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Biodiversity Conservation in Metacommunity Networks: Linking Pattern and Persistence

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ABSTRACT: A central goal of conservation science is to identify the most important habitat patches for maintaining biodiversity on a landscape. Spatial biodiversity patterns are often used for such assessments, and patches that harbor unique diversity are generally prioritized over those with high community similarity to other areas. This places an emphasis on biodiversity representation, but removing a patch can have cascading effects on biodiversity persistence in the remaining ecological communities. Metacommunity theory provides a mechanistic route to the linking of biodiversity patterns on a landscape with the subsequent dynamics of diversity loss after habitat is degraded. Using spatially explicit neutral theory, I focus on the situation where spatial patterns of diversity and similarity are generated by the structure of dispersal networks and not environmental gradients. I find that gains in biodiversity representation are nullified by losses in persistence, and as a result the effects of removing a patch on metacommunity diversity are essentially independent of complementarity or other biodiversity patterns. In this scenario, maximizing protected area and not biodiversity representation is the key to maintaining diversity in the long term. These results highlight the need for a broader understanding of how conservation paradigms perform under different models of metacommunity dynamics.

Keywords: biodiversity, complementarity, conservation planning, metacommunities, neutral theory.

Introduction

Habitat loss is a widespread consequence of human activities and a global threat to biodiversity (Pimm et al. 1995; Rosenzweig 1995, 2001; Vitousek et al. 1997; Dirzo and Raven 2003; Whittaker et al. 2005). A basic premise of conservation biology is that habitat units have unequal biological value; some are more important than others for maintaining total biodiversity and thus have a higher priority for protection. Understanding how to identify those

critical patches—and effectively allocate conservation resources—remains an important theoretical and applied problem.

A common approach to conservation planning uses biodiversity patterns (among other criteria) to prioritize habitat units for protection. This approach generally favors patches that harbor biological uniqueness (high complementarity) over those with high community similarity to other areas (Margules and Pressey 2000; Myers et al. 2000; Possingham et al. 2000; Faith et al. 2004; Margules and Sarkar 2007). More informally, conservationists and biologists are intuitively drawn to areas with high endemism. This thinking often leads to a focus on small areas with many endemics and patch sets with high complementarity at the expense of more “redundant” local communities embedded in larger, spatially homogeneous areas. Indeed, with systematic planning, large proportions of gamma diversity can often be represented in small subsets of total area. On a global scale, this line of reasoning leads one to consider large areas with high alpha diversity and low beta diversity, such as the Amazon basin, as conservation priorities despite a higher overall rate of habitat contraction.

This focus on biodiversity patterns assumes that after some habitat is lost, current diversity patterns will persist in the remaining areas. However, biologists have long been concerned that removing a patch can cause a dynamic response in the rest of the landscape and a secondary loss of biodiversity (Bierregaard et al. 1992; Tilman et al. 1994; Hanski 1999; Cabeza and Moilanen 2001; Cabeza 2003), which is often called an extinction debt. These concerns trace back at least to island biogeography theory (MacArthur and Wilson 1967; Laurance 2008) and the ensuing single large or several small (SLOSS) debate (Diamond 1975; Simberloff and Abele 1976; Saunders et al. 1991). Since that time, metapopulation theory has directly addressed the persistence problem both conceptually and in applied contexts (Hanski 1999). Despite increasingly sophisticated methods to plan for the persistence of non-

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interacting multiple species metapopulations (Nicholson et al. 2006; Nicholson and Possingham 2007; Drechsler et al. 2008), less is known about the connection between biodiversity pattern and persistence when ecological interactions on the community level, such as competition, drive both the generation of patterns and the dynamic response to habitat loss. Nevertheless, community patterns of diversity, similarity, and complementarity still constitute the primary biological information used for conservation prioritization.

Metacommunity theory (Hubbell 2001; Leibold et al. 2004; Holyoak et al. 2005) provides a mechanistic route to connecting observable properties of patches on a landscape (e.g., biodiversity patterns) with the nonobvious effects of removing those patches on biodiversity persistence. It differs from classical metapopulation theory because in a metacommunity, multiple species can promote or interfere with the persistence of others on a landscape. Despite a recent surge of interest in metacommunities, there is still great untapped potential for the paradigm to inform conservation approaches.

Spatial biodiversity patterns can arise across a metacommunity due to species sorting along environmental gradients or to spatial structure and dispersal limitation (Loreau and Mouquet 1999; Leibold et al. 2004; Cottenie 2005; Economo and Keitt 2008, 2010). When only properties of the local environment control local community structure, removing a patch should result in the loss of only biotic elements unique to that patch, consistent with the approach of maximizing representation. However, when the areas, arrangements, and connectivity of habitat patches (spatial structure) drive biodiversity patterns, removing a patch is more likely to have cascading secondary effects on biodiversity persistence in the metacommunity. From a conservation perspective, a significant problem arises if these secondary effects are correlated with the metrics used for prioritization, such as complementarity. Because patch connectivity drives both the structure of local communities (i.e., complementarity) and their dispersal contributions to other patches, such correlations might be expected.

Spatially explicit ecological neutral theory (Hubbell 2001; Condit et al. 2002; Chave 2004; Rosindell and Cornell 2007; Economo and Keitt 2008, 2010) presents a case where beta diversity in a landscape is driven solely by patterns of connectivity, without variation in the environment or biogeographic history. Here I use it to ask a basic question: are spatial biodiversity patterns useful in building reserves that maintain biodiversity on a landscape in the long term when those patterns are driven by variation in patch connectivity? The premise of this study is not that conservation planning paradigms should be redesigned around neutral theory. Rather, neutral theory is a well-

established model that highlights a set of ecological processes (i.e., dispersal limitation, spatial structure, competition, and stochastic drift) with poorly understood conservation implications. This study can be viewed as the first step in a wider and more synthetic investigation of biodiversity representation and persistence across a range of metacommunities, with different ecological dynamics that range from neutral to purely environmentally determined. Furthermore, at least in some contexts, neutral theory accurately predicts quantitative aspects of biodiversity loss after habitat contraction (Halley and Iwasa 2011).

Following recent work (Economo and Keitt 2008, 2010; Muneepeerakul et al. 2008), I represent a neutral metacommunity as local communities (nodes) arranged in a network and connected by links reflecting dispersal of individuals. Networks are widely used in landscape ecology to represent complex patterns of patch connectivity (Urban and Keitt 2001; Bodin and Norberg 2007; Urban et al. 2009) and can be used as a scaffold for building spatially explicit ecological theory. However, despite the widespread interest in landscape networks, little is known about how metacommunity dynamics play out in a spatial network context, much less about their conservation implications (Cumming et al. 2010).

