

Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks

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Habitat loss fragments metacommunities, altering the movement of species between previously connected habitat patches. The consequences of habitat loss for ecosystem functioning depend, in part, on how these changes in connectivity alter the spatial insurance effects of biodiversity. Spatial insurance is the maintenance of biodiversity and stable ecosystem functioning in changing environments that occurs when species are able to move between local habitat patches in order to track conditions to which they are adapted. Spatial insurance requires a combination of species sorting dynamics, which allow species to disperse to habitats where they are productive, and mass effect dynamics, where dispersal allows species to persist in marginal habitats where environmental conditions do not support growth. Here we use a spatially explicit metacommunity model to show that the relative contribution of species sorting and mass effects to spatial insurance changes with the rate of dispersal. We then simulate different sequences of habitat loss by removing habitat patches based on their betweenness centrality (the degree to which a patch serves as a connection between other patches in the metacommunity). We demonstrate that the sequence of habitat loss has a large, non-linear impact on diversity, ecosystem functioning and stability. Spatial insurance is lost because habitat fragmentation impedes species sorting, while promoting mass effects and dispersal limitation. We find that species sorting dynamics, and thus spatial insurance, are most robust to the removal of habitat patches with low betweenness centrality. These findings advance our understanding of how habitat connectivity facilitates the maintenance of biodiversity and ecosystem functioning, and may prove useful for the design of habitat networks.

Stemming habitat loss is paramount to the conservation of biodiversity (Gonzalez et al. 2009, Butchart et al. 2010, Pereira et al. 2010, Rands et al. 2010, Hooper et al. 2012, Haddad et al. 2015) and ecosystem services (Gonzalez et al. 2009, Butchart et al. 2010, Pereira et al. 2010, Rands et al. 2010, Cardinale et al. 2012, Hooper et al. 2012). The ecological impacts of habitat loss will depend in large part on the geometry of remnant area (Keil et al. 2015) and the degree of habitat fragmentation (Haddad et al. 2015). Maintaining the ability of species to move and disperse among habitat patches, i.e. habitat connectivity, may lessen the impacts of habitat loss on biodiversity and ecosystem functioning through the spatial insurance effects of diversity (Loreau et al. 2003, Staddon et al. 2010, Hanski 2011).

The spatial insurance hypothesis posits that dispersal is crucial for governing patterns of diversity at local and regional scales which in turn influence the function and stability of ecosystems in single habitat fragments, and across a network of fragments, at the scale of the metacommunity (Loreau et al. 2003, Gonzalez et al. 2009, Shanafelt et al. 2015). Our ability to manage fragmented landscapes effectively requires that we understand how habitat loss erodes connectivity, and how this imparts direct and indirect

effects on the link between biodiversity and ecosystem functioning.

Metacommunity models explain how dispersal mediates species coexistence and how biodiversity patterns affect ecosystem function across a network of local communities (Leibold et al. 2004, Gonzalez et al. 2009). In the absence of dispersal, local diversity is low and productivity in a habitat patch will fluctuate depending on whether the environment is suitable for the species that are present. But, with increasing dispersal, more productivity is sustained because greater species diversity can be maintained via species sorting and mass effects. Species sorting occurs when dispersal among habitat patches allows species to remain productive by tracking their environmental niches across space and through time. When dispersal is high enough, mass effects can allow species to persist in patches where the environment is unfavourable. These mass effects contribute to species diversity and can allow species to persist in habitat patches as the environment changes. Together, these persistence mechanisms determine patterns of biodiversity and productivity across the metacommunity.

Loss of connectivity may also impact ecosystem functions that sustain ecosystem services important for human

well-being in transformed landscapes (Gonzalez et al. 2011, Cardinale et al. 2012, Hooper et al. 2012, Gonzalez 2013, Balvanera et al. 2014). For example, local biodiversity loss can alter the rate of production and the standing stock of biomass (Cardinale et al. 2011). This has implications for a wide range of ecosystem services linked to productivity, such as carbon storage (Kremen 2005, Mitchell et al. 2013, Ziter et al. 2013). In addition, biodiversity loss may impact the stability of ecosystem functioning as communities with low diversity are less resistant to environmental fluctuations, (Isbell et al. 2011, 2015), leading to more variable population and aggregate biomass (Gonzalez and Loreau 2009, Hector et al. 2010).

Habitat connectivity across a landscape can be represented as a set of habitat patches that are organized into a spatial network based on the pattern of potential dispersal among them (Urban and Keitt 2001). The structure of spatial habitat networks governs their response to habitat loss (Gonzalez et al. 2011). Robust network structures maintain habitat connectivity even after a large fraction of patches have been removed (Albert et al. 2000, Dunne et al. 2002). Networks with a few highly connected patches and many poorly connected patches are robust to the loss of random patches but vulnerable to the loss of highly connected patches (e.g. patches with high betweenness centrality; Thompson et al. 2014). Beyond assessments of the robustness of structural connectivity, network models provide a powerful method to examine the robustness of biodiversity and ecosystem functions to habitat loss when paired with metapopulation or metacommunity models (Bode et al. 2008, Holland and Hastings 2008, Ranta et al. 2008, Economo and Keitt 2010, Gilarranz and Bascompte 2012, Thompson et al. 2014, Grilli et al. 2015).

Here we extend the work of Thompson et al. (2014) to examine how habitat loss impacts biodiversity and the productivity and stability of ecosystems. We use realistic habitat networks and explore the contribution of species sorting and mass effects to biodiversity and ecosystem functioning in changing environmental conditions. We predict that the degree to which these persistence mechanisms are altered will depend on the connectivity of the habitat patches in the metacommunity and the order that they are removed from the landscape. Specifically, we expect the loss of patches with the greatest centrality (i.e. individual habitat patches that contribute the most towards metacommunity connectivity by serving as stepping-stones for dispersing individuals), to have the greatest impact on the biodiversity and ecosystem functioning. We further predict that the effects of habitat loss will be greatest when metacommunities are connected by intermediate dispersal rates, as these allow for both species sorting and mass effects, which are important for the spatial insurance effects of biodiversity in intact habitat networks.

