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Robustness of the spatial insurance effects of biodiversity to habitat loss

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ABSTRACT

Definitions: *Spatial insurance*: Improvement of maintenance of species diversity and ecosystem functioning in heterogeneous environments because species can track their optimal environments by dispersing between habitat patches. *Betweenness centrality*: Value of an individual habitat patch in adding to the connectivity of the metacommunity by being a stepping-stone for dispersing individuals. *Robustness*: The proportion of patches that must be removed to change each response variable beyond a given threshold.

Question: In fragmented landscapes, how do spatial patterns of habitat loss affect the robustness of the insurance effects on biodiversity? Does the underlying pattern of habitat connectivity in metacommunities play a role in maintaining biodiversity and ecosystem function in the face of habitat loss?

Mathematical method: Using a spatially explicit version of a resource competition metacommunity model, we simulated habitat loss in metacommunity networks composed of habitat patches connected by links for dispersal.

Key assumptions: Species differ in their environmental preferences. Local environmental conditions fluctuate asynchronously so that species must disperse in order to persist and maintain productivity. Habitat patches are lost sequentially, resulting in gradual fragmentation of the metacommunity.

Results: Habitat loss reduces the amount of spatial insurance conferred by the habitat structure on biodiversity by preventing species from dispersing to environmentally suitable areas. The robustness of metacommunities to habitat loss decreases dramatically when the patches with high betweenness centrality are lost. Metacommunities are generally most robust when the pattern of habitat connectivity is random and when the habitat patches that are lost have low betweenness centrality.

Keywords: centrality, connectivity, dispersal, ecosystem function, environmental change, extinction, habitat fragmentation, metacommunity, network, stability.

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INTRODUCTION

Destruction of natural habitat is the major direct cause of biodiversity declines worldwide (IUCN, 2014) and is projected to increase over the next century (Millennium Ecosystem Assessment, 2005). The fragmentation of remaining habitat and the spatial arrangement of the surrounding landscape can compound the effects of habitat destruction, resulting in further biodiversity loss over time (but see Fahrig, 2003; Yaacobi *et al.*, 2007; Gavish *et al.*, 2012). For example, habitat isolation is one consequence of habitat fragmentation that drives biodiversity loss (Hanski *et al.*, 2013; Dobert *et al.*, 2014) because it increases rates of local extinction and reduces rates of re-colonization. Patterns of landscape fragmentation are typically the result of both habitat loss and fragmentation, which have interdependent effects on biodiversity (Didham *et al.*, 2012).

Loss of biodiversity may also impact ecosystem function and erode associated ecosystem services essential for human well-being (Gonzalez *et al.*, 2009, 2011; Cardinale *et al.*, 2012; Hooper *et al.*, 2012; Balvanera *et al.*, 2014). For example, local biodiversity loss can reduce the efficiency with which communities convert nutrients into plant biomass (Cardinale *et al.*, 2011), which has implications for a wide range of ecosystem services such as carbon storage and primary productivity (Kremen, 2005). Moreover, biodiversity loss may decrease the stability of ecosystem functioning (Cardinale *et al.*, 2012), resulting in ecosystems with more variable aggregate biomass through time (Gonzalez and Loreau, 2009; Hector *et al.*, 2010).

Maintaining functional connectivity, or the ability of species to disperse among habitat fragments, may slow biodiversity loss and so mitigate the negative impacts of habitat loss and fragmentation (Loreau *et al.*, 2003; Staddon *et al.*, 2010; Hanski, 2011). The spatial insurance hypothesis posits that dispersal mediates diversity at local and regional scales and so directly affects the function and stability of ecosystems in single habitat fragments, and across many fragments, at the scale of the landscape (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). Our ability to manage fragmented landscapes effectively requires that we understand how habitat loss erodes the role connectivity plays in maintaining biodiversity and ecosystem functioning.

Patterns of landscape fragmentation can be modelled as spatial networks (Fagan and Calabrese, 2006; Dale and Fortin, 2010; Gonzalez *et al.*, 2011), wherein nodes represent habitat patches and links represent dispersal potential or pathways. The structure of habitat networks depends on the spatial distribution of links among nodes (Rayfield *et al.*, 2011) and has been shown to affect ecological dynamics of the resident species (e.g. Holland and Hastings, 2008; Ranta *et al.*, 2008; Economo and Keitt, 2010; Gilarranz and Bascompte, 2012). One important aspect of network structure is the degree to which links are regularly or randomly distributed among the nodes. Ranta *et al.* (2008) found that increasing the randomness of links among populations reduced synchrony of the population fluctuations. Holland and Hastings (2008) also found that randomizing the structure of habitat networks reduced synchrony among predator–prey dynamics across the network.

Another important measure of network structure is patch centrality (Carroll *et al.*, 2011). Centrality metrics rank the importance of habitat patches (or links) based on their local or regional position within the network (Bunn *et al.*, 2000; Estrada and Bodin, 2008; Carroll *et al.*, 2011). For example, betweenness centrality (Freeman, 1977) identifies habitat patches that are used as stepping stones to facilitate movement across the entire network. Protecting patches with high betweenness centrality may have a disproportionately large effect on maintaining regional landscape connectivity. And, local biodiversity can be higher in habitat patches with high regional centrality because they are more accessible to species distributed in different regions of the landscape (Economo and Keitt, 2010).