I use this process-based framework to evaluate biodiversity loss in a metacommunity as habitat patches are removed and the system dynamically responds to a new equilibrium. The main concern of this article is the correlation between the immediate costs to biodiversity representation from losing a patch (i.e., the biodiversity actually located in the patch) and the long-term effects of removing that patch on biodiversity persistence across the remaining network. More generally, I investigate the connection between the perceived conservation value of areas on the basis of biodiversity patterns and their long-term abilities to maintain diversity. When spatial structure and dispersal limitation generate patterns of alpha and beta diversity, I find that there is little such connection.

Theory and Methods

Neutral Metacommunity Theory

The theoretical approach used in this article is one realization of ecological neutral theory (Hubbell 2001), which has diversified into a family of models that share certain features. Aside from a few exceptions (Gilbert et al. 2006; Hubbell et al. 2008; Halley and Iwasa 2011), it has generally not been applied to conservation-related questions. The basic unifying idea of neutral theory is that diversity is maintained in a balance between input of new diversity, from speciation within the system or colonization from

outside the system, and loss of diversity due to stochastic extinction when a species' population "drifts" to 0. The rate of input and the total number of individuals in the system generally control the equilibrium level of diversity. In smaller communities, new species arise less frequently and existing species more often drift to extinction, which reduces equilibrium diversity levels. If dispersal is limited (i.e., individuals are not well mixed), close relatives cluster together and spatial patterns can arise. Ecological drift and speciation are differentiating forces leading the community composition of different areas to diverge over time, while the exchange of dispersing individuals is a homogenizing force. The balance of these opposing forces sets the equilibrium spatial diversity patterns (Hubbell 2001; Economo and Keitt 2008).

The spatial design of the metacommunity has important consequences for predicted diversity patterns. Previous work has assumed a large input pool and a small local community that receives migrants (Hubbell 2001; Etienne 2005) or an infinite two-dimensional landscape (Rosindell and Cornell 2007). Here we use a network construction (Economo and Keitt 2008, 2010) that distributes the individuals among a set of local communities connected by dispersal. The structure of the underlying landscape, the locations and arrangements of habitat patches (e.g., islands in an archipelago, mountaintops in a range), and the matrix of intervening habitat interact with the dispersal ability of the organisms involved to determine the spatial structure of the metacommunity and the network.

It is important to note that in a neutral scenario, any spatial patterns in diversity (other than pure sampling effects) are governed by the spatial structure of the metacommunity. The network approach is ideal for the current problem in that it allows complex spatial structures to be represented and produce similarly complex biodiversity patterns. At equilibrium, a local community can have more alpha diversity (on average) than other patches only if it is larger or has greater connectivity with other patches, which is essentially a realization of the original idea of island biogeography. Thus, it is well suited for representing a case where patterns of connectivity, and not other factors such as environmental variation or historical biogeography, produce biodiversity patterns.

The basic neutral dynamic studied here uses a standard set of assumptions from neutral theory; those assumptions are important to note, however, as even within the neutral theory paradigm there are a growing number of variations in the literature that can affect outcomes. I represent the metacommunity as a network of local communities of equivalent size (N_k individuals per community) that do not fluctuate in time (zero-sum dynamics; Hubbell 2001; Etienne et al. 2007b). This formulation does not require that the underlying landscape itself be structured into

equivalently sized units or even that it be a highly discretized "island" landscape. Rather, I partition the landscape into equally sized units so we can easily compare the effects of removing different equally sized amounts of habitat from across the metacommunity. A single large habitat patch would be represented as a tight cluster of smaller nodes with very high connectivity among them. There could be no structure at all (panmixia) within the cluster, which effectively behaves as a single large node. The zero-sum assumption is important, as it implies a constraint on competition for space and/or resources in the community within a trophic level. In general, this approach is most relevant to situations where the structure of the metacommunity is relatively stable (other than the habitat destruction). This excludes systems that are characterized by recurrent extinction of whole local communities.

In each generation, every individual dies and is replaced with a new individual of the species of a parent alive in the previous generation (Fisher-Wright dynamics). A new individual in patch i has a parent in patch j with probability m_{ij} and a parent in the same patch with probability m_{ii} . Note that $\sum_j m_{ij} = 1$. For a network with n nodes, the set of all probabilities (all m_{ij}) make up an $n \times n$ migration matrix \mathbf{M} . By random chance, not every individual will produce the same number of offspring in a given generation, and species abundances will change over time through drift. We set the additional constraint that $m_{ij} = m_{ji}$, or that dispersal is symmetric among pairs of nodes.

New species arise in the landscape randomly as single individuals with a fixed per-individual-generation probability of ν . This input can be interpreted as the speciation process or as colonization from a large source pool (Bell 2000). The speciation interpretation implies that the network is a closed biogeographic province, while the colonization interpretation implies that the network is an open landscape embedded within a larger province. The key is that there is an input of novelty (which I refer to from now on as speciation) that is necessary for nonzero equilibrium diversity. Although different speciation models have been proposed (Etienne et al. 2007a; Rosindell et al. 2010) and would be interesting to examine in a spatial context, the point process has the advantage of the dual interpretation and is the focus of this article.

The neutral processes described above can be modeled analytically to give equilibrium diversity levels within a local community, between different communities, and in the whole metacommunity (Economo and Keitt 2008). This approach, which was adapted from population genetics (Malécot 1948), has several advantages over simulation, namely, the speed of computation and the accessibility of parameter space. However, relative to simulation, it is constrained in both model assumptions

and predicted patterns, as it is limited to diversity indices (and not, e.g., species abundance curves) as its currency.

With inputs of the migration matrix, speciation rate, and local community sizes, the method calculates the equilibrium probability of identity in state, f_{ij} , which is the probability that two randomly chosen individuals from community i and community j are the same species. The set of all f_{ij} can then be used to calculate diversity patterns across the metacommunity (see below). Following recent work (Economio and Keitt 2008, 2010), we use the following equation describing the probability of identity in the current generation ($t + 1$) as a function of the probability of identities in the previous generation (t):

$$f_{ij,t+1} = (1 - \nu)^2 \left[\sum_{k,l,k \neq l} m_{ik} m_{jl} f_{kl,t} + \sum_k m_{ik} m_{jk} \left(1 - \frac{1}{N_k} \right) f_{kk,t} + \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k} \right) \right]. \quad (1)$$

Two sampled individuals are of the same type if neither has speciated since the previous generation (the first term) and (1) they were from parents of the same type from different patches (the first summation), (2) they were from different parents of the same type located in the same patch (second summation), or (3) they had the same parent (coalesced) in the previous generation (third summation). When the system is in a steady state, the equilibrium probability of identity for a given (i, j) pair is $\hat{f}_{ij} = f_{ij,t+1} = f_{ij,t}$. After substituting these into equation (1), we can rearrange the equation to bring all the probabilities of identities \hat{f}_{ij} on one side as

$$(1 - \nu)^{-2} \hat{f}_{ij} - \sum_{k,l} m_{ik} m_{jl} \hat{f}_{kl} + \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k} \right) \hat{f}_{kk} = \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k} \right). \quad (2)$$