Material and methods

We simulated habitat loss in spatially explicit metacommunity networks using a resource competition model (Thompson et al. 2014) that is based on the model used to develop the spatial insurance hypothesis (Loreau et al. 2003, Gonzalez et al. 2009, Shanafelt et al. 2015). The metacommunity

networks consist of M habitat patches distributed randomly in geographic space with X and Y coordinates drawn from uniform distributions with the range $[1, 1000]$, following Fournier et al. (2017; Fig. 1). We assume that patches with a Euclidean distance of less than 200 are connected by a link. Networks were discarded if they contained patches that occupied the same geographical coordinates or if they contained isolated patches.

Resource competition metacommunity model

The dynamics of the species in this metacommunity are determined by the following equations, which govern resource competition:

$$\frac{dN_{ij}(t;a)}{dt} = N_{ij}(t;a) \left[e \cdot c_{ij}(t) R_j(t;a) - m \right] + A_{ij}(t;a) - a N_{ij}(t;a) \quad (1)$$

$$\frac{dR_j(t;a)}{dt} = I - \ell R_j(t;a) - R_j(t;a) \sum_{i=1}^S c_{ij}(t) N_{ij}(t;a) \quad (2)$$

where $N_{ij}(t;a)$ is the biomass of species i and $R_j(t;a)$ is the abundance of the limiting resource in patch j at time t , given dispersal rate a . There are S species in the metacommunity, which compete for this resource. Species convert this resource to new biomass with an efficiency of e , and $c_{ij}(t)$ is the rate of consumption by species i in patch j at time t . All species die at a rate of m ; $A_{ij}(t;a)$ is the amount of biomass of species i that arrives in patch j through immigration from other patches at time t . At each time step t , a given proportion of the biomass in patch j is lost to emigration, which is determined by the rate of dispersal a . The rate of resource input to each patch is given by I , and ℓ is the rate of resource loss.

Dispersal between habitat patches is assumed to be passive (i.e. dispersing individuals do not choose patches based on suitability), constrained by the network links, and decreases with the distance between patches such that:

$$A_{ij}(t;a) = a \sum_{k \neq j}^M \left\{ \frac{\exp(-\alpha d_{kj})}{\sum_{f \neq k}^M \exp(-\alpha d_{kf})} N_{ik}(t;a) \right\} \quad (3)$$

This dispersal kernel allows for more than one link to be traversed during a single time step of the model. All dispersal between source patch k and destination patch j is based on the network distance d_{kj} between those patches, calculated as the effective resistance distance which integrates the travel distances (link lengths) of all possible pathways between two patches into a single measure (McRae 2006, McRae et al. 2008). Effective resistance distance between a pair of patches is lower when dispersal can occur across multiple pathways. The strength of the exponential decrease in dispersal with network distance d_{jk} is controlled by the parameter α . We assume an equal emigration rate from all patches, and so the amount of biomass immigrating to patch j from patch k also depends on the distance d_{kf} from patch k to each other patch f . During dispersal there is no net loss of biomass because the regional sum of emigration and immigration is the same. When patches lose all connections with other patches in the metacommunity, immigration $A_{ij}(t;a)$ becomes zero. We assume that emigration continues after a patch becomes isolated, but that this biomass is lost from the metacommunity.

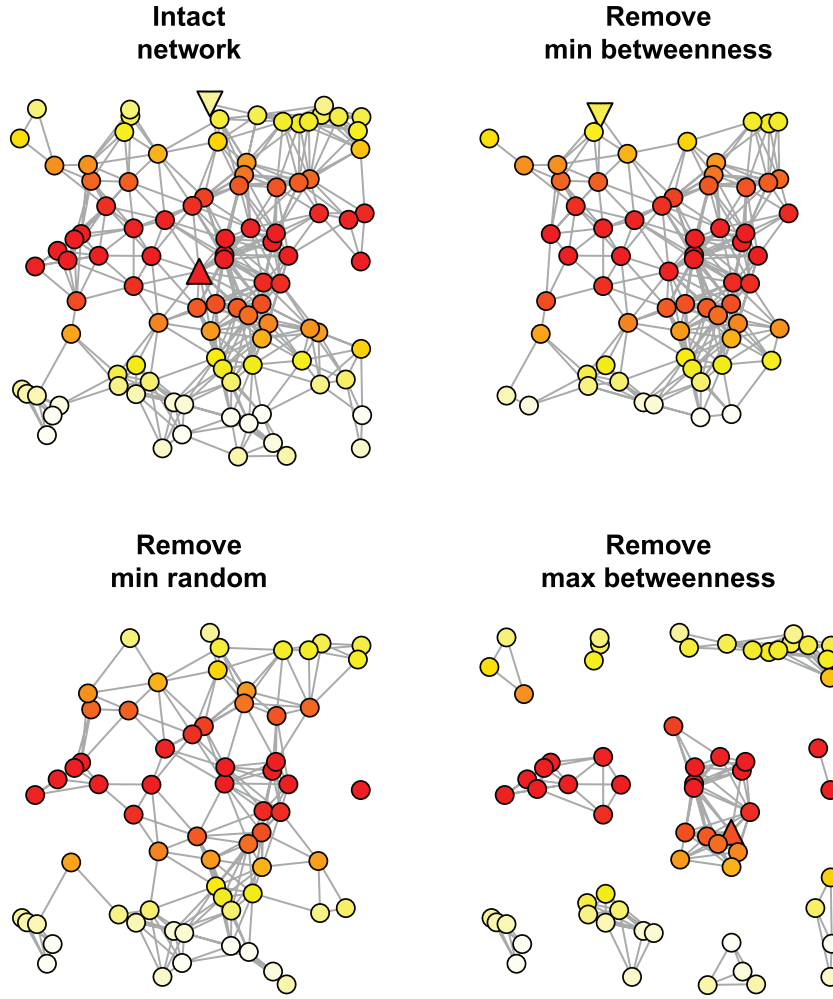


Figure 1. Example metacommunity network with links that have a Euclidean distance of less than 200. Metacommunities are shown as intact networks, and after 14 patches have been removed based on the three removal sequences: removing the patch with the minimum betweenness centrality; removing a random patch; and removing the patch with the maximum betweenness centrality. The next patch to be deleted in each of the removal sequences is shown as the yellow down pointed triangle (min betweenness) or the red up pointed triangle (max betweenness). The environmental conditions ($t = 1$) are illustrated by the pale yellow to red colour scale of the patches.