The structure of habitat networks can define the robustness of fragmented landscapes to further habitat loss (reviewed in Gonzalez *et al.*, 2011). Robustness is generally attributed to network structures that maintain connectivity even when some nodes are removed (Albert *et al.*, 2000; Dunne *et al.*, 2002). Many networks are sensitive to the selective loss of the most connected nodes yet robust to the random loss of nodes (Cohen and Havlin, 2010).

We hypothesize that robust landscapes are able to maintain levels of biodiversity and ecosystem function despite the loss of some habitat patches. However, the impact of losing any given habitat patch will depend on its local biodiversity and centrality.

To assess robustness involves simulating different patterns of habitat loss by sequentially removing patches based on different criteria such as their area (Urban and Keitt, 2001) or centrality (Estrada and Bodin, 2008). We examine the robustness of metacommunities, or networks of local communities embedded in fragmented landscapes (Economo and Keitt, 2008, 2010), across a range of network structures spanning regular to random patterns of connectivity (Holland and Hastings, 2008). We are interested in the degree to which habitat network structure can mediate impacts of habitat loss on biodiversity and ecosystem functioning. We simulate different patterns of habitat loss in these fragmented landscapes by using different node removal sequences that target randomly, strongly or weakly connected nodes based on their betweenness centrality. We show that biodiversity and ecosystem function are sensitive to habitat loss and that betweenness centrality is a key measure influencing the robustness of the spatial insurance hypothesis in fragmented landscapes (Dunne *et al.*, 2002).

METHODS

Resource competition metacommunity model

We modelled habitat loss in metacommunity networks using a resource competition model previously used to develop the spatial insurance hypothesis (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). The metacommunity networks consist of M habitat patches connected by $2 \times M$ links. Habitat patches are represented as points with fixed locations on a ring with a radius of one (Fig. 1). Each link has an associated length corresponding to the Euclidean distance between the locations of the connected patches. The networks were constructed first as regular lattices, where each patch was connected to its first- and second-order nearest neighbours. A given percentage of links were then randomly rewired to create random network structures that had a variety of shortcuts across the ring of habitat patches (Holland and Hastings, 2008).

The metacommunity dynamics are determined by the following equations governing resource competition:

$$\frac{dN_{ij}(t)}{dt} = N_{ij}(t)[ec_{ij}(t)R_j(t) - m] + A_{ij}(t) - aN_{ij}(t), \tag{1}$$

$$\frac{dR_j(t)}{dt} = I - lR_j(t) - R_j(t) \sum_i^S c_{ij}(t)N_{ij}(t), \tag{2}$$