Note that the migration probabilities (m_{ij}) and the population sizes (N_k) are given a priori and the set of all \hat{f}_{ij} are the only unknowns. Thus, for a network of n nodes, there are n^2 unknowns (i, j pairs), each with an equation that can be written in the form of equation (2). This linear system of equations can then be solved directly for the vector \mathbf{f} of all \hat{f}_{ij} . As there are n^2 equations, for anything larger than a few nodes it is most convenient to solve these equations computationally. I coded the left side of equation (2) as $n^2 \times n^2$ matrix \mathbf{X} and the right side as vector \mathbf{q} of length n^2 and solved the equation $\mathbf{X}\mathbf{f} = \mathbf{q}$ for the vector \mathbf{f} . The elements of \mathbf{X} and \mathbf{q} are given by

$$X_{(ij),(kl)} = (1 - \nu)^{-2} \delta_{ik} \delta_{jl} - m_{ik} m_{jl} + \delta_{kl} m_{ik} m_{jk} \left(\frac{1}{N_k} \right), \quad (3)$$

$$q_{(ij)} = \sum_k m_{ik} m_{jk} \left(\frac{1}{N_k} \right). \quad (4)$$

There is one row and one column of \mathbf{X} for each pair of nodes, and the notation $X_{(ij),(kl)}$ is used to indicate an element that is in the row for node pair (i, j) and the column for node pair (k, l) . Likewise, there is one element of the vector \mathbf{q} for each node pair (i, j) . Here, δ_{ij} is the Kronecker delta, where $\delta_{ij} = 1$ when $i = j$ and $\delta_{ij} = 0$ when $i \neq j$ (and thus, the term $\delta_{ik} \delta_{jl}$ adds $(1 - \nu)^{-2}$ to only the diagonal of \mathbf{X} and the term δ_{kl} adds the third term to only columns of \mathbf{X} where $k = l$). I conducted these calculations using Matlab.

The probability of identity f_{ij} is equivalent to the Simpson concentration (Simpson 1949) that forms the basis for a family of community diversity statistics. From the set of all f_{ij} we can calculate the Simpson's index of a local community i as f_{ii}^{-1} (alpha diversity) and that of the entire metacommunity (gamma diversity) as the inverse of the mean probability of identity ($\langle f_{ij} \rangle^{-1}$) taken over all i and j nodes. The name "Simpson's index" has been variably assigned to different quantities in the ecological literature; here I use it to refer to the inverse of the probability of identity, in effective species numbers, that would be calculated as $(\sum_i p_i^2)^{-1}$ from species frequency data if p_i were the frequency of the species i in the community. These can then be used in the diversity analyses described below.

To summarize, the input parameters in the model described above are the migration matrix \mathbf{M} representing the topology and edge weights (dispersal probabilities) of the network, the local community size N_k , and the speciation rate ν . I created several different networks, and these are discussed in a following subsection. For each topology, I varied both migration and speciation rates from 10^{-10} to 10^{-1} . The local community size N_k controls levels of gamma diversity but does not directly control patterns of alpha and beta diversity, and thus for most of the trials in this article, I set each node to 2,000,000 individuals and held it constant. In the appendix, N_k is varied and its (minimal) effect demonstrated. Note again that holding N_k constant does not mean that patches in a landscape do not vary in size but merely that I partitioned them into equal-sized units.

Measuring Biodiversity Representation and Persistence in a Metacommunity

Before introducing the metrics used in this article, it is important to discuss what they are trying to measure in

a metacommunity and how this relates to conservation. Conservation efforts often seek to maintain gamma diversity in a landscape. This gamma diversity can be concentrated within many similar communities (alpha diversity) or found in the differences among communities (beta diversity). Complementarity (Pressey and Nicholls 1989; Margules and Pressey 2000), a metric familiar to conservation biologists but more rarely used by community ecologists, reflects the amount of diversity that a given patch or set of patches adds to another set of patches. Here I use it to measure the contribution of single communities to the gamma diversity of the landscape. If the community is composed of widespread, commonly occurring species, it will have low complementarity, while a community with many endemics will have a high complementarity. Note that complementarity is not the same as similarity or distinctness; a community composed of a single endemic species is maximally distinct, as is a community composed of two endemic species, but the latter has a higher complementarity because it contributes more to gamma diversity. It is easy to see why an alpha diversity dominated landscape would appear more redundant than one composed of unique and complementary local communities. In the former, patches could be lost while diversity is still maintained in the remaining patches, while in a landscape with maximal beta diversity, all patches are needed to maintain gamma diversity. Thus, complementarity is the focus of many biodiversity-based analyses as a measure of conservation value, but more specifically it measures representation value without regard to importance for biodiversity persistence.

I focus on several quantities calculated from a metacommunity: (1) the initial gamma diversity of a metacommunity at equilibrium, γ_0 ; (2) the initial gamma diversity of all patches except node i , γ_i ; and (3) the new gamma diversity of the metacommunity after i is removed and the rest of the metacommunity relaxes to a new equilibrium, γ'_i .

From the model output, we can calculate Simpson's index for a local community (alpha) and for the whole metacommunity (gamma), as shown above. These indices, and all diversities in this article, are expressed in effective species numbers (Hill 1973). Effective species numbers have several important conceptual and quantitative advantages over the raw probabilities of identity, which are well discussed elsewhere (Jost 2006; Economo and Keitt 2008; Jost et al. 2010). To calculate a given γ_h (i.e., gamma diversity of the metacommunity without node h), we again use the average probability of identity ($\langle f_{ij} \rangle^{-1}$) over all (i, j) but with $i, j \neq h$.

The initial primary cost to gamma diversity of removing a patch i is the complementarity, $c_i = \gamma_0 - \gamma_i$. Mathematically, it measures representation value, the contribu-

tion of one patch to metacommunity gamma diversity on the basis of current biodiversity patterns (or alternatively, representation loss if it is removed). Complementarity is often used for sets of multiple patches, but we focus on one patch (or more specifically, the complementarity of one patch with the set of all other patches) here to compare the representation and persistence losses due to individual node removals.

After a patch is removed, secondary biodiversity changes may occur in the remaining patches as the metacommunity relaxes to a new equilibrium. These secondary costs to persistence, κ_i , can be written as the difference between the pre- and postrelaxation gamma diversity of the reduced metacommunity, $\kappa_i = \gamma_i - \gamma'_i$. The total long-term reduction in biodiversity Λ_i due to node removal is the sum of the representation loss and persistence loss $\Lambda_i = c_i + \kappa_i = \gamma_0 - \gamma'_i$. Here I evaluate whether the representation loss (complementarity, c_i) is correlated with persistence loss κ_i across patches and whether the perceived conservation value c_i is predictive of the total long-term biodiversity costs of removing a node Λ_i .

