

LETTER

Species diversity in neutral metacommunities: a network approach

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Abstract

Biologists seek an understanding of the processes underlying spatial biodiversity patterns. Neutral theory links those patterns to dispersal, speciation and community drift. Here, we advance the spatially explicit neutral model by representing the metacommunity as a network of smaller communities. Analytic theory is presented for a set of equilibrium diversity patterns in networks of communities, facilitating the exploration of parameter space not accessible by simulation. We use this theory to evaluate how the basic properties of a metacommunity – connectivity, size, and speciation rate – determine overall metacommunity γ -diversity, and how that is partitioned into α - and β -components. We find spatial structure can increase γ -diversity relative to a well-mixed model, even when θ is held constant. The magnitude of deviations from the well-mixed model and the partitioning into α - and β -diversity is related to the ratio of migration and speciation rates. γ -diversity scales linearly with metacommunity size even as α - and β -diversity scale nonlinearly with size.

Keywords

β -Diversity, biodiversity scaling, diversity partitioning, island biogeography, metacommunities, neutral theory, patch networks.

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INTRODUCTION

Understanding variation in species diversity and community composition is a central problem in biology (Brown 1995; Rosenzweig 1995). Neutral ecological theory links biodiversity pattern to an elementary set of ecological and evolutionary processes (Hubbell 2001). Despite this simplicity, the theory holds promise for generating a set of baseline expectations, and serves as a useful touchstone for building more complex theory (Alonso *et al.* 2006). Recent work has extended several dimensions of the model including the mechanism of speciation (Hubbell 2005; Etienne *et al.* 2007b; Mouillot & Gaston 2007), the density dependence of population dynamics (Volkov *et al.* 2005), the zero-sum assumption (Etienne *et al.* 2007a), among others (Chave 2004). Here, we focus on the model of space underlying the theory, moving beyond simple spatial templates to develop theoretical results for metacommunities with more complex structure.

The neutral perspective views diversity as an outcome of stochastic speciation, migration and ecological drift caused by birth–death dynamics of individuals. This occurs in a spatial context where a local community receives migrants

from a metacommunity (Hubbell 2001). Various implementations of this general idea can be found in the literature, focusing on different aspects of neutral pattern (Chave 2004; McGill *et al.* 2006). McGill *et al.* (2006) classify neutral metacommunity models as either *spatially implicit*, where the local community draws migrants from a separate pool of individuals, or *spatially explicit*, where the metacommunity is an actual set of local communities with connections among them. The degree to which the behaviour of a truly spatially explicit metacommunity deviates from the spatially implicit model is an open question. A somewhat different definition for spatially explicit is used in the broader metacommunity literature, for example by Leibold *et al.* (2004): ‘A model in which the arrangement of patches or distance between patches can influence patterns of movement or interaction.’ The theoretical approach we present is spatially explicit according to both definitions.

Spatially explicit neutral models have been explored with stochastic simulation and with analytic theory (Durrett & Levin 1996; Bell 2000; Hubbell 2001; Chave & Leigh 2002; Chave *et al.* 2002; Houchmandzadeh & Vallade 2003; McGill *et al.* 2005; Zillio *et al.* 2005; Rosindell & Cornell 2007). However, little attention has been paid to how the

internal structure of spatially explicit metacommunities determines equilibrium spatial patterns under neutrality. As neutral theory emphasizes the role of dispersal limitation, the number and strengths of connections a local community has with other communities will influence patterns of species diversity and similarity. Beyond these primary connections, the position of a community in the broader metacommunity may have a cascading influence on the local community.

Most spatially explicit applications of neutral theory have been focused on two dimensional continuous habitats, some specifically inspired by spatially extended lowland forest communities (Chave & Leigh 2002). While this is a logical approach for metacommunities extended in continuous space, many real metacommunities are characterized by discontinuous, or patchy internal structure. Habitats can be distributed unevenly in space from landscape-level scales to the largest scales, their distribution on and among continents. Network theory is a versatile framework for representing these complex structures, where habitat patches, islands, or even continents, are nodes in a graph, and edges represent some rate of individual movement. Network tools are commonly used in landscape ecology (Urban & Keitt 2001), metapopulation ecology (Hanski 1999), and a variety of other fields where a set of units has heterogeneous connections among them (Albert & Barabási 2002).