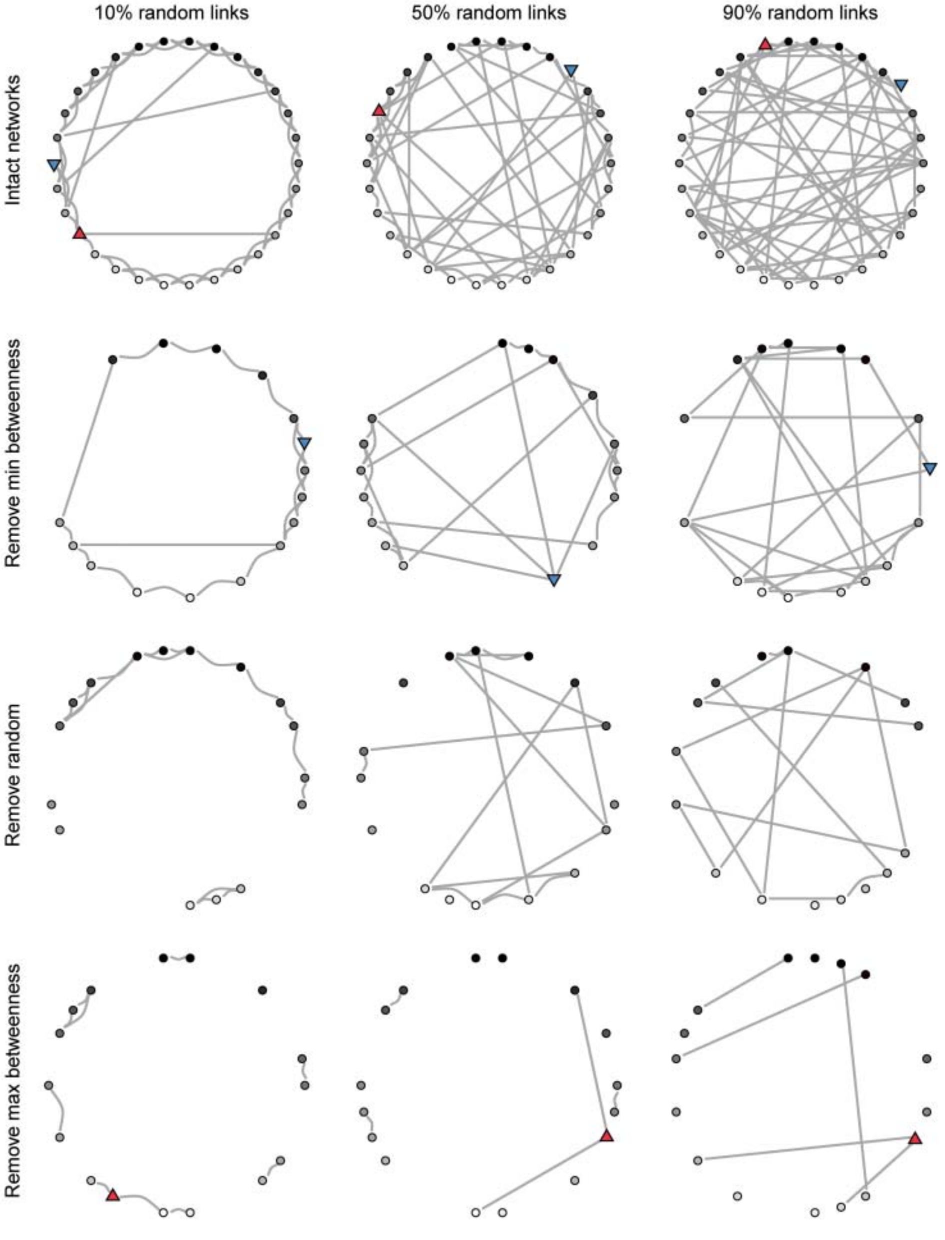

Fig. 1. Example metacommunity networks with 10%, 50%, and 90% random links. Metacommunities are shown as intact networks, and after 14 patches have been removed based on the three removal sequences: removing the patch with the minimum betweenness centrality; removing a random patch; and removing the patch with the maximum betweenness centrality. First- and second-order neighbour links are shown with curved lines for clarity, but distances are calculated based on Euclidean (straight-line) links. The next patch to be deleted in each of the centrality removal sequences is shown as the downward pointing triangle (minimum betweenness) or the upward pointing triangle (maximum betweenness). The grey scale of the patches illustrates the autocorrelated environmental conditions ($t = 1$).

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

Dispersal occurs via the network links and decreases with distance from source patch such that:

$$A_{ij}(t) = aN_{ij}(t) \sum\nolimits_{k \neq j}^{M} \frac{\exp(-Ld_{kj})}{\sum\nolimits_{f \neq k}^{M} \exp(-Ld_{kf})}. \tag{3}$$

This depends on the shortest network distance (computed as the weighted shortest path based on link length) between source patch k and the destination patch j. The distance dependence limitation L determines the strength of the exponential decrease in dispersal with distance d_{kj}. Because we assume equal emigration from all patches, the proportion of dispersing biomass to patch j from patch k is also dependant upon the distance from patch k to each other patch f. If patch j loses all connections with other patches in the network, $A_{ij}(t)$ will be equal to zero. We assume that emigration continues once patches become isolated, but that this biomass is lost from the metacommunity.

The environmental conditions E_j in each patch j fluctuate through time (e.g. temperature), following a sinusoid with a period T such that:

$$E_j(t) = \frac{1}{2}\left[\sin\left(Einit_j + \frac{2\pi t}{T}\right) - 1\right]. \tag{4}$$

We assume that the initial conditions $Einit_j$ span a regular gradient between zero and one, but are autocorrelated [Moran's $I = 0.43$ (Moran, 1950)] in space so that the environments $E_j(t)$ in nearby patches are similar at any time t (Fig. 1). We assume that the consumption rate $c_{ij}(t)$ of species i is determined by the match between its environmental optimum H_i and the local environmental conditions $E_j(t)$ such that:

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

where the environmental optima H_i of the S species are equally spaced across the one-dimensional range of environmental conditions.

Landscape fragmentation simulations

We simulated 30-patch networks with nine species and the following model parameters: $e = 0.2$, $m = 0.2$, $I = 150$, $l = 10$, $N_{ij}(t = 1) = 10$, and $R_j(t = 1) = 9$. We set an extinction threshold to be $N_{ij} = 0.1$; populations below this were assumed extinct with a biomass of zero. We used the Euler method with $\Delta t = 0.08$ to approximate continuous dynamics. Each environmental fluctuation had a period $T = 40{,}000$, which was chosen to be large enough to cause competitive exclusion of all but one species if there is no dispersal. We set the dispersal rate to be $a = 0.01$, a rate that allows for tracking of local environmental conditions. This allowed all species to persist in all patches, with maximum community biomass, and minimal temporal variation of biomass at both local and regional scales (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). This provides a best-case scenario with which to examine the impacts of different habitat loss sequences.