The environmental conditions in each patch fluctuate through time following a sinusoid with a period T :

$$E_j(t) = \frac{1}{2} \left[\sin \left(E_j^{init} + \frac{2\pi t}{T} \right) - 1 \right] \quad (4)$$

where $E_j(t)$ is the environmental conditions in patch j at time t . The initial conditions E_j^{init} are equally spaced across the sinusoidal wave and are autocorrelated in space so that nearby patches have similar environmental conditions (Fig. 1). The consumption rate $c_{ij}(t)$ of species i in patch j is determined by the match between its environmental optimum H_i and the local environment $E_j(t)$ at time t :

$$c_{ij}(t) = \frac{1.5 - |H_i - E_j(t)|}{10} \quad (5)$$

where the environmental optima H of the S species are equally spaced across the range of environmental conditions.

Calculating metacommunity processes

We calculate the proportional contributions of base growth, species sorting, and mass effects to total metacommunity

production. The production of biomass in the metacommunity at time t with dispersal rate a is calculated as:

$$\phi(t; a) = \sum_{j=1}^M \sum_{i=1}^S e \cdot c_{ij}(t) R_j(t; a) N_{ij}(t; a) \quad (6)$$

The proportion of metacommunity biomass production that is due to base growth is calculated as:

$$Base\ growth(t; a) = \min \left\{ \frac{\phi(t; 0)}{\phi(t; a)}, 1 \right\} \quad (7)$$

where $\phi(t; 0)$ is the production of biomass production in a metacommunity without dispersal (i.e. $a = 0$) at time t . Because low rates of dispersal can reduce biomass production through source-sink effects, it is possible for $\phi(t; 0) > \phi(t; a)$, in which case we assume that all biomass production is due to base growth. The proportion of metacommunity biomass production due to species sorting is calculated as:

$$Species\ sorting(t; a) = \frac{\sum_{j=1}^M \sum_{i \in S_j^{(rad)}} e \cdot c_{ij}(t) R_j(t; a) N_{ij}(t; a) + A_{ij}(t; a) - a N_{ij}(t; a) - \phi(t; 0)}{\phi(t; a)} \quad (8)$$

where

$$S_j^*(t; a) = \left\{ i \left| \frac{dN_{ij}(t; a)}{dt} - A_{ij}(t; a) \geq 0 \right. \right\} \quad (9)$$

That is, the proportion of overall biomass production $\phi(t)$ that is produced by the subset of species $S_j^*(t; a)$ that have positive growth without immigration in patch j at time t , beyond that which is produced through base growth. We only consider species that have positive growth without immigration in order to exclude sink populations. Therefore, this measure quantifies biomass production that occurs because dispersal has allowed species to track their environmental optima. The proportion of metacommunity biomass production that is due to mass effects is calculated as:

$$\text{Mass effects}(t; a) = \frac{\sum_{j=1}^M \sum_{i \in S_j^*(t; a)} e \cdot c_{ij}(t) R_j(t; a) N_{ij}(t; a) + A_{ij}(t; a) - a N_{ij}(t; a)}{\phi(t; a)} \quad (10)$$

where

$$S_j^{\dagger}(t; a) = \left\{ i \left| \frac{dN_{ij}(t; a)}{dt} - A_{ij}(t; a) < 0 \right. \right\} \quad (11)$$

That is, the proportion of overall biomass production $\phi(t; a)$ that is produced by the subset of species $S_j^{\dagger}(t; a)$ that have negative growth without immigration in patch j at time t .

Simulation parameters

We simulated landscape fragmentation in metacommunities with the following parameters: $M = 30$, $S = 9$, $e = 0.2$, $m = 0.2$, $I = 10$, $N_{ij}(1; a) = 10$, $R_j(1; a) = 9$, $L = 1$, and $\alpha = -0.05$. We set an extinction threshold of $N_{ij} = 0.1$, below which, populations were assumed extinct, and were set to zero abundance. We approximated continuous dynamics by

using the Euler method with $\Delta t = 0.08$. The environmental fluctuations had a period of $T = 40\,000$, which was large enough to cause competitive exclusion of all but one species, in the absence of dispersal. These values correspond to those that have previously been used to explore the impacts of habitat loss on the spatial insurance effects of biodiversity (Thompson et al. 2014). Previous studies have shown that the spatial insurance effects seen in this model are robust to variation in parameter values (Loreau et al. 2003, Gonzalez et al. 2009, Shanafelt et al. 2015, Thompson and Gonzalez 2016). We first calculated the relative strength of the three metacommunity processes in the intact networks over 17 dispersal rates a ranging from 0.0001 to 1. We then ran habitat loss simulations at three dispersal rates which corresponded to the points where the dominant metacommunity process switches from base growth to species sorting ($a = 0.0005$), where species sorting dynamics are maximized ($a = 0.005$), and where mass effects become dominant ($a = 0.015$; Fig. 2).

Habitat loss

We simulated habitat loss through the sequential removal of habitat patches. When a habitat patch was removed, we also removed all links associated with it. The remaining network remains unchanged. The loss of habitat patches and associated links alters the connectivity of the remaining network, so we recalculate the effective network distances after each patch removal. Therefore, after habitat loss, dispersal is re-routed through the remaining links and patches. Prior to removing any habitat, the simulation was run for 100 000 time steps to allow the initial transient dynamics to subside. After this, we removed a habitat patch every 40 000 time steps,