The present study examines how the network structure of metacommunities determines patterns of diversity and similarity among individual communities undergoing ecological drift, speciation and dispersal. Central to the neutral theory are stochastic biological rates interacting with spatial constraints, and while spatial complexity complicates neutral expectations, it also provides an opportunity to make use of spatial pattern to discriminate neutral processes from competing ideas in ecology. Neutral pattern should respond to the structure of island archipelagoes and the shape of domain boundaries – the geographic structure of the metacommunity.

We develop analytical theory which predicts equilibrium diversity patterns within and among localities in metacommunities with a diverse set of spatial structures. Following previous spatially explicit theory (Chave & Leigh 2002), we borrow tools from population genetics and derive spatially explicit predictions for a family of diversity indices based on the Simpson concentration (Simpson 1949). By connecting this approach to network theory, we facilitate the investigation of a broad set of questions about neutral diversity patterns in structured geographies.

In this paper, we focus on a basic question about spatially explicit metacommunities; how the broad scale structure of the network controls patterns of α -, β - and γ -diversity. Using a well-mixed metacommunity as a benchmark, we

investigate the effects of spatial structure on overall metacommunity γ -diversity. Metacommunity diversity can be partitioned into within α -community components and among β -community components (Whittaker 1972; Lande 1996; Magurran 2004). We investigate how the basic components of the model – connectivity, speciation, and metacommunity size – determine spatial pattern under neutrality.

THEORY: NEUTRAL BIODIVERSITY PATTERN IN A NETWORK OF COMMUNITIES

The resemblance, if not identity, of ecological neutral theory to the more mathematically mature neutral theory of population genetics (Kimura 1983) allows concepts and quantitative tools from the latter to be adapted by ecologists. Indeed much of the extant ecological neutral theory has been inspired at least in part by population genetics (Hubbell 2001; Chave 2004; Hu *et al.* 2006). Here, we follow a mathematical approach used in population genetics and based on the concept of probability of identity to derive novel theory for species diversity in networks of communities.

A common construction of neutral theory assumes point speciation, with new species arising randomly as one individual, with zero-sum stochastic community dynamics. This model maps on exactly to the infinite alleles model of population genetics (Kimura & Crow 1964; Hubbell 2001). A useful concept in population genetics is the *probability of identity in state* of two alleles chosen from a population. In this model, two alleles are identical in state if – looking backwards in time – their lineages coalesce into a common ancestor before a mutation has occurred in either lineage. This probability depends on both the *coalescence time*, how far back in time existed most recent common ancestor, and the rate at which mutations accumulate on the lineages. Coalescence times will normally be dependent on population sizes, migration rates and the spatial separation of the sampled alleles, as the lineages have to move to the same location before coalescing (Hudson 1991).

Identity probabilities underlie population genetics statistics describing patterns of genetic diversity (Nei 1987). Interestingly, we can convert these into diversity statistics that are traditionally used by ecologists, a connection that has been made before in the context of neutral theory (Chave & Leigh 2002; Condit *et al.* 2002; Etienne 2005; He & Hu 2005; Hu *et al.* 2006). The Simpson concentration, by definition, is the probability that two individuals chosen at random from a set are the same type (Simpson 1949). In ecology, this is applied to individuals chosen from a community (Magurran 2004) and is usually calculated directly from the set of species frequencies. Therefore to the extent that genetic models map on to ecological models,

theory for allelic probabilities of identity in state also mechanistically predict community diversity. We develop this further and show how a host of metrics describing diversity patterns in metacommunity with network structure can be analytically found using population genetics theory.

