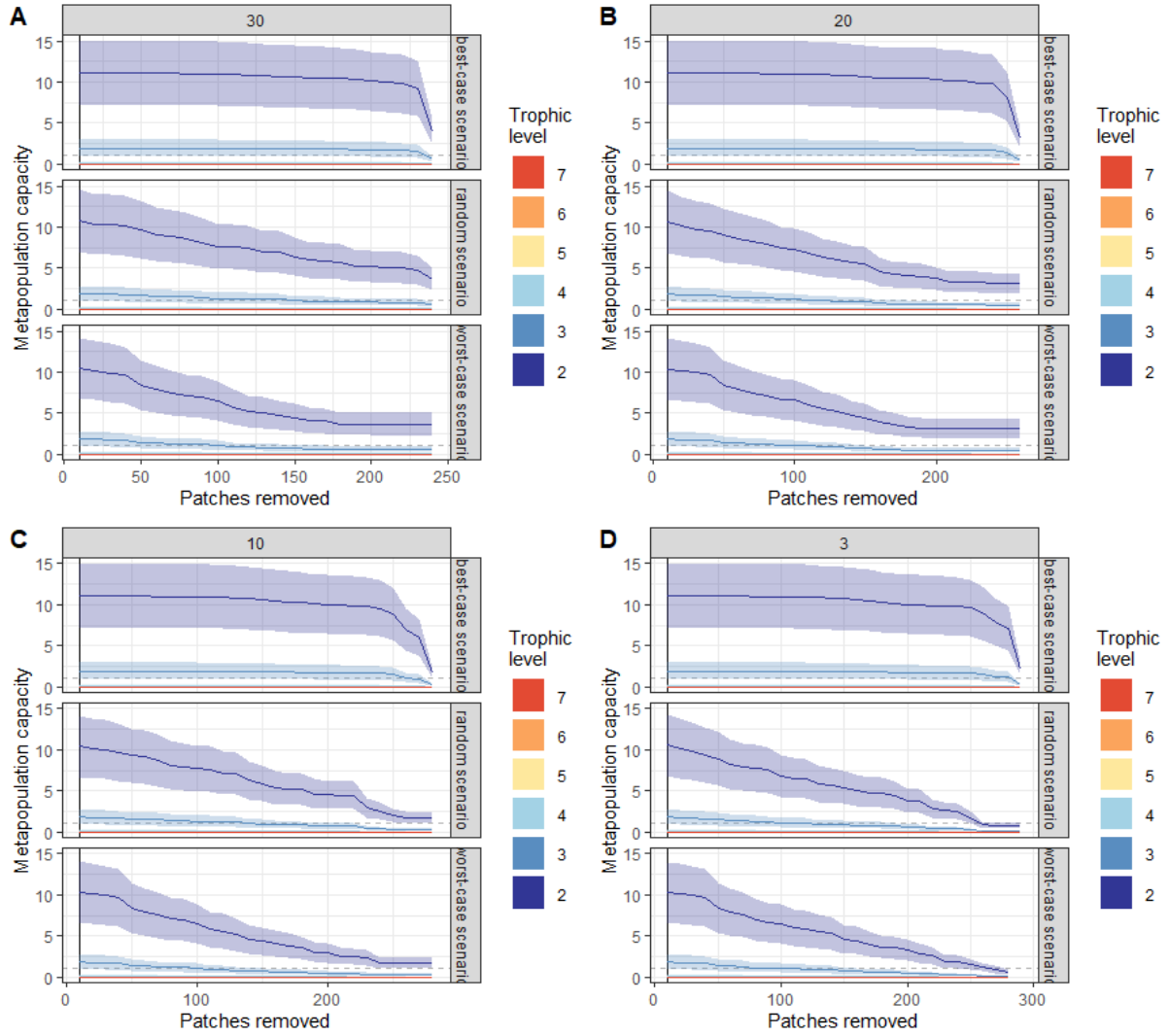


Figure 5. Metapopulation response to habitat loss with different number of corridors,  $\alpha=1$ ,  $\beta=5$  (Concave). With 30 (A), 20 (B), 10 (C) and 3 (D) corridors. The x-axis shows number of patches removed and the y-axis shows long-term persistence (metapopulation capacity). Colors indicate species' trophic level, see legend. Line indicates the mean for that trophic level and the color around shows the standard deviation range for that trophic level. Horizontal dashed line indicates where the threshold for long-term species persistence is, a metapopulation capacity of 1. Vertical line indicates when the metapopulation capacity for the top species drops below this threshold. Each row is one scenario; "best-case scenario", "random scenario", "worst-case scenario".