We compared networks that varied in the proportion of links that were randomly rewired (10, 30, 50, 70, and 90%) and a spatially implicit case, as a baseline reference. In this spatially implicit case, the patches have no explicit location in space or connectivity structure, and we assume equal dispersal between all patches in the metacommunity. The spatially implicit networks match those that have been previously used to demonstrate the spatial insurance hypothesis (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). In the spatially explicit networks, distance dependent limitation L was set to 1.

Habitat loss

Each simulation ran for 100,000 time steps to allow initial transient dynamics to subside. We then simulated habitat loss by removing a single patch from the network, as well as its connections to other patches, every 20,000 time steps until only two patches remained. We compared three patch removal sequences: removing the patch with the lowest betweenness centrality, removing a random patch, and removing the patch with the highest betweenness centrality (Fig. 1). The betweenness centrality of a patch is computed as the proportion of shortest paths between all pairs of patches that include that patch (Freeman, 1977; White and Borgatti, 1994). The shortest paths were weighted by link lengths. Habitat patches with high betweenness centrality can be considered as key stepping-stones, as they are included in the largest number of shortest paths. For example, in Fig. 1, in the intact network with 10% random links, the patch indicated by the downward pointing triangle has no betweenness centrality because it does not act as a stepping-stone between other patches in the metacommunity. In comparison, the patch indicated by the upward pointing triangle has the highest betweenness centrality because it connects patches in the lower and right-hand part of the network to patches in the upper left side of the metacommunity. Betweenness centrality was recalculated each time a patch was removed to account for the effect of removing that patch on the betweenness centrality of patches in the remaining network. Only the random removal sequence could be used for the spatially implicit networks.

Response variables and analysis

All response variables were calculated based on sampled data taken every 1000 time steps, excluding the first 100,000 time steps. The number of connected components in each metacommunity was calculated to track changes to the network structure. A connected component is defined as a subset of patches in the metacommunity that are all either directly or indirectly connected. Patches in different components are not connected and therefore would not be able to exchange individuals during metacommunity simulations.

The number of species and community biomass were calculated at both local and regional scales. Here we present only the mean local community biomass because regional biomass is lost with every patch removal, and so does not reflect the response of the metacommunity to patch removal. The temporal coefficient of variation (CV) of community biomass was calculated, both locally and regionally, for time steps between each patch removal. All reported variables are based on 100 replicate simulations, each with a new randomly generated network as an initial condition.

We calculated network robustness as the proportion of patches removed that is required to change each response variable beyond a given threshold (Dunne *et al.*, 2002). These thresholds were: ≥50% of initial number of species, ≥75% of initial mean local biomass, and when local and regional biomass CV was ≤0.1 and 0.05 respectively. These threshold values were chosen to emphasize differences between networks and patch removal sequences.

All analyses and simulations were conducted in *R* v.3.1.1 (R Development Core Team, 2014) with networks generated using the *iGraph* package v.0.7.1 (Csardi and Nepusz, 2006).

RESULTS

Connected components

The number of connected components had a unimodal shape in both the maximum betweenness and random patch removal sequences (Fig. 2); initially increasing due to the removal of patches that bridge two or more connected components and subsequently decreasing as single-patch components were removed. The maximum betweenness patch removal sequence resulted in the largest numbers of connected components (up to 11 components) for the smallest fraction of patches removed (50% of patches) across all levels of link randomness. The network remained intact as a single connected component under the minimum betweenness patch removal sequence.

Number of species

Local and regional number of species declined from 9 to 1 species as patches were removed (Fig. 3), and species loss occurred with fewer patch deletions in the spatially explicit metacommunities than in the spatially implicit case. The decline in number of species was most gradual in the minimum betweenness removal sequence and most rapid in the maximum

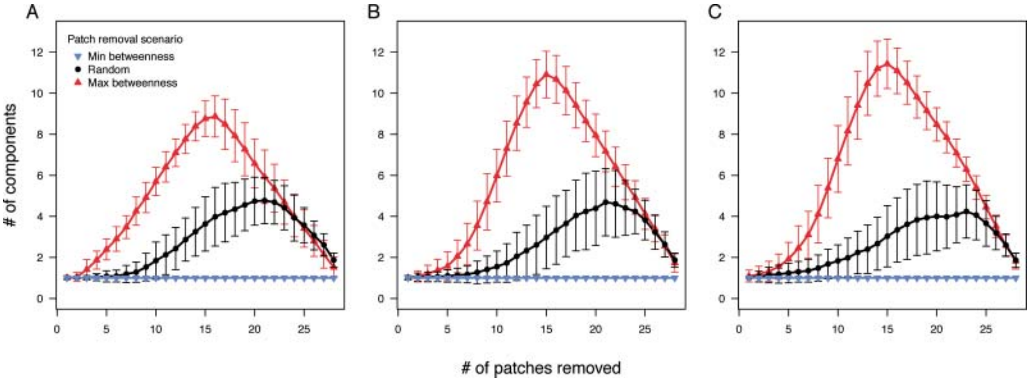

Fig. 2. The number of connected components resulting from the removal of patches in the three removal sequences (▼ = minimum betweenness patch removed; ● = random patch removed; ▲ = maximum betweenness patch removed) in metacommunity networks with 10% (A), 50% (B), and 90% (C) random links. Error bars represent ± one standard deviation around the mean for 100 replicate networks.