Neutral ecological dynamics in a network of communities correspond to *migration matrix* models (Bodmer & Cavalli-Sforza 1968) in population genetics. In this representation, a network of n local populations is represented by a stochastic backward migration matrix (M). Each m_{ij} reflects the fraction of individuals in a given subpopulation i that originated from a parent in subpopulation j in the previous generation, and $\sum_j m_{ij} = 1$. Edge weights m_{ij} , and local population sizes N can vary to capture the underlying spatial structure of the metacommunity. In the following derivation, directed networks (matrices where some $m_{ij} \neq m_{ji}$) are permitted but descendants of individuals in each node must be able to eventually reach every other node ($m_{ii} \neq 1$). Speciation rate v takes the place of mutation, and reflects the per generation probability of change in state of a single individual.

The *probability of identity in state* (f_{ij}) for alleles sampled from communities i and j under the infinite alleles model can be calculated with a recursive equation originally discovered by Malécot (1951, 1970, and developed extensively by later authors (Nagylaki 1980; Nagylaki 1982; Laporte & Charlesworth 2002) The equation for the probability of identity in state f'_{ij} in the current generation in terms of the set of f_{ij} in the previous generation can be written as a recursion:

$$f'_{ij} = (1 - v)^2 \left[\sum_{k,l} m_{ik}m_{jl}f_{kl} + \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right) (1 - f_{kk}) \right] \tag{1}$$

where k and l index over all n nodes. This converges to an equilibrium (Nagylaki 1980):

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

We rearrange this equation to the form:

$$\hat{f}_{ij} = (1 - v)^2 \left[\sum_{k,l,k \neq l} m_{ik}m_{jl}\hat{f}_{kl} + \sum_k m_{ik}m_{jk} \left(1 - \frac{1}{N_k} \right) \hat{f}_{kk} + \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right) \right] \tag{3}$$

Two sampled alleles are the same type if neither has mutated since the previous generation (the first term), and (i) they were from parents of the same type from different patches (the first summation) or (ii) they were from different parents

of the same type located in the same patch (second summation), or (iii) they had the same parent (coalesced) in the previous generation (third summation).

Equation (3) is linear and may be further rearranged and written in the form:

$$(1 - v)^{-2} \hat{f}_{ij} - \sum_{k,l} m_{ik}m_{jl}\hat{f}_{kl} + \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right) \hat{f}_{kk} = \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right). \tag{4}$$

For a network of n nodes, there are n^2 (i, j) pairs, and thus n^2 linear equations in this form describe the system at equilibrium. As there are n^2 unknowns in n^2 equations, the system can be solved for the vector \vec{f} of all \hat{f}_{ij} . For the analyses in this paper, we coded the left side of eqn (4) as a $n^2 \times n^2$ matrix X , and the right side as a vector \vec{q} of length n^2 , where

$$X_{(ij),(kl)} = (1 - v)^{-2} \delta_{(ij),(kl)} - m_{ik}m_{jl} + \delta_{k,l} m_{ik}m_{jk} \left(\frac{1}{N_k} \right) \tag{5}$$

$$q_{(ij)} = \sum_k m_{ik}m_{jk} \left(\frac{1}{N_k} \right) \tag{6}$$

and where δ_{ij} is the Kronecker delta ($\delta_{ij} = 1$ when $i = j$ and $\delta_{ij} = 0$ otherwise), and solved the formula $X\vec{f} = \vec{q}$ for \vec{f} with MATLAB. Migration and speciation rates as well as local community sizes can take on any value without loss of computational efficiency. This allows the exploration of large regions of parameter space inaccessible to simulation. The limitations are mainly in the number of nodes n in the network; as the matrix of length n^2 must be computationally tractable. However, if most nodes in the network are connected to a relatively small number of other nodes (likely a common biological situation) large networks can be computed with sparse matrix methods. In this paper, we used sparse matrix routines for networks with > 30 nodes.

The set of all \hat{f}_{ij} represent the probability two individuals, randomly chosen from within local patches i and j at any locations in the network, are identical in state. In terms of the neutral ecological model, it is the equilibrium probability they are the same species. From these values, we can calculate a number of diversity metrics of ecological interest for the local and metacommunity.