Network Construction

I first constructed a 10-node network with three clusters of nodes. I varied migration rate (entries m_{ij} of the migration matrix \mathbf{M}) within this topology under two models. (1) In the node-independence model (fig. 1a), to represent two scales of hierarchical structure (within and among clusters), I assigned to within-cluster links a weight of m_0 , and to among-cluster links I assigned a weight of $0.1m_0$. (2) In the cluster-independence model (fig. 1b), I kept clusters internally panmictic and assigned links among clusters a common weight of m_0 . In both cases, I changed the migration rate systematically by varying m_0 across 10 orders of magnitude. The difference between the two is that in the first model, the limit of no migration makes every node an independent unit, and in the second the limit makes every cluster of nodes an independent unit.

I also examined three larger networks with a diversity of topologies and complexity in the pattern of edge weights (fig. 3). Only symmetric networks were considered, in that migration was equal in both directions between a pair of nodes, but different pairs could have different migration strengths. The grid network topology is simply a 7×7 lattice. The modular network was generated by randomly assembling several subnetworks and then randomly adding a few links between the subnetworks. The random graph was constructed by randomly assigning links between pairs of nodes with a probability p ; in this case, $p = 0.085$. I varied edge weights (m_{ij}) by randomly assigning nodes into three categories of isolation (isolated [I], intermediate [M], and connected [C]). If two nodes had an edge between

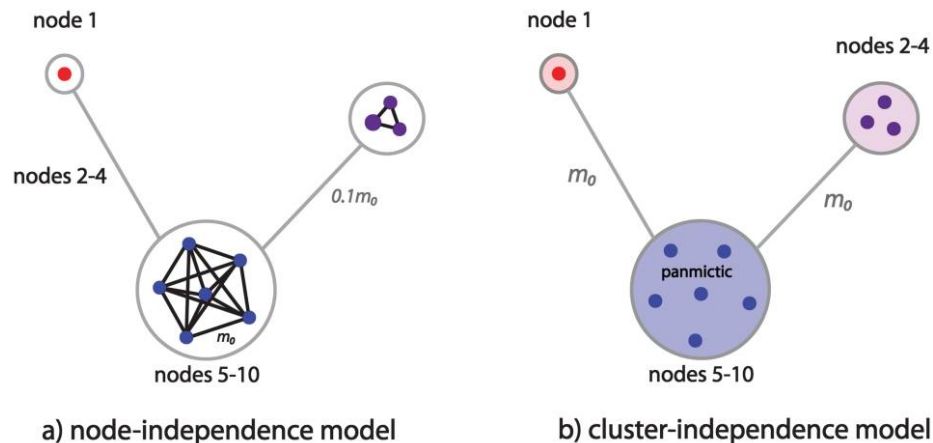


Figure 1: A simple 10-node metacommunity with three clusters. I varied migration rates in this network under the following two models: (a) node independence, with varying the weights of all edges with the parameter m_0 but where connections are stronger within than among clusters, and (b) cluster independence, with panmixia maintained within the different-sized clusters but with varying migration rates between them. The first represents a hierarchical landscape with two levels of structure, and the second is a landscape with three different-sized habitat units that vary in connectivity among them, again with the parameter m_0 .

them, then they were assigned values based on the categories of each node (I/I, $0.0001m_0$; I/M, $0.0005m_0$; I/C, $0.001m_0$; M/M, $0.001m_0$; M/C, $0.005m_0$; and C/C, $0.01m_0$). The parameter m_0 was then varied to examine different overall levels of migration. The probability of no migration was adjusted accordingly as $m_{ii} = 1 - \sum_{j, i \neq j} m_{ij}$. The model reserves in figure 4 represent all 1,022 possible subsets of the 10-node network in figure 1a.

Node Removal Procedures

I followed two basic procedures to investigate the effect of removing nodes on biodiversity loss. First, I examined the effect of removing single nodes on metacommunity diversity and whether that effect is related to complementarity (representation value) of the node. Second, to evaluate how the effects observed in single-node removals scale to removals of many nodes, I examined how well subsets (model reserves) of the network that have varying levels of biodiversity representation preserve biodiversity in the long term.

The basic procedure is as follows: (1) initiate a metacommunity with a given spatial structure and parameter values and calculate the neutral diversity equilibrium; (2) analyze current biodiversity patterns in that metacommunity and calculate the complementarity of each node or, in the case of multiple node removals, the gamma diversity of a subset of nodes; (3) remove one (figs. 2–4) or more (fig. 5) nodes from the network and solve for the new equilibrium diversity patterns in the metacommunity

with reduced size; and (4) analyze the new biodiversity patterns and calculate changes relative to initial diversity levels.

Results

Single-Patch Removals

In general, neutral processes in this type of metacommunity create three types of equilibrium pattern controlled by parameter values (Economo and Keitt 2008, 2010). When connectivity is very high relative to speciation rate, local communities are homogenized: each community represents all of the gamma diversity of the metacommunity, and the complementarity of each patch is 0 ($c_i = 0$). In the other extreme, when speciation rate is very high relative to migration rates between nodes, each node becomes its own distinct local community (under the node-independence model) and the metacommunity has maximum complementarity. At intermediate levels of connectivity and speciation (for the topologies considered here, this occurs roughly when ν and edge weights m_{ij} are within several orders of magnitude) complex patterns of diversity and complementarity form.

It is simple and instructive to consider what happens to diversity when a node is removed in the two extreme cases of maximum complementarity and maximum similarity. This will provide context for the effects of removing patches from a landscape with complex biodiversity patterns. In a completely well-mixed metacommunity, gamma diversity (Simpson's index in effective species numbers)