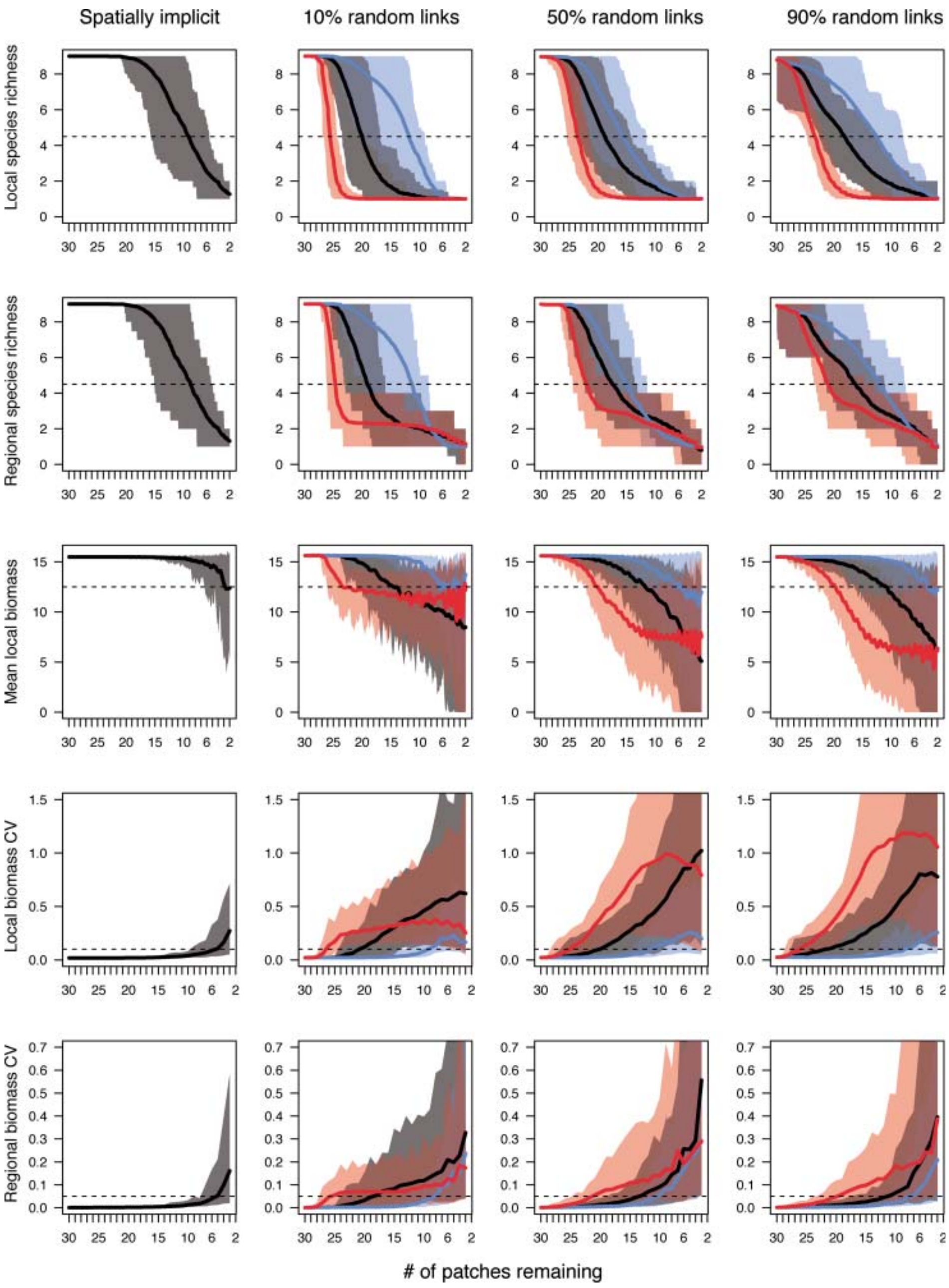

Fig. 3. Change in the five response variables (local number of species, regional number of species, mean local biomass, local biomass CV, and regional biomass CV) as patches are removed from spatially implicit metacommunity networks and spatially explicit metacommunity networks with 10%, 50%, and 90% random links. Mean values (lines) and 95% quantiles (shaded areas) from 100 replicate networks are shown for the three removal sequences (blue = minimum betweenness patch removed; black = random patch removed; red = maximum betweenness patch removed). The threshold value for calculating robustness, seen in Fig. 3, for each response variable is indicated with the dashed line.

betweenness removal sequence. Loss of species was similar at both local and regional scales but the decreases were slightly greater at local scales, especially under the maximum betweenness removal sequence.