α -diversity

As discussed before, f_{ii} is equivalent to the Simpson concentration λ or a local community i . In population genetics, this is also related to the heterozygosity ($1 - f_{ii}$) of a population. This can be written as Simpson's diversity index α_i :

$$\alpha_i = 1 - f_{ii}. \tag{7}$$

For many purposes such as diversity partitioning, a raw Simpson's index is undesirable as a measure of α -diversity as it converges to one as diversity increases unbounded, with highly misleading behaviour (Jost 2006). The index can be linearized by converting to an *effective number of species* or Hill number (Hill 1973), which is the species richness that would produce a given Simpson's index if all species abundances were equal:

$$D(\alpha_i) = f_{ii}^{-1}. \quad (8)$$

The average α -diversity expressed as Simpson's index and as an effective number of species over the whole metacommunity are:

$$\alpha_M = (1 - \bar{f}_{kk}) \quad (9)$$

$$D(\alpha_M) = (\bar{f}_{kk})^{-1} \quad (10)$$

where both averages are taken over all k .

γ -diversity

Metacommunity diversity, or γ -diversity, can be calculated with similar averages. Averaging the whole f_{ij} vector gives the Simpson concentration for the metacommunity, which can be used to give the Simpson's index and effective number of species for the whole metacommunity:

$$\gamma = 1 - \bar{f}_{ij}, \quad (11)$$

$$D(\gamma) = (\bar{f}_{ij})^{-1} \quad (12)$$

where both are averaged over all (i,j) pairs.

β -diversity

β -Diversity, broadly speaking the component of diversity reflected in differences among locations or samples, can also be calculated using the Malécot equation. γ -diversity can be partitioned into independent α - and β -components with multiplicative (Whittaker 1972) or additive (Lande 1996) methods. Given the scaling problems of using raw Simpson diversity indices, we can partition total metacommunity (gamma) diversity into α - and β -components in terms of Hill numbers. There is one caveat, problems of concavity arise when calculating metacommunity-wide (but not node specific) figures for α -, β - and γ -diversity based on Simpson's index when community weights are unequal (e.g. when local community sizes are variable, see Jost (2006) for further discussion). This paper will consider only networks where nodes are the same size.

Multiplicative partition

An *effective number of communities*, the number of distinct communities with the average α -diversity needed to account for overall γ -diversity, can be calculated as follows. In

panmixia, this is 1, if all communities are distinct, this is n , the number of local communities:

$$C_e = \frac{D(\gamma)}{D(\alpha_M)} = \frac{\bar{f}_{ij}}{\bar{f}_{kk}} \quad (13)$$

where averages are taken over all i, j and k nodes.

Additive partition

Additive partitioning calculates a β -diversity value in the same units as α - and γ -diversity. The average effective number of species in a local site (α) and effective number of species of the metacommunity (γ) can be used to back calculate the β -contribution.

$$D(\beta) = D(\gamma) - D(\alpha) = (\bar{f}_{ij})^{-1} - (\bar{f}_{kk})^{-1} \quad (14)$$

Pairwise similarity

Similarity of two local communities i and j can be described with the Morisita–Horn index of overlap (Horn 1966):

$$MH_{ij} = \frac{2f_{ij}}{(f_{ii} + f_{jj})} \quad (15)$$

ANALYSIS AND RESULTS

The theory described in the previous section can be used to investigate equilibrium diversity patterns generated by neutral processes in complex habitat networks much more quickly than simulation methods for large area of parameter space. In the rest of this paper, we solve eqn (3) under various conditions to explore how the basic dimensions of the model, migration rate, network topology, speciation rate and network size, drive α -, β - and γ -diversity patterns in spatially explicit metacommunities. We focus on spatial structure on the scale of the metacommunity, or more specifically divisions that break the metacommunity into tens or hundreds of units, rather than fine scale patchiness.

Both migration rate and network topology contribute to connectivity, an important driver of dynamics in landscape (Brooks 2003), metapopulation (Hanski 1999) and metacommunity ecology (Leibold *et al.* 2004). The exchange rates among communities can have variable effects on community diversity depending on the underlying model of community dynamics assumed (Mouquet & Loreau 2002, 2003; Cadotte 2006).