Lastly, when the Bayesian network took on a convex shape, the metapopulation for all trophic levels increased to the point that almost every trophic level avoided extinction (Figure 6). Increasing the presence of corridors did increase the point at which the species at the highest trophic level went extinct, from the last instance of patch removal to never going extinct. Increasing the number of corridors did also increase metapopulation capacity.

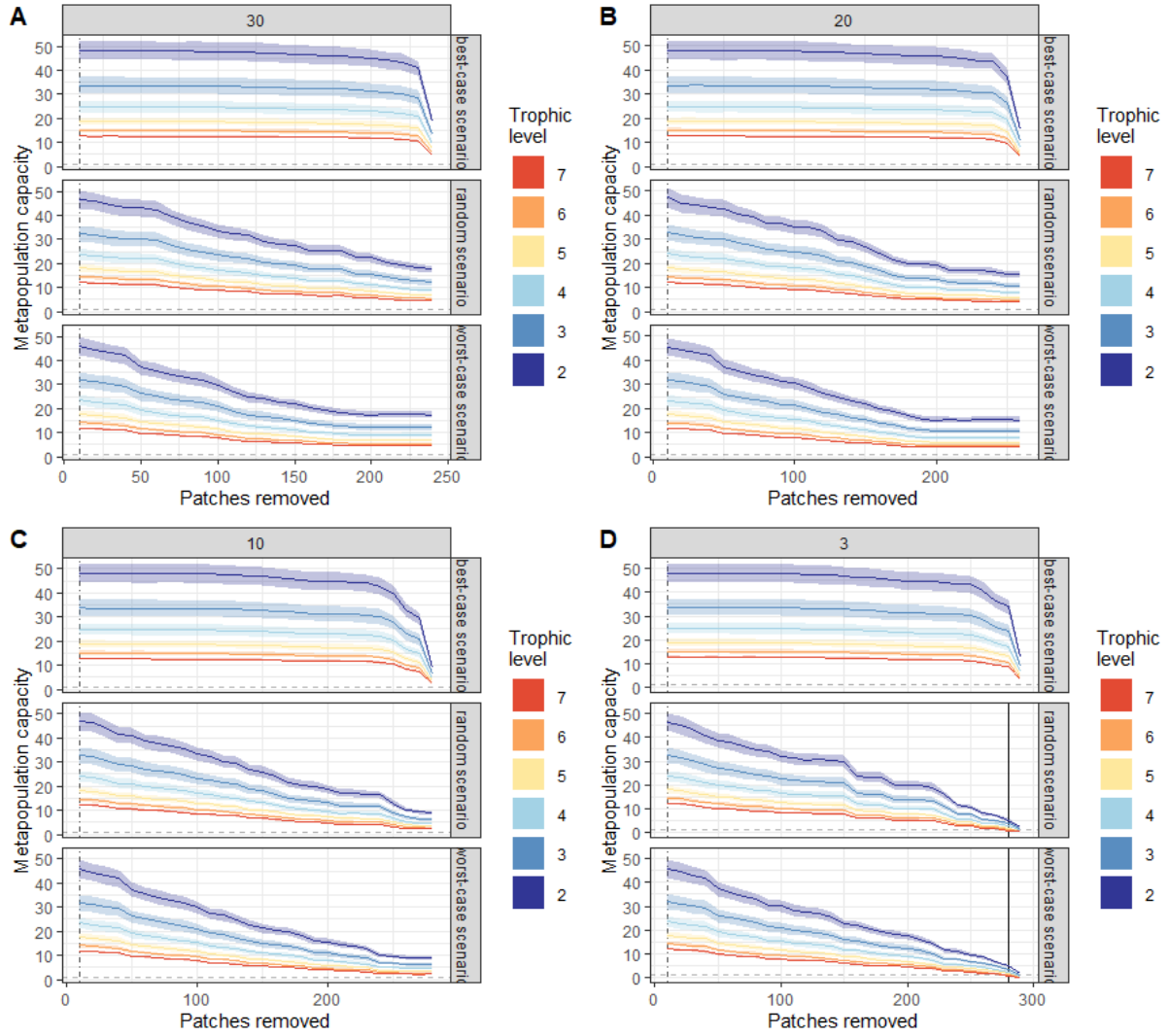


Figure 6. Metapopulation response to habitat loss with different number of corridors,  $\alpha=5$ ,  $\beta=1$  (Convex). With 30 (A), 20 (B), 10 (C) and 3 (D) corridors. The x-axis shows number of patches removed and the y-axis shows long-term persistence (metapopulation capacity). Colors indicate species' trophic level, see legend. Line indicates the mean for that trophic level and the color around shows the standard deviation range for that trophic level. Horizontal dashed line indicates where the threshold for long-term species persistence is, a metapopulation capacity of 1. Vertical line indicates when the metapopulation capacity for the top species drops below this threshold. Each row is one scenario; "best-case scenario", "random scenario", "worst-case scenario".