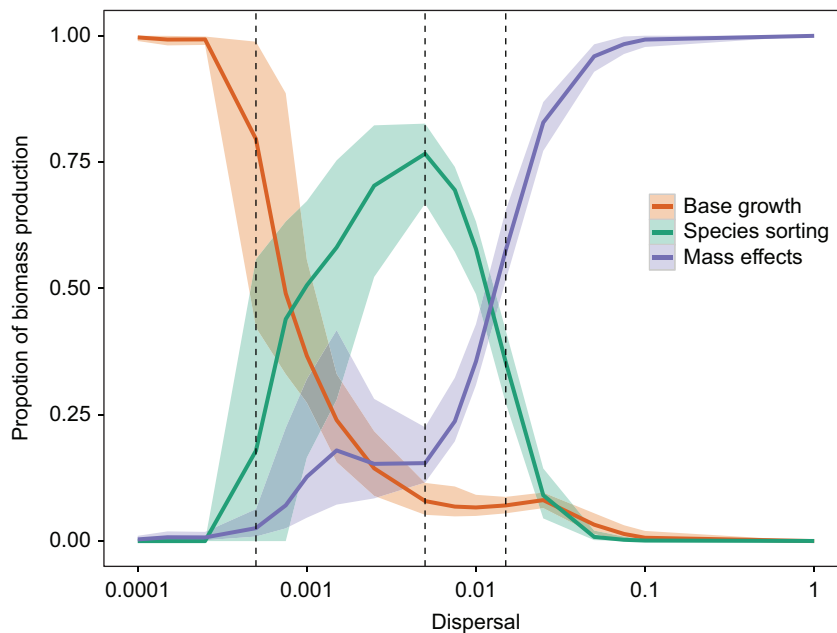


Figure 2. The change in the proportion of biomass production from species exhibiting base growth (red), species sorting (green), and mass effects (blue) over the range of dispersal rates in the intact networks. Solid lines represent mean values across one hundred replicate simulations and ribbons represent the range between the 2.5th and 97.5th percentiles of the data. Vertical dashed lines indicate the three dispersal rates used in the habitat loss simulations.

which corresponded to one sinusoidal environmental fluctuation. We compared three patch removal sequences where we removed: the patch with the lowest betweenness (min betweenness removal sequence), a random patch (random removal sequence), or the patch with the highest betweenness centrality (max betweenness removal sequence; Fig. 1). The betweenness centrality of a patch is the proportion of shortest paths between all pairs of patches in the network that include the patch (Freeman 1977, White and Borgatti 1994). Betweenness centrality was recalculated following each patch removal to account for the effect of removing the patch on the connectivity of the remaining habitat network. In the event that only pairs of connected patches and isolated patches remained in the network during the max betweenness removal sequence (i.e. the betweenness centrality of all patches was zero), we removed a randomly-selected patch from the connected pairs of patches in order to further fragment the landscape.

Response variables and analysis

Response variables were calculated based on sampled data taken every 2000 time steps, excluding the first 100 000 time steps. We report the average value of each response variable for all time steps in between each habitat patch removal event. Four measures of structural connectivity were calculated based on the network components in the metacommunity: the number of network components, the average size (number of patches) in each network component, the mean environmental range of the network components at each time step, and the mean environmental range of the entire network. The environmental range of a network component is defined as $(\max(E_j(t)) - (\min(E_j(t))))$, for all patches that comprise that network component. The same equation was used to calculate the environmental range of the entire network, but for all patches regardless of connectivity. A network component is a set of patches that are either directly or indirectly connected by network links. Nodes in different network components are not connected. All intact networks consist of one network component, but the loss of habitat patches can result in the fragmentation of the metacommunity into multiple network components.

We calculated species richness at local and regional scales, the proportion of remaining patches that are occupied by at least one species, the average biomass of the remaining patches, and the temporal variability of biomass at both local and regional scales. The temporal variability of biomass was calculated as the coefficient of variation (CV) of biomass across all time steps between each patch removal. Patches that did not contain species were not included in our calculation of average local temporal biomass variability. All reported variables are based on 100 replicate simulations, each with a new randomly generated initial network. Effective resistance distance between pairs of nodes was calculated in Circuitscape (Shah and McRae 2008). All other analyses and simulations were conducted using R (R Development Core Team 2015). Metacommunity networks were generated using the iGraph package (Csardi and Nepusz 2006). All code for the simulations and figures is available on GitHub (https://github.com/plthompson/SIH_fragmentation).

Results

Fragmentation of the metacommunity

Removing patches results in the fragmentation of the network into smaller component networks (Fig. 3a). The max betweenness removal sequence breaks the network into the largest number of components and reduces the mean size and environmental range of components with the fewest patches removed (Fig. 3a–c). When patches are removed randomly or based on max betweenness, the number of components initially increases and the mean component size decreases as multi-patch components break apart. The mean range of local environmental conditions present in components decreases linearly when subject to random node removals and exponentially when subject to max betweenness patch removals, reaching zero when only single-patch components remain. When patch removal is based on min betweenness, the network remains connected in a single component that decreases in size linearly and retains the full range of local environmental conditions until half the patches have been removed. Removing patches initially has little effect on the overall range of environmental conditions present in the entire network (Fig. 3d). This environmental range only begins to decrease after at least half of the patches have been removed. This decrease occurs fastest in the min betweenness sequence while the loss of environmental range is similar in the random and max betweenness scenarios.

Species diversity

The species richness in each habitat patch (local), and in the entire network (regional), decreases non-linearly as habitat is lost (Fig. 4a–f). The patch removal sequence determines the local and regional richness in the fragmented networks when dispersal is high, and to a lesser extent when dispersal is intermediate. The initial patch removals cause the greatest loss of regional species richness in the max betweenness sequence. However, subsequent patch removals cause greater declines in regional species richness in the min betweenness sequence, which results in lower regional species richness compared to the max betweenness sequence. Local species richness has the steepest decline in the max betweenness sequence and the most gradual decline in the min betweenness sequence.

Ecosystem function and stability

The mean biomass in each habitat patch decreases as habitat is lost when dispersal rate is intermediate or high (Fig. 4k–l); biomass declines most rapidly in the max betweenness removal sequence. When dispersal is low, the mean local biomass in the intact network is lower than at higher dispersal rates (Fig. 4j). As patches are removed, mean biomass of metacommunities with low dispersal remains fairly constant around 50 (corresponds to base growth).