Network connectivity can be a local property reflecting how connected a given node is to other nodes, or a global statistic characterizing the structure of a network. The former corresponds to the biogeographic concept of patch or island isolation while the latter refers to a landscape or metacommunity level property. In this paper, we focus on the latter, network-level connectivity, and how it determines

diversity patterns as measured by standard α -, β - and γ -diversity concepts.

Migration rate

In the spatially implicit model, the diversity of a panmictic metacommunity is controlled by the fundamental biodiversity parameter $\theta = 2\nu N_m$, while the diversity of a local community is controlled by θ , the local community size, and the migration rate into the local community (Etienne 2005). A basic question about the spatially explicit model is how structuring the metacommunity by restricting dispersal affects overall metacommunity γ -diversity. In addition, we seek to establish what determines the partitioning of that γ -diversity into within α -community components and among β -community components. For the purposes of this analysis, we use additive partitioning methods (eqns 10, 12, 14).

We consider the effect of restricting migration rates (mathematically represented by edge weights – values of the M matrix) on diversity patterns in two test networks representing topological extremes: a linear chain of communities (Fig. 1a), and a network where every node is connected to every other node. The latter network corresponds to the island model of population genetics, and we refer to it as the island graph (Fig. 1b).

Equilibrium diversity levels were calculated for networks of 20 local communities with a local community size of 20 000 individuals and a range of m values (1×10^{-7} – 1×10^{-2}). All edges m_{ij} in the network were set to equal weight. Figure 2

plots the results for a range of theta values on the two networks. The diversities are additively partitioned and presented in terms of effective number of species (eqns 10, 12, 14).

We find γ -diversity always decreases monotonically with increasing migration rate (edge weight). The relative magnitude of the decrease is also a function of the diversity parameter θ , with the spatial effect having a greater relative impact on metacommunities with substantial dispersal limitation (low m_{ij} values). This can be understood straightforwardly by examining the mathematics of diversity in a well-mixed metacommunity. The Simpson's index of a well-mixed metacommunity is, to a very good approximation (Kimura & Crow 1964; Hubbell 2001; He & Hu 2005):

$$\gamma = \frac{\theta}{\theta + 1}, \quad (16)$$

which can be converted to an effective number of species,

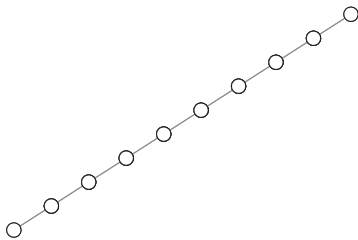
$$D(\gamma) = \theta + 1 = 2N_m\nu + 1. \quad (17)$$

Now consider if this metacommunity were split into a set of n smaller communities, each with size N_m/n and no migration among them. The effective number of species of such a system would be:

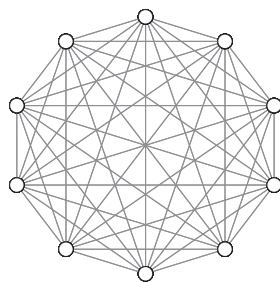
$$D(\gamma) = n \left(2 \frac{N_m}{n} \nu + 1 \right). \quad (18)$$

Subtracting eqn (17) from eqn (18), we find the difference in γ -diversity in the limit of no migration is $n - 1$ effective species. As migration is increased and the metacommunity

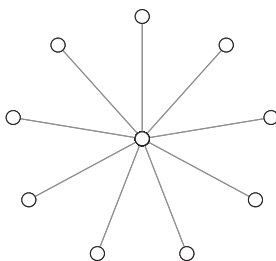
(a) Chain



(b) Island



(c) Star



(d) Random

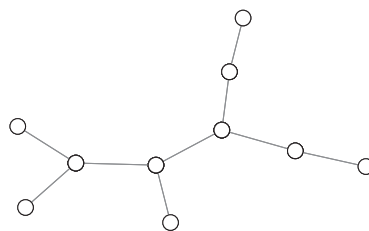


Figure 1 Network topologies appearing in this paper, (a) chain graph, (b) island graph, (c) star graph, (d) randomly assembled network. The networks used in the analyses have more nodes than those shown here, but have the same basic structure. The random graph is generated by arbitrarily connecting nodes but limiting the number of edges in the network.