## 5 Discussion

Understanding how fragmentation of landscapes affect population's biodiversity and finding a way to counteract the impact it has on species persistence, both direct and indirectly, is a must for a sustainable future (Thomas et al., 2004; Ebenman & Jonsson, 2005; Haddad et al., 2015). In this study I looked at how the implementation of corridors in a landscape subjected to habitat fragmentation affect metapopulations ability to survive habitat loss. When just looking at the effect the presence of corridors has on metapopulation survivability, we can see that the number



of corridors do affect the metapopulations ability to survive habitat loss, when just implementing a few corridors. Implementing 10 corridors increased the amount of trophic levels that remained above the threshold for long-term species persistence and the metapopulation capacity for all trophic levels. . This corroborate with other findings about the effect migration and links between patches has on metapopulation persistence against habitat loss (Dunne et al., 2002; Häussler et al., 2020). However, implementing just three corridors did not seem to be enough to withstand the effect of habitat loss. This could be due to which corridors are chosen to pair together and how close they are together. These results were based on a Bayesian network where the species baseline extinction probability were linear to the amount of fractions lost. What happens when the baseline extinction change from a linear to a concave (faster response to small losses) relationship?

Changing the Bayesian network to a concave shape caused, for all landscapes with and without corridors, almost all trophic levels (except trophic level 2) to fall below the threshold for long-term species persistence at the start of the patch removals (*Figure 5*). However, the general trend that an increasing amount of corridors caused the metapopulation capacity for all trophic levels (in this case, only one trophic level) to increase, is still there. So it seems that the effect corridors has on metapopulations persistence against habitat loss do increase with increasing amount of corridors, in the same manner in both instances. But that is not entirely true, a major difference between the Bayesian network with the linear shape and the concave shape is that increasing the number of corridors, in the landscape with a linear shape, increased the number of trophic levels above the extinction threshold. For the landscape with the concave shape, increasing the number of corridors only increased metapopulation capacity for one trophic level. Changing the Bayesian network to a sigmoidal shape (*Figure 4*), generated very similar results to those acquired when the Bayesian network had a linear shape (*Figure 3*). Implementing just 10 corridors increased the metapopulation capacity for all trophic levels and the amount of trophic levels that remained above the extinction threshold. The difference we can see is that overall, a sigmoidal shape causes all trophic levels to have a generally higher metapopulation capacity, which causes more trophic levels to avoid extinction compared to the Bayesian network with the linear shape. Despite the difference, these results still indicate that the presence of corridors do have a noticeable effect on metapopulation survivability.

These results, when the Bayesian network took on a sigmoidal shape, were very similar to the results for the landscape with a convex shape, in terms of increasing the metapopulation

capacity compared to the linear shape (*Figure 6*). However, the relationship between corridors and number of trophic levels above extinction threshold that we saw in the linear and sigmoidal shape, does not exist in the convex shape. This difference is due to the shape causing almost all trophic levels to stay above the extinction threshold right from the start. Which meant that increasing the number of corridors only increased the metapopulation capacity marginally. Nevertheless, an increased effect on metapopulation persistence can be seen when comparing the landscape with 10 corridors and the landscapes with three and zero corridors. These trends with different shapes of the Bayesian network do corroborate with the results Häussler et al (2020) retrieved when they tested different alphas and betas, which one would expect considering it is the same method and model used, but with different landscape matrixes.

When just looking at the species at the highest trophic level and at which level of patch removal they go extinct, the results shift slightly. But first, why should we only look at the species at the highest trophic level? This is because Häussler et al. (2020) found that habitat destruction affects the species with the highest trophic level the most, due to them having fewer available patches to colonize and due to them having to deal with reduced prey availability. Because they are the most vulnerable species in the landscape, they also are the most critical from a conservation standpoint. In a landscape with no corridors and an alpha and beta that is equal to 1 (linear shape), the number of patches removed before the species with the highest trophic levels went extinct was 40 patches in the worst-case scenario and 70 patches in the random scenario. When adding just three corridors to this landscape, an additional 50 patches could be removed before extinction (from 80 to 130). However, this effect decreased from almost double the amount of patches to just a few patches when increasing the number of corridors to 10, 20 and 30. When changing alpha and beta to 5 (sigmoidal shape), almost the same results was seen, with the difference being that the number of patches for the top species to go extinct was higher for all scenarios and number of corridors. The same results could however not be seen when changing alpha and beta to either 1 and 5 (concave shape) or 5 and 1 (convex shape). This was because the topmost species either went extinct at the start of the patch removal, when alpha and beta is 1 and 5, or was extant in all scenarios, for all number of corridors above three. This outcome, when habitat loss affect the food web from top to bottom (species at the highest trophic level first) has been seen prior to this study (Häussler et al., 2020; McWilliams et al., 2019; Ryser et al., 2019).