Local biomass is a positive saturating function of the species richness in a patch, as long as dispersal rates are sufficient to allow multiple species to co-exist ($a > 0.0005$;

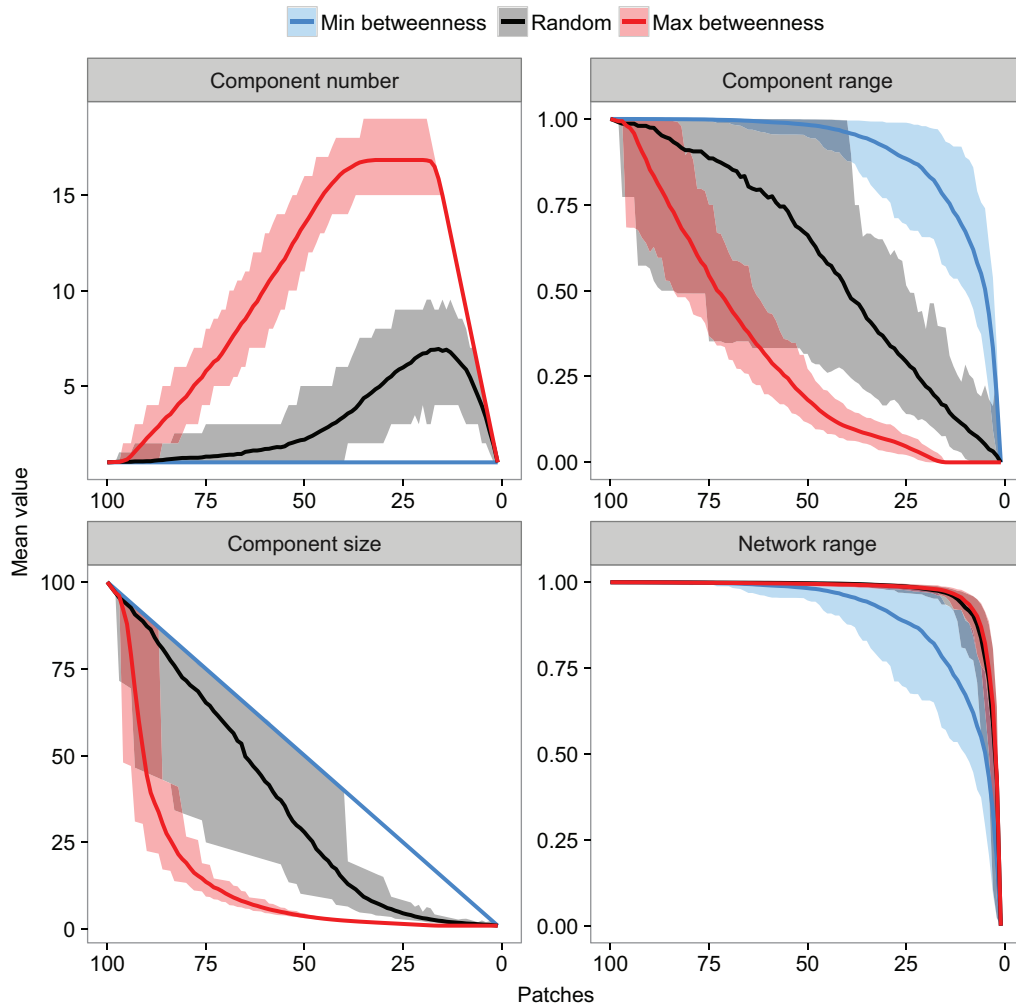


Figure 3. The change in four measures of network structure—component number (a), component environmental range (b), component size (c), and network environmental range (d) as habitat patches are removed according to the three sequences: removing the patch with the minimum betweenness centrality (blue); removing a random patch (black); and removing the patch with the maximum betweenness centrality (red). Lines represent mean values across one hundred replicate simulations and ribbons represent the range between the 2.5th and 97.5th percentiles of the data.

Fig. 5). The sequence of patch removal has little effect on the shape of this relationship. But the patch removal sequences differ in how much diversity is lost with each patch removal, so a given amount of patch loss causes communities to be at different points on this curve (e.g. the symbols on Fig. 5 indicate the position after 70 patches are lost).

The temporal variability of biomass, as measured by the CV, increases as habitat is lost except at local scales, when dispersal is low (Fig. 4m–r). Biomass variability increases most steeply in the max betweenness removal sequence and most gradually in the min betweenness sequence. These differences between the removal sequences are more pronounced at the local scale compared to the regional scale. When dispersal is low, the intact community has higher biomass variability, and, at the local scale, this variability remains largely constant as habitat is lost.

Metacommunity dynamics and habitat loss

Changing the rate of dispersal has striking nonlinear effects on the relative contribution of the different persistence

mechanisms to biomass production (Fig. 2). Base growth is responsible for the majority of biomass production at low dispersal rates ($a \leq 0.0005$), but its contribution decreases as dispersal increases. Species sorting occurs over the intermediate range of dispersal rates, and is responsible for the majority of biomass production when dispersal rates are greater than 0.0005 and less than 0.015. Mass effects contribute to biomass production at all but the lowest dispersal rates, but become the dominant effect when the dispersal rate exceeds 0.01.

Overall, habitat loss results in the loss of species sorting dynamics, which are replaced by a combination of mass effects and base growth, depending on the dispersal rate and patch removal sequence (Fig. 6). The onset of this shift in the relative importance of persistence mechanisms is triggered by the fewest patch removals in the max betweenness sequence, and most patch removals in the min betweenness sequence.

When dispersal is low ($a = 0.0005$; Fig. 6a, d, g), base growth contributes ~ 80% of biomass production and species sorting contributes the remaining ~ 20% in the intact network. As patches are removed, species sorting dynamics