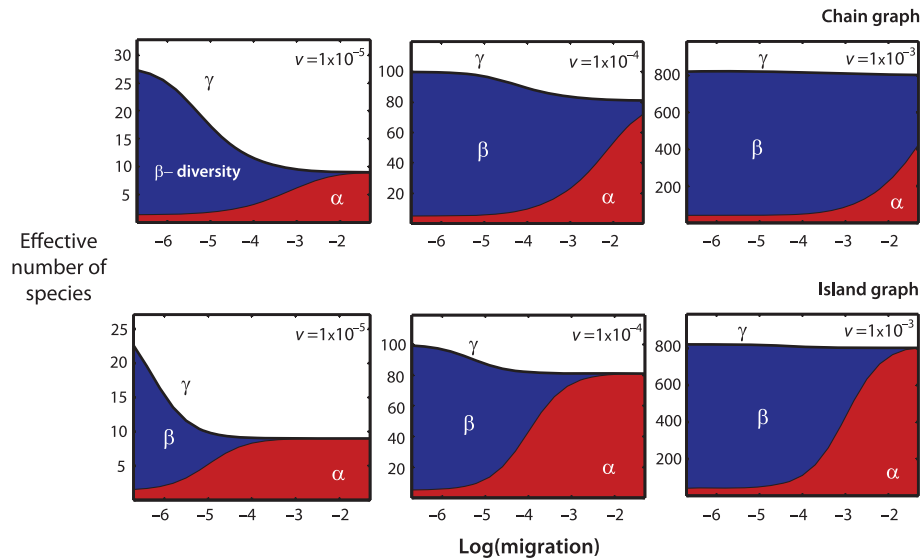


Figure 2 γ -diversity (black line), partitioned additively into α -diversity (red) and β -diversity (blue) in a network of 20 nodes plotted as a function of migration rate. The plots represent the equilibrium solution calculated using eqns 10, 12, 14, over a range of migration values (2×10^{-7} – 5×10^{-2}) and theta (8, 80 and 800). Individual node sizes were set to 20 000 individuals and not varied, theta was tuned by varying speciation rate (v). Notice γ -diversity converges to $\theta + 1$ as migration increases. Each edge in the network was set to the same migration value for a given calculation. The top row is for a network with chain structure, and the bottom row island structure (see Fig. 1). Notice γ -diversity converges to $\theta + 1$ as migration increases.

becomes more and more panmictic, this effect reduces to zero.

The implications are that for systems where the total expected effective number of species is much higher than the number of patches ($\theta + 1 \gg n - 1$), the degree of spatial isolation of those patches will have little relative – but a similar absolute – effect on γ -diversity. If the effective number of species in the metacommunity is small compared with the number of patches ($\theta + 1 \ll n - 1$), then spatial division can have a relatively large effect.

Metacommunity γ -diversity can be additively partitioned into within α -community components and among β -community components, as is represented in Fig. 2. Intuitively, higher migration rates among communities increases α -diversity at the expense of β -diversity, which can result in a profound increase in local diversity when migration is high. This is consistent with previous results highlighting the role of immigration in local diversity maintenance (MacArthur & Wilson 1967; Loreau & Mouquet 1999; Hubbell 2001). In terms of coalescence, as migration probabilities become larger, the distribution of coalescence times between individuals chosen from different communities becomes more similar to the distribution of times chosen from the same community.

Network topology

Even when the strengths and number of connections are held constant, the geometry of connections can have a

significant effect on the distance between nodes and the spread of information on a network (Watts & Strogatz 1998; Albert & Barabási 2002). To investigate this effect on diversity patterns, we hold migration rates and number of links constant while changing the architecture of the network. We consider three graphs with markedly different topologies, a linear chain graph, a randomly assembled graph, and a star graph (Fig. 1). The point of interest here is that for different topologies, node pairs are on average more or less isolated from each other, even when the total number and strengths of links are held constant. In other words, more or fewer intermediate nodes/edges must be traversed to travel between two randomly chosen nodes. Longer path length between two communities implies longer coalescence times between lineages chosen from those two communities, as lineages must move to the same patch before coalescing.