## **5.1 Conclusions**

When introducing a sufficient amount of corridors to a separated landscape, the general trend was that the metapopulation capacity for all trophic levels increased, and therefore caused more trophic levels to rise above the threshold for long-term species persistence. By just increasing the number of corridors from zero to three almost doubled the amount of patches that has to be removed before the species with the highest trophic level went extinct. This caused the metapopulation to be able to withstand habitat loss, even after a large fraction have been removed. When changing how the species basal extinction probability reacted to resource extinction from a linear function to concave, convex or sigmoidal, the number of corridors had, in general, a smaller effect.

## **6 Societal and ethical considerations**

This study aims to work towards the UN developmental goal 15 “Life on land” and most specifically to halt the biodiversity loss. The results from this study shows that there is an effective way to counteract the devastating aftermath of habitat fragmentation, which reduces biodiversity considerably. By increasing the application span of connections between two separated landscapes (e.g. through bridges over highways) more organisms are able to migrate between, which will decrease species extinction probabilities and therefore preserve (hopefully increase) biodiversity. One can also use this study as a foundation to further analyse migration in fragmented landscapes. The next step could be to study how increased connectivity between even more fragmented landscapes will affect metapopulations ability to survive habitat loss. One could also study more precisely which patches should be connected to achieve optimal survivability. Because there are so many different variables and parameters that can possibly affect the results, adjusting certain variables and parameters may change the results acquired. Additionally, because the landscape and food webs used in this study are constructed (not based on a real food web), one should be careful when trying to apply and compare these results to the real world. This model created by Häussler et al. (2020) do fortunately offer the user to be able to apply a real food web and landscape to the model (e.g. Serengeti food web used in Häussler et al. (2020)) to acquire results that are applicable to that location with that food web.

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## 8 References

- Albert, R., Jeong, H. & Barabási, A.L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382.
- Dunne, J.A., Williams, R.J., Martinez, N.D. (2002). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5, 558-567.
- Ebenman, B., Jonsson, T. (2005). Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology and Evolution*, 20.
- Eklöf, A., Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75, 239-246.
- Eklöf, A., Tang, S., Allesina, S. (2013). Secondary extinctions in food webs: a Bayesian network approach. *Methods in Ecology and Evolution*, 4, 760-770.
- Gilpin, M., Hanski, I. (1991). *Metapopulation dynamics: empirical and theoretical investigations*. Biological Journal of the Linnean Society, 42.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzales, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D. et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1.
- Hanski, I. (1994). A practical model of metapopulation dynamics. *Journal of Animal Ecology*, 63, 151-162.
- Hanski, I., Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, 404, 755–758.

Häussler, J., Barabás, G., Eklöf, A. (2020). A Bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions. *Ecology Letters*, 23, 1849-1861.

Jensen, F.V. (1996). *An introduction to Bayesian networks*. New York: Springer-Verlag, 36.

Leibold, M., Chase, J. (2018) *Metacommunity ecology*. Princeton University Press, 59.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., et al. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, 7: 601-613.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237-240.

McWilliams, C., Lurgi, M., Montoya, J.M., Sauve, A., Montoya, D. (2019). The stability of multitrophic communities under habitat loss. *Nature Communications*, 10.

Ovaskainen, O., Hanski, I. (2001). *Theoretical population biology*, Elsevier, 60, 281-302.

Ryser, R., Häussler, J., Stark, M., Brose, U., Rall, B.C., Guill, C.(2019) The biggest losers: habitat isolation deconstructs complex food webs from top to bottom. *Proceeding of the royal society B*, 286.

Solé, R.V., Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proc. R. Soc. Lond*, 268, 2039-2045.

Soulé, M.E., Estes, J.A., Berger, J. and Del Rio, C.M. (2003). Ecological effectiveness: conservation goals for interactive species. *Conservation Biology*, 17, 1238-1250.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L. et al. (2004). Extinction risk from climate change. *Nature*, 427, 145–148.