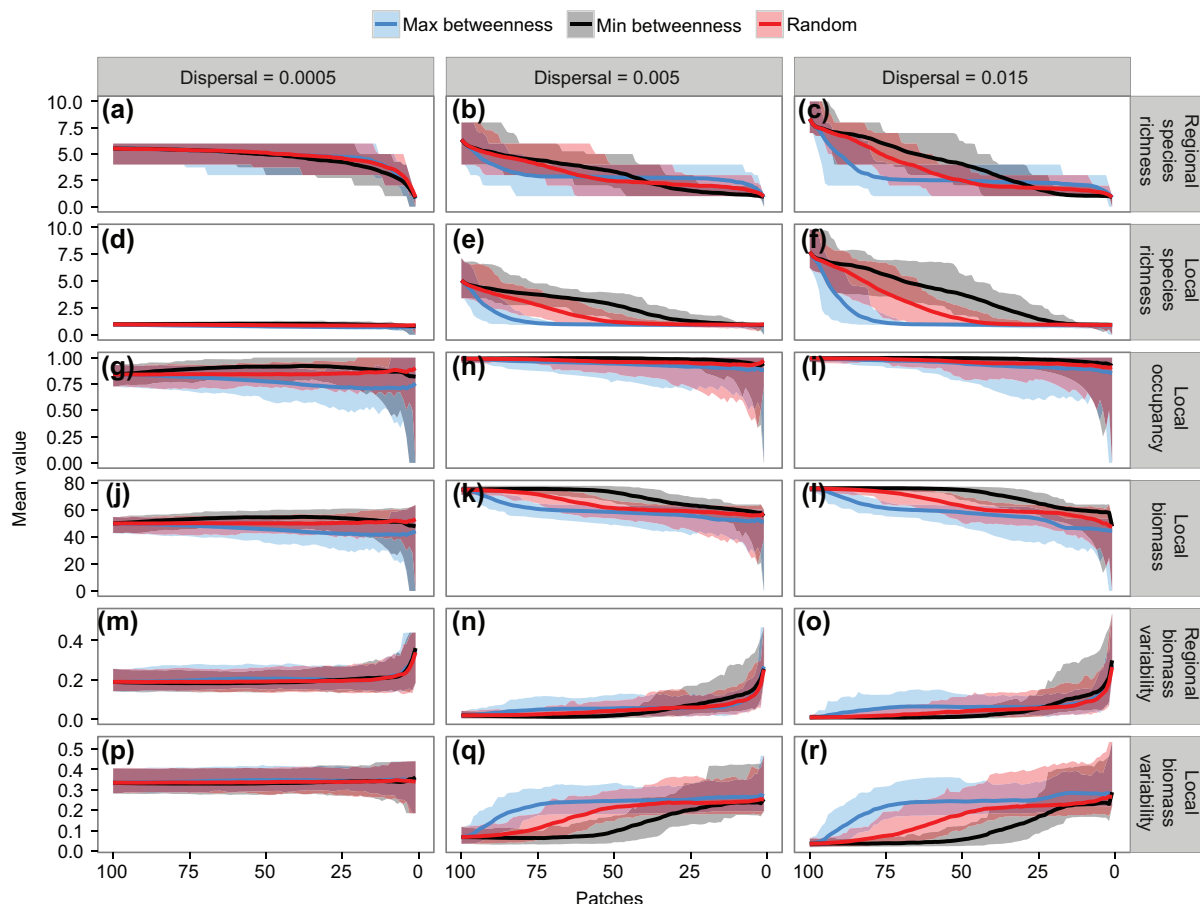


Figure 4. The response of six measures (rows) of metacommunity diversity, biomass production and stability at local and regional scales to habitat patch deletion, for three dispersal rates (columns). Each panel shows impact of the patch removal sequence minimum betweenness centrality (blue); random (black); and maximum betweenness centrality (red) on each response variable. Lines represent mean values across one hundred replicate simulations and ribbons represent the range between the 2.5th and 97.5th percentiles of the data.

become weaker, and base growth contributes proportionately more to biomass production, along with a small contribution from mass effects. With intermediate dispersal ($\alpha = 0.005$; Fig. 6b, e, h), species sorting dynamics contribute the majority ($\sim 75\%$) of the biomass production in the intact network. As patches are removed, the dynamics shift from species sorting to mass effects, and finally, to base growth, when the network is fully fragmented. With higher dispersal ($\alpha = 0.015$; Fig. 6c, f, i), mass effects and species sorting contribute $\sim 55\%$ and 40% of the biomass production of the intact network and the contribution from base growth is $\sim 5\%$. Patch removals weaken the strength of species sorting, so that a greater proportion of biomass is produced through mass effects until all that remains are single-patch components driven by base-growth.

Discussion

We find that habitat destruction causes non-linear losses of species richness and ecosystem functioning, and destabilizes biomass production at local and metacommunity scales. This occurs because habitat loss shrinks and fragments the metacommunity, limiting dispersal independent growth, impeding species sorting dynamics, while promoting mass

effects and dispersal limitation. The degree to which habitat loss impacts the community depends on the pattern of habitat loss and the rate of dispersal, such that metacommunities that are well connected by dispersal are most sensitive to the effects of habitat loss. As expected, removing highly connected habitat patches quickly erodes the contribution of species sorting dynamics, and has the greatest consequences for the diversity and functioning of the metacommunity. However, when we prioritize the conservation of the most connected habitat patches, species sorting dynamics are maintained, and species richness, ecosystem functioning, and stability are preserved. The effects of removing connected habitat patches can be interpreted as a function of the consequences for local (alpha) and regional (gamma) biomass stability as well as spatial asynchrony among local populations (beta stability; Wang and Loreau 2014, 2016). Our results demonstrate that conserving connected habitat can increase local stability and maintain species sorting dynamics, thereby producing a net increase in regional stability.

Prior to habitat loss, the degree to which species exhibit dispersal limitation, species sorting and mass effects depends on the rate of dispersal (Fig. 2) (Loreau et al. 2003, Leibold et al. 2004). At low dispersal rates, species are limited in their ability to move between patches in response to the