The chain and star graphs (Fig. 1) represent extremes in topological connectivity, in that a chain has relatively long path lengths and a star graph – where nodes are at most two links away no matter the network size – has short paths. As an intermediate case, we generate random graphs by haphazardly connecting nodes, while constraining the network to have a given number of edges (in this case $n - 1$) and every node reachable by some path from every other node. This generates graphs with tree-like structure (Fig. 1d).

We considered networks with 100 local communities of 20 000 individuals, and 99 edges total. Larger networks are

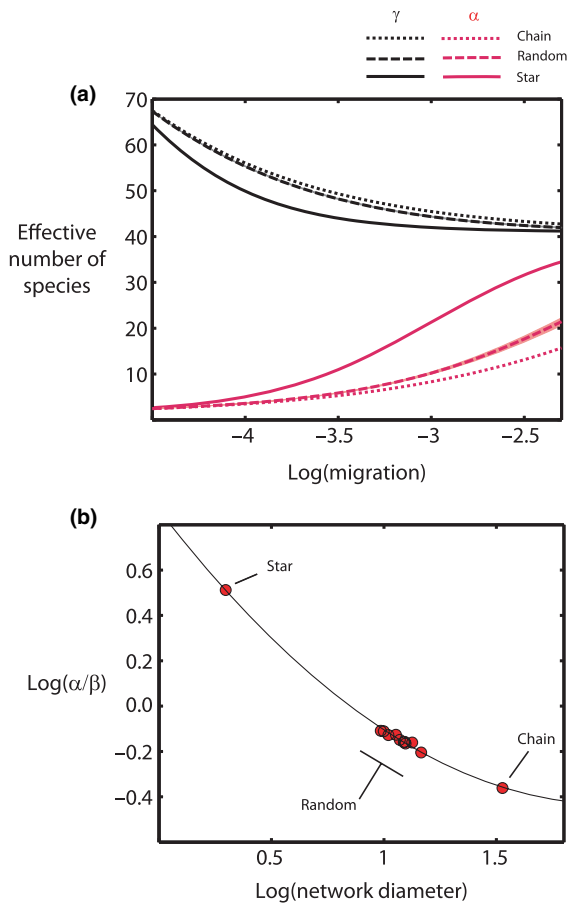


Figure 3 (a) The effect of network topology on diversity patterns is demonstrated by examining the diversity levels on networks with otherwise similar parameter values (100 nodes, 99 links, $\nu = 1 \times 10^{-5}$, local pop. sizes = 20 000). α -diversity (red) and γ -diversity (black) in metacommunities with star, chain, or random topologies, are plotted for a range of migration rates. Values for the random network line are averages of 10 different networks, and the pink/grey shading reflects standard deviations. The difference between the black and red lines is β -diversity using an additive definition. (b) $\log(\alpha/\beta)$, an index of geographic differentiation, plotted as a function of network diameter (average minimum path length between all pairs of nodes) for the networks and parameter values considered in Fig. 3a, with $\log(\text{migration})$ set to -2.5 . The curve is a quadratic fitted for visualization purposes.

used than in Fig. 2, as topological differences of small networks will have little variation in path lengths. In general, we expect the larger the network, the more topological variation will affect have consequences for diversity pattern. Figure 3a demonstrates the effect of different network topologies on diversity patterns in a metacommunity. The plot is structurally similar to those in Fig. 2 but represents several networks simultaneously. α -diversity (red) is highest for a given migration rate in the networks with shorter path lengths (star, random) and lowest in the chain graph. For

higher migration rates, the difference is pronounced. The effect is not as dramatic as the migration parameter itself – for networks of this size – but it underscores the importance of metacommunity geometry in diversity patterns, something impossible to capture in a spatially implicit model.