The robustness of diversity was lower in the spatially explicit metacommunities than in the spatially implicit ones; the latter retained more than half their species until 75% of the patches had been removed (Fig. 4A, B). The robustness of local and regional diversities followed the same general patterns with removal sequence and link randomness but differences among removal sequences were greater for local diversity. The minimum betweenness removal sequence yielded the most robustness, with metacommunities subjected to it retaining more than half of the species regionally until an average of 63% of the patches had been removed in the 10% random link networks. The maximum betweenness sequence was most destructive, with removal of an average of 22% of the patches resulting in the loss of half of regional species in the 10% random link networks. The random removal sequence produced intermediate robustness, with the removal of an average of 39% of the patches resulting in the loss of half the species regionally in the 10% random link networks. Robustness increased with link randomness in the random and maximum betweenness patch removal sequences, but robustness showed a unimodal dip in the minimum betweenness removal sequence. The greatest difference in retention of species occurred when link randomness was low.

Biomass

Mean local biomass declined as patches were removed (Fig. 3), and biomass began to decline with fewer patch deletions in the spatially explicit metacommunities than in the spatially implicit case. The initial biomass was most robust in the minimum betweenness patch removal sequence and was the least robust in the maximum betweenness sequence. However, although biomass began to decline after only a few patches were removed in the maximum betweenness removal sequence, this decline slowed so that biomass remained at a relatively constant level as the remaining patches were removed. This asymptote occurred with fewer patch deletions under low link randomness, resulting in a negative relationship between final biomass and link randomness (Fig. 3). This asymptote did not occur in the random removal sequence, and once biomass began to decline it did so relatively constantly as further patches were removed. Therefore, unless networks had high link randomness (90%), the final biomass when only two patches remained was higher in the maximum betweenness removal sequence than in the random removal sequence. The decline in biomass only reached an asymptote in the minimum betweenness removal sequence in networks with low link randomness (10%), and in all cases the highest biomass was retained in the minimum betweenness removal sequence. Biomass robustness showed similar patterns to species diversity robustness but the unimodal dip of the minimum betweenness sequence was less pronounced (Fig. 4C).

Local biomass variability (CV) increased as patches were removed (Fig. 3), and this increase was greater in the spatially explicit metacommunities than in the spatially implicit case. The maximum betweenness removal sequence showed sharp increases in local biomass variability with the removal of only a few patches, but these increases slowed, and then local biomass CV declined as subsequent patches were removed. As with biomass, this asymptote occurred with fewer patch deletions in networks that had low link randomness, resulting in a positive relationship between final biomass CV and link randomness (Fig. 3). The random