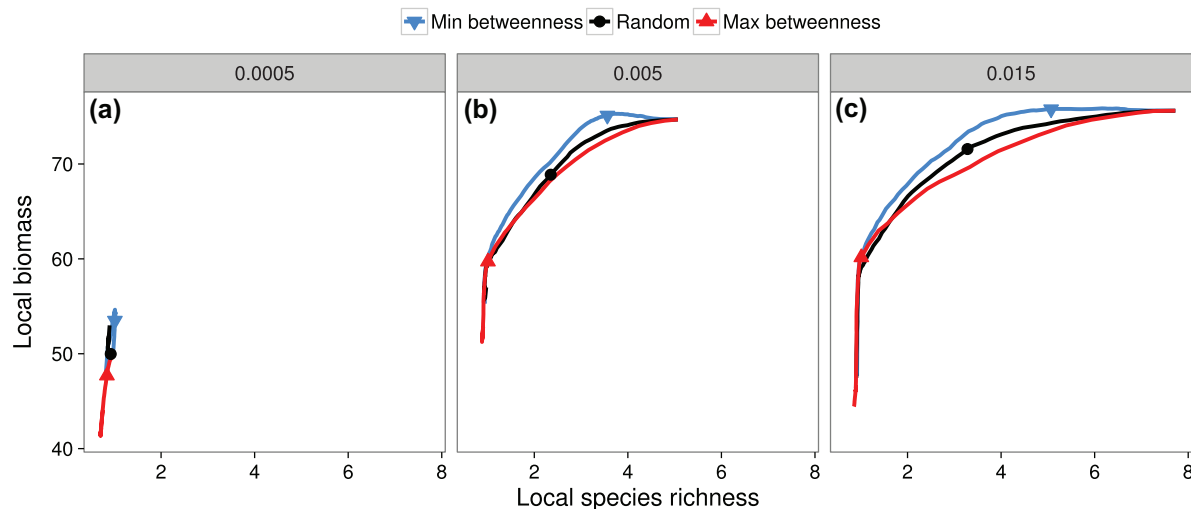


Figure 5. The relationship between local species richness and local biomass, for three dispersal rates (columns). The patch removal sequence is indicated by the colour of the lines: minimum betweenness centrality (blue); random (black); and maximum betweenness centrality (red). The mean values after 10 patches have been removed is indicated by the symbols: minimum betweenness centrality (blue down pointing triangle); random (black circle); and maximum betweenness centrality (red up pointing triangle). Lines represent mean values across one hundred replicate simulations. Variation across replicates is omitted for clarity, but the three removal sequences are all within 1 standard deviation.

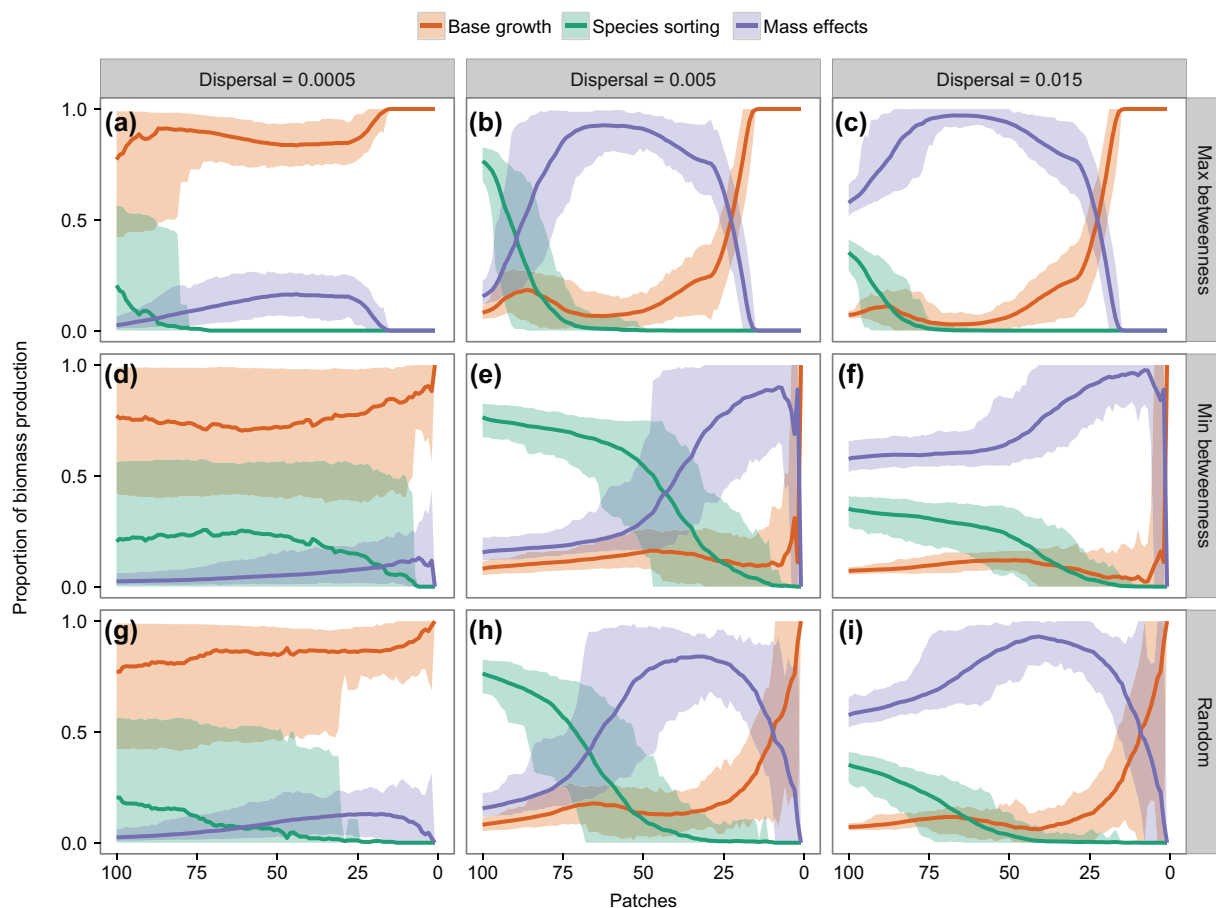


Figure 6. The proportion of biomass production from species exhibiting base growth, species sorting, and mass effects at different levels of habitat loss (number of patches remaining). Three different dispersal rates are shown (rows) that represent cases where the predominant dynamic is base growth (0.001), species sorting (0.01), and mass effects (0.1). The columns represent the different scenarios of habitat loss, depending on whether habitat loss targets patches with the minimum betweenness centrality, at random, or with the maximum betweenness centrality. Lines represent mean values across one hundred replicate simulations and ribbons represent the range between the 2.5th and 97.5th percentiles of the data.

environment. Competitive exclusion limits the number of species in each community, and biomass production decreases when the environment becomes unfavourable for those species. Intermediate rates of dispersal result in species sorting, which allows species to move away during periods of unfavourable local environmental conditions, and sustain higher rates of biomass production. In addition, as long as there are patches that are favourable for growth, this ensures that species will persist in the metacommunity. While species sorting allows species to establish in favourable environments, mass effects allow them to persist in unfavourable environments. Mass effects increase local diversity, and provide additional stability for biomass production by ensuring that local communities are less affected by changes in the environment.