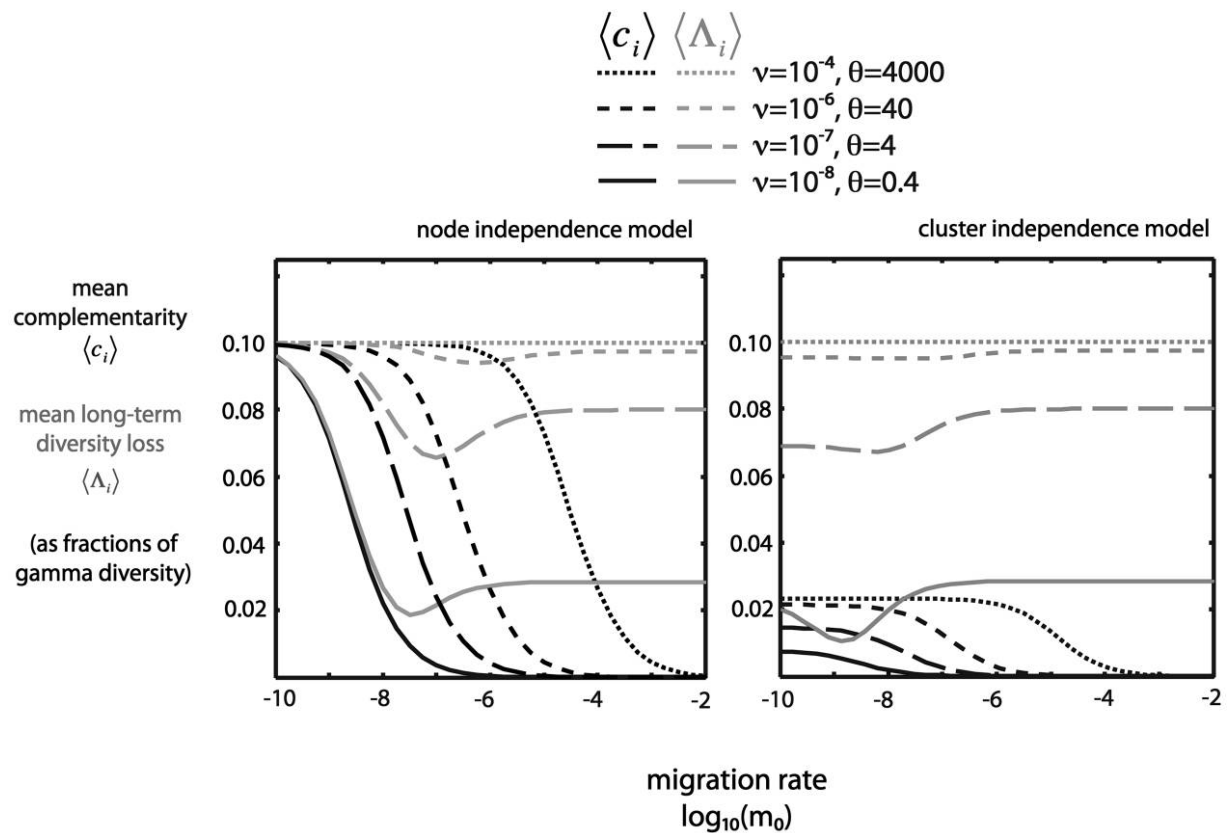


Figure 2: For the networks in figure 1, mean complementarity (black lines) across the metacommunity measures the average representation value of nodes and generally decreases with migration. Mean long-term diversity loss (gray lines), however, is decoupled from complementarity. To facilitate comparison across parameter values, both $\langle c_i \rangle$ and $\langle \Lambda_i \rangle$ were expressed as fractions of gamma diversity, as both scale with total diversity (and speciation rate). The fact that $\langle \Lambda_i \rangle$ remains near γ_0/n (here, 0.10 on the Y-axis because $n = 10$) shows diversity loss is proportional to the fraction of the metacommunity removed, although at low diversity (when θ is on the order of 1), a proportional loss is not possible because diversity is already near the minimum of one effective species (see text). Similar calculations for more parameter values are presented in the appendix.

is controlled to a very good approximation by the fundamental biodiversity parameter, as $\gamma_0 = \theta + 1 = 2N\nu + 1$ (Hubbell 2001; He and Hu 2005; Economo and Keitt 2008). Here N is the total number of individuals in the metacommunity, but from now on we use $N = N_k n$, where n is the number of nodes in the network and N_k is the (constant) local community size. Even if there is no dispersal limitation and the metacommunity is well mixed, the individuals could be arranged in space and, in this case, $\alpha = \gamma$ and $\beta = 0$. In a network context, this situation would arise when the entries of the migration matrix \mathbf{M} are all equal to $1/n$, where n is the number of equally sized nodes in the network. Here, removing a node has no apparent effect on gamma diversity because all of the gamma diversity is represented in every node, $\gamma_0 = \gamma_i = \alpha$, and the complementarity of each node is 0. However, the high alpha diversity observed in each node is

maintained solely because it is part of a greater panmictic metacommunity. Removing any node will change equilibrium gamma diversity because the total metacommunity size has changed and thus it will lower the diversity of all other nodes. The new gamma diversity is $\gamma'_i = \theta' + 1 = 2(n-1)N_k\nu + 1$, and the long-term diversity loss from removing node i is $\Lambda_i = \gamma_0 - \gamma'_i = 2N_k\nu$. This shows that in the absence of dispersal limitation, the biodiversity pattern (redundancy) observed on the landscape is entirely misleading for determining the effects of losing patches on biodiversity.

In the other extreme, when nodes are completely disconnected or the per-generation probability of migration ($1 - m_{ii}$) is much less than the probability of speciation (ν), each node becomes its own distinct community (maximal beta diversity), with a diversity as if it were its own well-mixed metacommunity: $\alpha_i = \theta_i + 1 = 2N_k\nu + 1$.

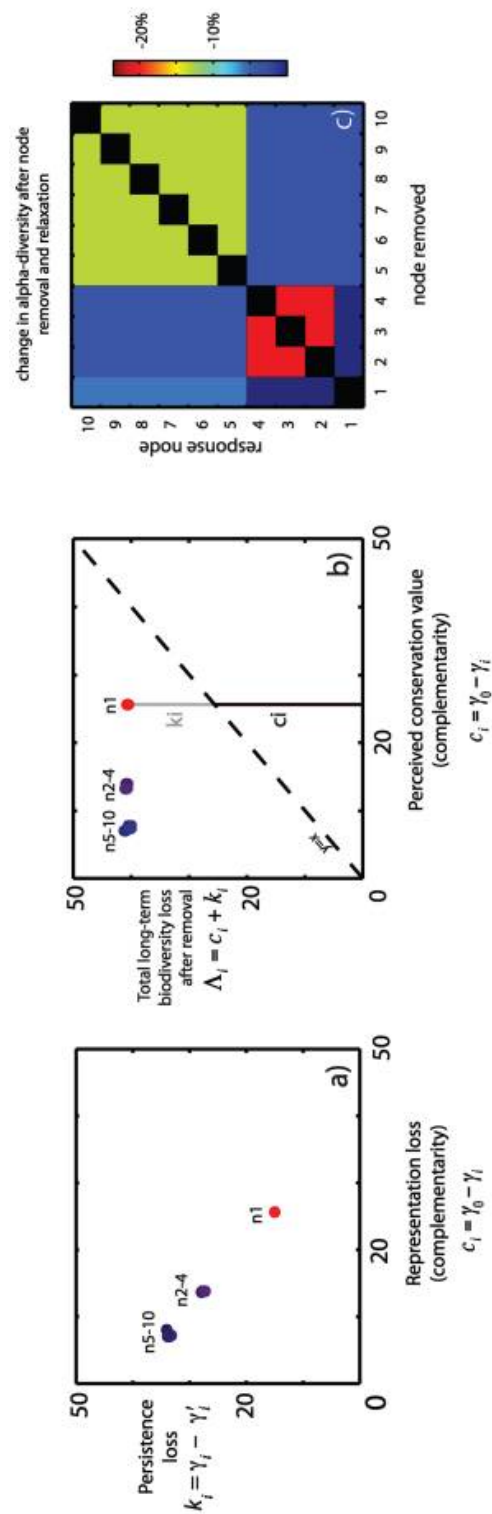


Figure 3: Biodiversity consequences of single-patch removals in the 10-node network (fig. 1a) for the parameter combination $\nu = 10^{-5}$, $m_0 = 10^{-4}$, and $N_k = 2,000,000$. a. There is a trade-off in the loss of biodiversity representation and subsequent loss of biodiversity persistence due to patch removal. A small random variation was added so that points are not completely overlapping. b. The perceived conservation value (equivalent to complementarity [c_i] and representation loss) varies across nodes even as long-term diversity loss (Λ_i) is relatively constant after reduction and relaxation to a new equilibrium. If complementarity accurately predicted value for long-term biodiversity maintenance, then the points would fall on the dashed line ($y = x$). c. This trade-off occurs because removing nodes from the large clusters (low c_i) results in a greater decrease in alpha diversity across other nodes. Here the color reflects the alpha diversity change in the node numbered on the Y-axis when the node on the X-axis is removed (node numbers correspond to numbers in fig. 1). Note that the loss of one node causes a reduction in diversity of γ_0/n (here, $\gamma_0 = 400$).