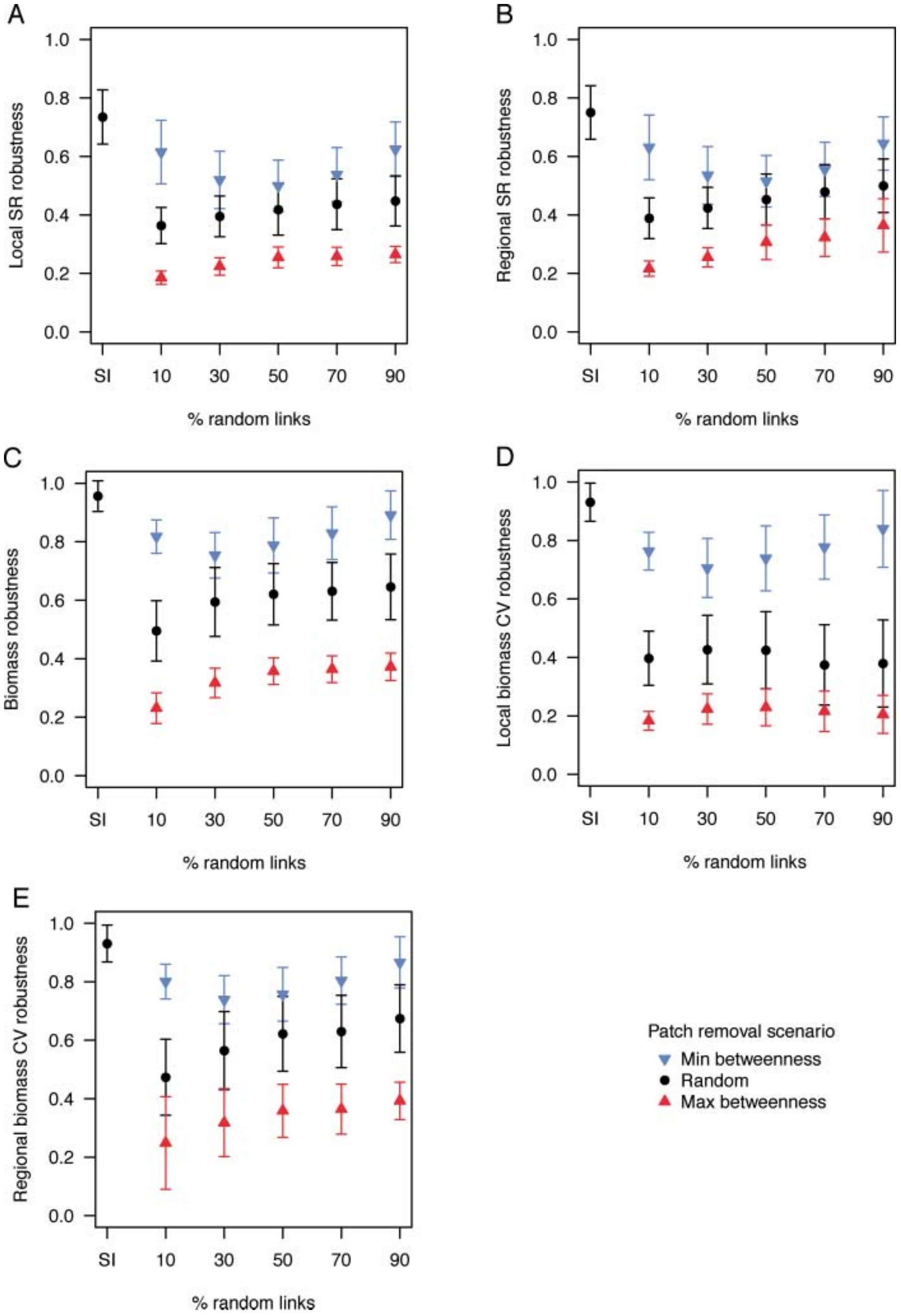

Fig. 4. Robustness for (A) local and (B) regional number of species, (C) mean local biomass, as well as (D) local and (E) regional biomass CV across metacommunity link randomness. SI indicates the spatially implicit metacommunities. Error bars represent ± one standard deviation around the mean based on 100 replicate networks.

patch removal sequence was less sensitive to initial patch deletion, but increases in biomass variability were more consistent, saturating only in networks with high link randomness (90%). Therefore, the final biomass CV, once all but two patches had been removed, was highest with the random patch removal sequence except in networks with high link randomness (90%). Initial patch removals had little effect on local biomass CV in the minimum betweenness removal sequence. In this case, biomass variability became noticeable only after half the patches had been removed. These increases tended to saturate at low CV, especially when link randomness was not high (<90%). The minimum betweenness removal sequence always resulted in the lowest local biomass variability. Local biomass CV robustness showed similar patterns to mean biomass robustness but robustness did not increase with link randomness in the random and maximum betweenness removal sequences (Fig. 4D).

Regional biomass variability (CV) was always lower than local biomass variability (Fig. 3). Unlike local biomass CV, increases in regional biomass variability did not reach an asymptote as patches were removed. In addition, the minimum betweenness removal sequence resulted in similar or higher regional biomass variability than the maximum betweenness removal sequence, when only a few patches remained (<6) and when network links were not highly random (<90%). Regional biomass CV robustness showed similar patterns to mean biomass robustness (Fig. 4E).

DISCUSSION

The diversity and ecosystem function of metacommunities in this study are more robust to the loss of random or least-connected habitat patches than loss of highly connected habitat patches. Fragility to the loss of highly connected nodes is a common property of many real-world networks (Dunne *et al.*, 2002; Cohen and Havlin, 2010). As expected, the more connected a habitat patch is, the more disruptive its loss will be to species' dispersal and, consequently, to the diversity and functioning of the metacommunity network. Previous assessments of landscape robustness have found that different node removal criteria have different effects on various aspects of the network structure, such as network diameter (Urban and Keitt, 2001), network modularity (Albert *et al.*, 2013), size of the largest connected component, and network cliqueishness (Estrada and Bodin, 2008). Our study goes further than these assessments by demonstrating both the structural and the functional consequences of habitat loss in fragmented landscapes.

The robustness of our metacommunities to habitat loss depends on the degree to which the removal of the patches disrupts the connectivity of the landscape. Because local environmental conditions change constantly, diversity and productivity can be maintained only when species are able to track favourable conditions through dispersal (Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). When habitat loss reduces landscape connectivity, species become restricted to subsets of the remaining patches. These subsets, or connected components, of the metacommunity contain only part of the environmental range of the intact metacommunity, and so species cannot track their environmental optima as the local conditions change over time. As a result, species diversity and biomass decline, and biomass becomes more temporally variable because species are trapped in habitat patches and are forced to fluctuate in response to local environmental conditions. The metacommunity is least robust to the removal of patches with the highest betweenness centrality because their removal causes the most abrupt changes to the connectivity of the habitat network. In the example shown in Fig. 1 (10% random links), the removal of a single patch with the highest betweenness centrality entirely disconnects the bottom-left region. Furthermore, removing 50% of the patches with the highest betweenness centrality results in a metacommunity of fifteen remaining patches that is isolated into, on average, nine subgroups, each comprised of one or two neighbouring habitat patches (Fig. 2A). In comparison, the metacommunity is most robust to the removal of patches with low betweenness centrality because network connectivity is always preserved, regardless of the number of patches removed (as shown in Fig. 1 and Fig. 2). However, although the metacommunities are structurally robust to the minimum betweenness removal sequence (at least in terms of the number of connected components; Fig. 2), patches can become more isolated if they are connected to other patches only by long pathways. Such isolation reduces the amount of dispersal to these patches, with negative consequences for diversity and productivity. Patch isolation is responsible for the reduced functional robustness of these networks compared with the spatially implicit metacommunities, i.e. the case where all patches remain equally connected.