Habitat loss alters the balance of these metacommunity processes by restricting the range of environmental conditions that species can access through dispersal, and thus preventing species from tracking their environmental optima as conditions change through time (Thompson et al. 2014). This occurs in two ways: 1) habitat loss reduces the overall range of environmental conditions in the metacommunity, and 2) habitat loss can cause the metacommunity to fragment, which restricts species to sub-components (Fig. 3a) of the remaining habitat network. Whereas all sequences of habitat loss result in a linear reduction in the overall range of environmental conditions in the metacommunity, habitat loss that fragments the landscape reduces the range of available environmental conditions much more quickly. Therefore, removing the patches with the highest betweenness results in the greatest changes to diversity and biomass dynamics of the metacommunity. In contrast, removing the patches with the lowest betweenness does not result in fragmentation, and so the dynamics of the metacommunity are less affected. Economo (2011) also found that the most connected patches were very important for the persistence of regional (gamma) diversity in metacommunities. He modelled neutral metacommunities and so species sorting was not at play. He found that regional diversity declined over the long term due to the extinction of widespread species that were no longer able to persist once their metapopulations were fragmented by the removal of highly connected patches.

The sequence of habitat loss only matters when dispersal rates are high enough to allow for species sorting as the local environments change. When dispersal between patches is limited, changes in structural network connectivity and the range of environmental conditions has little effect on a local community (left column of Fig 4), and so its diversity and biomass is largely unaffected by the removal of neighboring habitat. These findings suggest that the consequences of habitat loss for real habitat networks will depend on how functionally connected the patches are by dispersal.

By altering the balance of species sorting, mass effects, and base growth, habitat loss reduces the number of species and the overall biomass that can be sustained. However, while species richness is relatively sensitive to the initial loss of patches, especially when patches of high betweenness are removed, biomass declines are more gradual and require greater habitat loss. This delayed biomass decline is due to the fact that ecosystem functioning is a positive saturating function of species diversity (Fig. 5), as has been found in

ecosystem experiments (Cardinale et al. 2011); initial loss of species from species rich communities results in little loss of biomass production. In this case, the reason for this relationship is because resource complementarity occurs through time as the environment changes (Loreau et al. 2003, Isbell et al. 2011): different species become productive as conditions become favourable for them and this increases the overall functioning of the community. As the community loses species, its ability to maintain productivity at all times through compensatory dynamics declines (Gonzalez and Loreau 2009), and biomass becomes increasingly variable through time (Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010). While the shape of the local biodiversity–ecosystem function relationship is not greatly affected by the three patch removal sequences, the loss of high betweenness patches causes the greatest loss of species diversity for a given loss of habitat (e.g. Fig. 5 – the symbols contrast the position on the curve after 70 patch deletions), and so the communities quickly move into the range where biomass is low and highly variable.

Despite the clear value of preserving habitat patches that are integral to the connectivity of the landscape, we find that targeting patches with low betweenness has some unintended consequences for biodiversity. When patches with minimum betweenness are targeted for removal, we see that high levels of habitat loss can lead to greater declines in regional diversity compared to when loss is random or when high betweenness patches are removed (Fig. 4, dispersal = 0.005 and 0.015). This occurs because patches with minimum betweenness tend to be those on the periphery of the network, and so their removal shrinks the extent, and overall range of environmental conditions that are present in the network (Fig. 3d). This emphasizes the need to consider environmental uniqueness of a habitat patch when making conservation decisions and account for potential trade-offs between connectivity of other features that make habitat patches ecologically important or rare.

The emphasis in our model is on spatial processes that allow species to persist and maintain ecosystem functioning in changing environments. However, there are clearly processes at play in real ecosystems that allow species to co-exist without dispersal, such as species that specialize on different resources (Tilman 1990), non-linear responses to environmental changes (Levins 1979), and the temporal storage effect (Chesson 2000). These processes should increase rates of base productivity compared to what we have in our model. However, these are non-spatial processes and so should not be greatly affected by the loss of neighbouring patches. Our metacommunities represent simplified habitat networks, in landscapes fragmented by humans, patch area and configuration can be very heterogeneous. We have assumed passive dispersal, but we expect that species sorting would be stronger, and mass effects weaker, if dispersing individuals chose patches based on their environmental preferences. We also expect that active dispersal would allow species sorting to be more robust to habitat loss, but future investigation is required to confirm this hypothesis. Nonetheless, our model allowed us to identify how habitat loss and connectivity can alter metacommunity processes by reducing the environmental heterogeneity that is available for species that allows them to persist and contribute to ecosystem functioning.

This should apply to real habitat networks, but the degree to which it does so will depend on the environmental heterogeneity and the functional connectivity of the network.

Conclusion

Habitat fragmentation is a global phenomenon with recent estimates indicating that more than 70% of the world's forest lies within 1 km of an edge (Haddad et al. 2015). Field data and experiments point to the impacts, often delayed, of altering connectivity on the diversity, composition and functioning of communities (Gonzalez and Chane-ton 2002, Tewksbury et al. 2002, Brudvig et al. 2009, Chisholm et al. 2010, Staddon et al. 2010, Haddad et al. 2015, Resasco et al. 2017). Our metacommunity model formalises a fragmented landscape as a dynamic spatial network of communities in which diversity and ecosystem function decayed rapidly and non-linearly as patches of high value to connectivity were lost. This finding suggests that network approaches to conservation should be used to restore and manage heavily fragmented landscapes (Opdam et al. 2006, Vos et al. 2008). These results, and our finding on the robustness of networks to habitat loss (Thompson et al. 2014), stress the value of conserving remnant ecosystems, but argue for the prioritization of fragments that play a disproportionately important role in the connectivity of the spatial network of habitat. For example, the management of patches with high centrality in the network can greatly reduce the loss of local and regional diversity and associated ecosystem functions. Conserving the connectivity of fragmented landscapes, by restoring the quality of the matrix between fragments or establishing corridors between influential clusters of patches, are practical means of maintaining the valuable spatial insurance effects of biodiversity for ecosystem function and services in uncertain and changing environments.

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