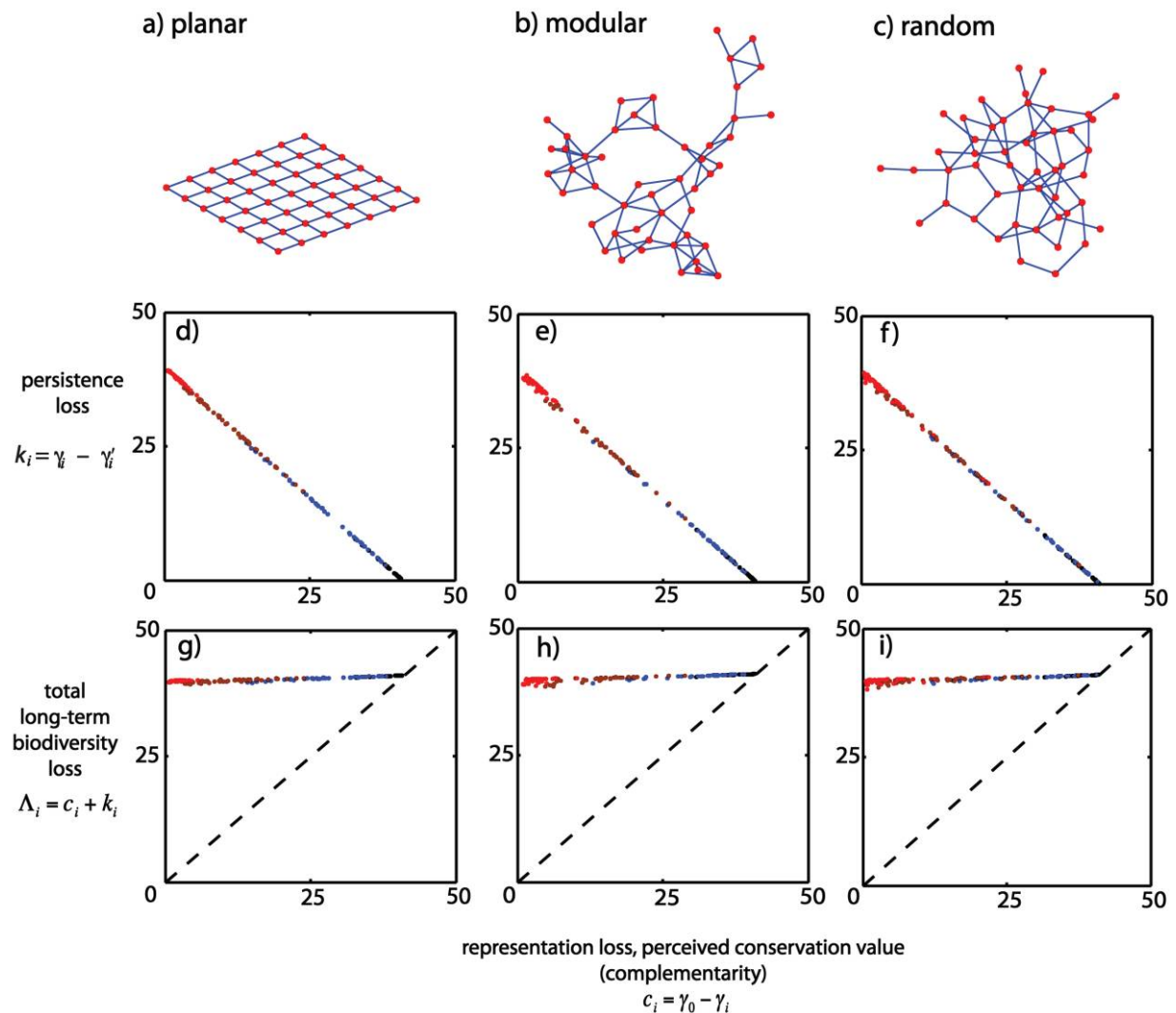


Figure 4: Biodiversity impacts of single-node removals in complex networks with different topologies (a–c) and variable link weights (see “Network Construction”). d–f, Nodes that are the most important for persistence are the least important for representation. Here m_0 varies in orders of 10 from black ($m_0 = 10^{-4}$) to blue to brown to red ($m_0 = 10^{-1}$), and points with the same color are from the same metacommunity. g–i, While there may be a good deal of variation in perceived conservation value (complementarity), there is very little variation in the effects of removing a community on total long-term biodiversity loss. In these examples, $\nu = 10^{-5}$ and $N_k = 2,000,000$, but similar plots with more parameter combinations are presented in figure A4.

The gamma diversity of the entire set of nodes is the sum of the diversity of individual nodes $\gamma_0 = n\alpha_i = n(2N_k\nu + 1)$ (diversities expressed in effective species numbers can be added if the communities are completely distinct). The complementarity is $c_i = \gamma_0 - \gamma_i = n(2N_k\nu + 1) - (n-1)(2N_k\nu + 1) = 2N_k\nu + 1$, and since removing a node has no secondary effects on other nodes, $c_i = \Lambda_i$. In this extreme, each node is as it appears: equally unique and important for maintaining gamma diversity of the landscape.

When comparing these two extreme cases, complemen-

tarity (c_i) is either 0 or $2N_k\nu + 1$ (which can also be written as 0 and γ_0/n), but the long-term effect on gamma diversity of removing a node (Λ_i) varies within a more modest range, either $2N_k\nu$ or $2N_k\nu + 1$ (or $\gamma_0/n - 1/n$ and γ_0/n). This suggests that biodiversity patterns are not predictive of diversity loss and that removing a node causes a proportional decrease in gamma diversity (at least when $2N_k\nu$ is not on the order of 1 or less; see more on that case below). When some groups of nodes are connected more strongly than others, due, for example, to their spatial arrangement or to the simple fact that groups of our