The initial distribution of links among habitat patches in fragmented landscapes has a weak ability to buffer biodiversity and ecosystem functioning against habitat loss. Our results show a trend of positive correlation between the randomness of network links and functional robustness (Fig. 4). This result is consistent with the effects of link randomness on population (Ranta *et al.*, 2008) and predator–prey synchrony (Holland and Hastings, 2008). However, the positive effects of link randomness are small compared with the negative effects of removing patches with high betweenness centrality. Furthermore, the positive effects of link randomness on functional robustness are not caused by structural robustness because the number of connected components increases with link randomness (Fig. 2). Rather, link structure affects metacommunity network robustness because it determines how much environmental heterogeneity is retained by the connected components as habitat is lost. Components containing subsets of patches that are more environmentally heterogeneous can sustain more diversity and function because there is a better opportunity to track changes in the environment through dispersal among patches. The environments in our metacommunities are spatially autocorrelated, so the environmental heterogeneity of connected patches increases with network randomness, resulting in the increased robustness of these networks. There is, however, a benefit to having a less random link structure during the minimum patch betweenness removal sequence. In this removal sequence, the remaining patches are connected, so the full range of environmental heterogeneity is always accessible. The benefit of networks with low link randomness is that most links are between patches with similar environments. Thus, conditions are generally favourable for dispersing individuals requiring an environment that matches their trait optimum. And so we see that the sensitivity of metacommunity robustness to link randomness depends on the spatial autocorrelation of local environments (Moran, 1953).

Our model is an obvious simplification of the dynamics of real metacommunities. But our approach allows us to identify how habitat loss will affect the spatial maintenance of biodiversity and ecosystem function (Chesson, 2000a; Loreau *et al.*, 2003; Gonzalez *et al.*, 2009). Other co-existence mechanisms that we did not model, such as the temporal storage effect (Chesson, 2000b), non-linear response to environmental fluctuations (Levins, 1979), or species that specialize on different resources (Tilman, 1990), would likely increase metacommunity robustness to habitat loss. We chose conditions that maximized the spatial insurance effects of diversity on ecosystem function by fixing dispersal rate, maintaining the asynchrony of local environmental conditions, and modelling species with environmental optima that are evenly spaced across the environmental range. However, spatial insurance will still occur as long as (1) the metacommunity is connected via dispersal, (2) local environmental variation is not completely spatially synchronous, and (3) species exhibit differential responses to these environmental conditions (Gonzalez *et al.*, 2009). We have extended previous research of the spatial insurance hypothesis by studying the role that network connectivity plays in the robustness of spatially explicit metacommunities. Our networks are still idealized models of real habitat networks embedded in fragmented landscapes, but we have shown that the core mechanisms of the spatial insurance hypothesis are retained when dispersal is limited by the constraints of dispersal distance and network structure.

The use of current network approaches in conservation biology promises to accelerate our understanding of biodiversity change and our ability to mitigate its impacts on ecosystem function. A recent application of network approaches to conservation is the design of ecosystem networks for sustainable landscapes (Opdam *et al.*, 2006; Vos *et al.*, 2008). Ecosystem networks are composed of mixed ecosystem types (forest, wetland, grassland, etc.) linked into a spatially coherent network through the movement of organisms and resources (Opdam *et al.*, 2006). Our model captures the essential features of ecosystem networks, and our results point to the value of a network perspective for the management of highly fragmented landscapes for biodiversity and associated ecosystem services. For example, we might manage patch centrality in a network of forest patches to sustain networks of pollinators required for pollination services, or complex communities of natural enemies for pest control in agricultural landscapes. Recent experimental results further strengthen the science of ecosystem networks (Tewksbury *et al.*, 2002; Brudvig *et al.*, 2009; Chisholm *et al.*, 2010; Staddon *et al.*, 2010) and stress the value of ecological corridors as a practical means of maintaining landscape connectivity and the spatial insurance effects of biodiversity.

CONCLUSION

Our analysis demonstrates how habitat loss within fragmented landscapes can reduce biodiversity and ecosystem function by eroding the spatial insurance effects of biodiversity. The impact of habitat loss depends on the degree to which species can track their environmentally optimal conditions within the habitat patches that remain. The loss of patches with high betweenness centrality hinders the ability of species to relocate to environmentally suitable habitat patches. The underlying distribution of links in metacommunity networks determines how habitat loss reduces the range of environmental heterogeneity in the residual network. It is the connectivity and heterogeneity of the landscape that governs how much biodiversity can be maintained and the degree to which this diversity can buffer environmental change. Together, these results suggest that robustness of fragmented landscapes to ongoing habitat loss can be maintained if conservation strategies focus on protecting or restoring landscape connectivity.

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