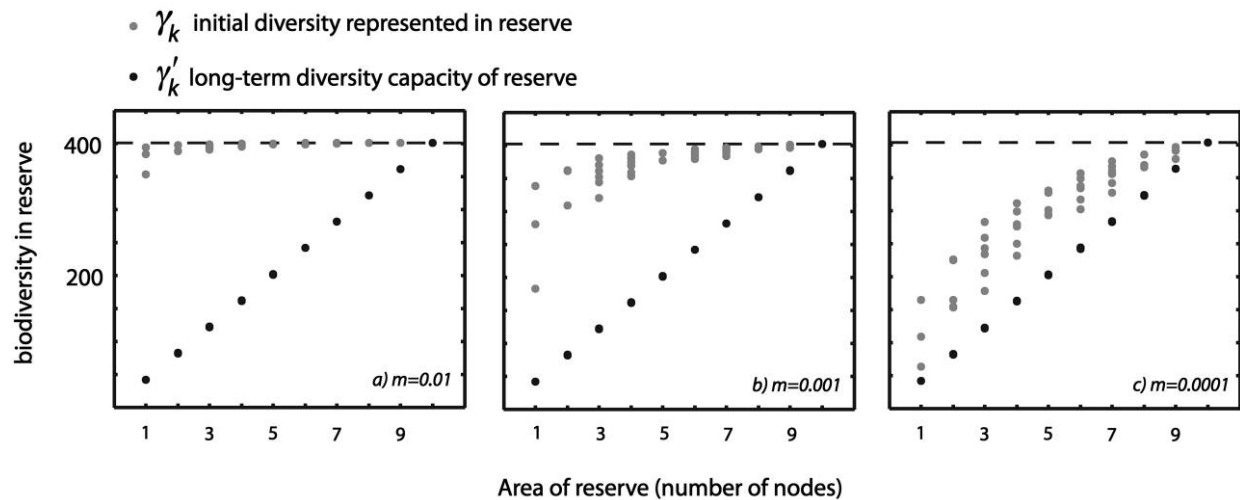


Figure 5: Biodiversity representation and persistence in reserves of different sizes. Initial diversity representation (gray circles) and diversity capacity at the new equilibrium (black circles) of all 1,022 possible subsets of the 10-node metacommunities in figure 2a plotted as a function of the number of nodes in the reserve, with migration rates increasing by an order of magnitude from *a* to *b* and from *b* to *c*. Diversity capacity is only a function of reserve area and not an initial representation of diversity; the black circles for a given area are superimposed on one another. Here, $\nu = 10^{-5}$ and $N_k = 2,000,000$.

equal-sized nodes could represent larger habitat units, complex patterns of alpha and beta diversity form. This could lead to certain areas receiving more conservation attention than others.

I examined biodiversity losses in the simple metacommunity depicted in figure 1 across a range of migration and speciation rates. As suggested by the argument above, for the node-independence model, the mean representation value of a single patch (mean complementarity across patches, $\langle c_i \rangle$) varies from $2N_k\nu + 1$ when each local community is distinct to 0 when migration is high, and it swamps any spatial structure (fig. 2). However, the mean long-term effects of losing a node on biodiversity ($\langle \Lambda_i \rangle$) are decoupled from complementarity and do not go to 0 at high migration. Moreover, $\langle \Lambda_i \rangle$ remains near $2N_k\nu$ or γ_0/n except when θ is on the order of 1, in which case it is reduced but still decoupled from complementarity (more on this case below). In the supplemental figures (appendix), I examine the same patterns for more parameter values, including variation in N_k (figs. A1, A3).

Figure 2 also depicts the same analyses for the cluster-independence model, and here the results are even more striking. Because in this case the clusters remain internally panmictic at low migration, the metacommunity never reaches the point where each node is distinct and mean patch complementarity is equal to γ_0/n . Yet, the cost of removing a node is again nearly constant at close to γ_0/n , except when metacommunity diversity is on the order of 1.

As mentioned above and as observed in figures 2 and A1–A3, when diversity is very low (θ on the order of 1 or less), Λ_i is reduced (as a fraction of gamma diversity) compared within more diverse metacommunities. While in most situations the removal of a node will cause a reduction in diversity of approximately γ_0/n , when metacommunity diversity is already near the minimum of 1, diversity cannot be further reduced and so removing a node necessarily will have little effect. For similar reasons, when migration and diversity are low in the node-independence model, complementarity does predict Λ_i (fig. 2). This occurs because a completely disconnected patch will always have at least one unique species to add to gamma diversity, while a cluster of connected patches may collectively support only a single shared species, and thus each is truly redundant because diversity cannot fall below 1 if the cluster is reduced (given the zero-sum assumption). However, this requires that the size of the patch be small enough and the speciation/colonization rate (ν) be low enough to support no diversity, yet migration between patches is $<\nu$ and the patch persists long enough in isolation for speciation/colonization to occur and reach equilibrium. Although this condition is important to note, this is one of the less biologically relevant regions of parameter space for this model, where the assumptions of zero-sum dynamics and neutral equilibrium will be strained. Furthermore, conservation problems dealing with one or a few spatially nonoverlapping species arranged in a landscape are probably not best addressed by

a neutral metacommunity model calculating equilibrium diversities.

It is helpful to examine more closely what is happening in the network for one of the parameter combinations ($\nu = 10^{-5}$, $m_0 = 10^{-4}$) that produces variation in complementarity in the node-independence model (fig. 1a). At initial equilibrium, communities in the smaller clusters (nodes 1–4) have the highest complementarity and nodes in the large cluster are more redundant: they share many species with other nearby nodes due to strong dispersal connections. In general, at neutral equilibrium, more isolated nodes have reduced alpha diversity and increased complementarity, while nodes that are highly connected to many others have high alpha diversity but low complementarity, as the node is colonized frequently but much of that diversity is shared across many other communities.

While removing nodes with high complementarity removes more uniqueness from that single patch (representation loss) than does removing a redundant node, the latter causes a greater persistence loss (fig. 3a). These effects compensate, and the diversity loss from node removal (Δ_i) is nearly constant even as complementarity varies (fig. 3b). This happens because removing a low-complementarity node causes a greater reduction in alpha diversity across many other nodes (fig. 3c).

To evaluate the generality of these results for larger and more complex networks, I examined the effects of node removals in several 49-node metacommunities with a variety of different network geometries (fig. 4). These networks all exhibit the same pattern as the smaller one: secondary effects compensate for complementarity such that ultimate biodiversity loss is similar across nodes. A broader exploration of parameter space for these networks is presented in figures A2 and A4.

This article is limited in scope to symmetric networks, where the connectivity (flow of individuals) into a node is similar to the outward connectivity of a node. Asymmetric networks (where dispersal in and out of nodes is unequal) produce complex-enough behavior that they deserve their own treatment. However, I can report that when there is asymmetric connectivity among nodes, removing different nodes has a much more variable effect on biodiversity change but there is also little consistent connection between representation and persistence.

Persistence in Reserve Networks

To examine these effects in groups of nodes, I considered how well initial diversity representation predicts the long-term diversity capacity of all 1,022 subsets (indexed by k) of the 10-node network (fig. 1a), which serve as model reserves. The secondary effects occur when the loss of habitat outside the reserve impacts diversity persistence

within the reserve. In this case, I calculate the diversity of a subset γ_k first when it is embedded within the initial metacommunity and then after the rest of the metacommunity is removed and the communities in the set relax to a new equilibrium γ'_k . Subsets of nodes (of equal area) that have a high complementarity will have greater representation and a higher γ_k . Again, regardless of the initial diversity in the reserve, the subset relaxes to an equilibrium diversity that is linearly dependent on subset size (fig. 5). When migration is high, small subsets of the metacommunity can represent nearly all of the gamma diversity in the metacommunity, but subsets with disproportionately high representation simply have a greater secondary loss of diversity. Within reserves of a given size, the connectivity of nodes and alpha and beta diversity levels may vary, but long-term diversity capacity is essentially constant. In general, when there is any significant connectivity in the community and diversity is at nontrivial levels, representation overestimates the diversity capacity of a subset of the metacommunity.

In summary, even in more complex scenarios, the effect of removing a single node varies between approximately $2N_k\nu$ and $2N_k\nu + 1$ even as complementarity varies between 0 and $2N_k\nu + 1$. This and the fact that groups of nodes have similar diversity capacity independently of initial biodiversity levels or spatial arrangements (fig. 5) indicate that metacommunity size primarily controls diversity levels. The fact that removing a certain fraction of individuals ($1/n$) from the metacommunity reduces diversity by nearly the same fraction (approximately γ_0/n) suggests that this relationship is linear. This accords with previous results that found that gamma diversity scales linearly with metacommunity size (Economo and Keitt 2008), independently of the internal connectivity structure of the metacommunity, which controls alpha and beta diversity. This also echoes results in population genetics that show that certain evolutionary quantities are invariant with geographic structure in neutral models (Nagylaki 1982). Thus, in the neutral case, the only situations where biodiversity patterns actually predict value for biodiversity maintenance are (1) where all patches are the same size and completely distinct and thus all equally required to maintain gamma diversity and (2) when metacommunity diversity is near the minimum of one effective species and removing a node cannot possibly reduce it much further.

Discussion

In a neutral metacommunity, the secondary effects of habitat loss work in direct opposition to the strategies of protecting unique communities and representing the most biodiversity in the smallest protected area. Communities with high connectivity to other patches develop high sim-

ilarity and thus appear to be redundant, but this apparent redundancy correlates with their importance in maintaining diversity across other patches. More isolated nodes have unique diversity within the patch, but removing them has a weaker effect on diversity persistence in other nodes in the network. Small subsets of the metacommunity may represent large proportions of total biodiversity due to high migration, but those subsets will simply experience a greater reduction in diversity after the rest of the habitat is lost. In other words, even in alpha diversity dominated landscapes, equilibrium gamma diversity is determined by metacommunity size (area), and thus seemingly identical communities are not redundant at all. If we consider again the Amazon basin, which is reducing in habitat area at a great pace, under neutrality we would expect that a loss of one-half of area will eventually result in a loss of one-half of gamma diversity, even if nearly all of the biodiversity were initially represented in the remaining area.

It is not an unusual result that more highly connected and central nodes are more important for maintaining persistence; this is commonly the case for metapopulations. In particular, these results are reminiscent of previous analyses that found that high-complementarity patches are concentrated in marginal areas of species ranges and/or in ecotones (Gaston et al. 2002), and thus they might be less important for maintaining species persistence due to source-sink or core-satellite dynamics for individual populations (Branch et al. 1995; Araújo and Williams 2001). However, the metacommunity approach used here includes the additional complication that species interact and compete for space or resources. Thus, one species' loss is another species' gain. In areas of low connectivity, individual species persist longer with more restricted ranges. Increasing connectivity does not increase long-term diversity maintenance of the landscape as a whole; it simply saves more alpha diversity at the expense of beta diversity. Thus, because representation and persistence are negatively correlated, there is no way to simultaneously prioritize for both other than by maximizing total protected area.

The secondary loss of diversity may not occur quickly after habitat fragmentation, with the relevant timescales depending on parameters such as speciation rates, generation times, and community sizes. This implies that there could be a significant extinction debt (Tilman et al. 1994) looming in already fragmented areas such as conservation hotspots (Myers et al. 2000), although diversity is reduced in this case because of increased extinction and a loss of speciation rate (Rosenzweig 2001). All else being equal, it might be better to preserve complementary patches over more redundant patches simply because the secondary effects (persistence losses) take some time to work through the system whereas the diversity loss from a highly com-

plementary patch happens immediately. Still, this reasoning begins to break down when one chooses between two areas of different size, as is often the case, because the areas will have different equilibrium diversities that would need to be examined. In general, if timescales of habitat change are faster than the time in which a community can reach equilibrium, conservation strategies must consider transient dynamics in addition to equilibria. An interesting extension to the current analysis would be to explicitly model both nonequilibrium landscape dynamics—for example, a given spatiotemporal pattern of future habitat contractions and expansions—and the resulting nonequilibrium changes in diversity.

It is instructive to ask why the neutral theory exhibits this conflict between representation and persistence and whether it is likely to depend on its most controversial aspect, the ecological equivalence of species. The key dynamic is that dispersal and colonization maintain local diversity at a much higher level than a locality could otherwise support. At the same time, that high connectivity homogenizes the local community with many other nodes, reducing its perceived conservation value, the complementarity. Removing a connected node leads to extinction of widespread species that are persisting tenuously as metapopulations in this high connectivity area, and thus the conservation value of the node is related to not only what uniqueness occurs there but also its contribution to the diversity of other patches.

This reasoning does not rely on ecological equivalence, but given the complexity of possible species interactions and differences, it is simply a useful starting point that now provides a baseline for more complicated theoretical investigation. It is unknown how departures from some of the assumptions will affect the results, and there is not a single niche-based foil to compare with neutral theory but rather a suite of different models emphasizing different processes. I speculate that the conflict between representation and persistence will hold with varying degrees for a range of nonneutral metacommunity models, when dispersal limitation and variation in patch isolation and not environmental heterogeneity produce differences in site complementarity. The challenge for experimental and theoretical metacommunity ecology is to seek generality across this vast theoretical space, which can be useful as a guide for conservation biology.

Even if, as these results suggest, biodiversity pattern-based conservation approaches do not work well at all in a neutral metacommunity, it certainly does not follow that complementarity-based approaches to conservation planning should be abandoned. If beta diversity in a landscape is due to environmental heterogeneity and not dispersal limitation (and it often is), ignoring complementarity would be misguided. However, if neutral theory reflects

one extreme in a continuum of possible metacommunity dynamics, many conservation analyses still depend on another extreme where biodiversity patterns are determined solely by intrinsic properties of a locality independent of spatial context.

This analysis suggests that when dispersal limitation drives spatial patterns of alpha and beta diversity, biodiversity may be in much greater peril than is currently recognized and our strategies for conserving it may be ineffective. An urgent task for ecological theory is to link observable biodiversity patterns to the biological dynamics generating them and use that light to reconcile our conservation strategies with community processes.

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