These topological differences can be measured with network statistics such as network diameter, which is variably defined in the literature as either the minimum distance between the furthest nodes, or the average minimum distance between two nodes, averaged over all node pairs (Albert & Barabási 2002; Amaral *et al.* 2005). We used the latter definition and calculated diameter for the networks considered in Fig. 3a, and find that networks with longer diameters have a greater allocation of diversity into the β -component (Fig. 3b). This appears a promising direction and further work is needed to investigate the quantitative relationship between diameter and other network statistics with diversity patterns across a broader range of network types. An open question is the extent to which such statistics can substitute for direct modelling of neutral dynamics.

Speciation rate (ν)

In the spatially implicit metacommunity, γ -diversity (in effective numbers of species) scales approximately linearly with speciation rate because of eqn (17). We investigate whether that scaling holds for metacommunities with internal dispersal limitation. Considering a chain graph identical to the one considered in Fig. 2, we held migration rates constant and varied speciation rate to examine its scaling with overall γ -diversity. The relationship between speciation rate and γ -diversity is found to deviate from the spatially implicit model (again by as many as $n - 1$ effective species), with a strong interaction effect with migration rate. Note we are using eqn (4) and not eqn (17), which is an approximation, to generate predictions for the well-mixed model. Considering migration and speciation together in Fig. 4a, we find that the deviations vary between zero and $n - 1$ and are related to the ratio of migration to speciation m/ν . This result is qualitatively robust to different network structures (island vs. chain, varying network size), but differ in quantitative details such as the actual values of m/ν that lead to a deviation of a certain magnitude.

Aside from the strong effect on γ -diversity, speciation rates have consequences for the allocation of diversity into among (β)- and within (α)-site components. Intuitively, higher speciation rates can be expected to promote geographic differentiation, with migration as an opposing, homogenizing force. Figure 2 demonstrates the control of migration rates on the tradeoff between α - and β -diversity, with local diversity making up increasing fraction of the total metacommunity diversity as migration rates are elevated.

Comparing panels in Fig. 2, it is clear that the transition from β - to α -diversity occurs at a higher migration rate when speciation rates are higher.

The joint effect of migration and speciation rate on differentiation can be considered on a chain graph ($n = 20$, local population sizes = 20 000), shown in Fig. 4b. The isoclines for a metric geographic differentiation $\log(\alpha/\beta)$, are parallel and with a slope of 1. This implies the ratio m/v is the relevant quantity with respect to the tradeoff between α - and β -diversity, when network size and topology are held constant. When m/v is large, α -diversity dominates, and β when m/v is small. Again, while m/v controls $\log(\alpha/\beta)$ for a given metacommunity structure (link structure and population sizes), different networks with the same m/v may differ in their allocation of diversity into α - and β -components.

Interestingly, we do not find the product of local population size and migration rate ($N.m$) being greater or less than one to have a strong effect on geographic differentiation, *per se*, after holding m/v constant (Fig. S1). This is in contrast to the commonly cited connection between $N.m$ and F_{ST} taken from analysis of the island model, although clearly the relationship is more complex when idealized assumptions are violated (Wilkinson-Herbots 1998; Whitlock & McCauley 1999). We do note that one of the assumptions from the $N.m$ result is that speciation (mutation) is weak compared with migration rates. If $N.m < 1$, then $N.v$ must be at least several orders of magnitude below 1. As metacommunity diversity is generally controlled by theta, and $\theta = 2nN.v$, n must be in the hundreds or thousands to recover a theta on the order of 1. So for subcommunities that are a significant fraction of the metacommunity (on the order of tens and hundreds), it is unlikely that a metacommunity would support much

diversity to differentiate if $N.m < 1$ and $m \gg v$. We limit the scope of our conclusions to the population structures and diversity statistics explored here, and emphasize the need for further examination of the issue.

Metacommunity size (N_m)

The number of individuals in a metacommunity is expected to directly control equilibrium diversity under neutrality. In the spatially implicit model, this relationship is linear because of the eqn (17). As we have demonstrated, diversity in spatially explicit metacommunities has a more complex relationship with migration and speciation rate than in the spatially implicit model. This is apparently not the case for network size. We grow metacommunities both by increasing the number of individuals in each subcommunity, and by increasing the number of nodes in the network, holding migration and speciation rates constant. Fig. 5a shows α -, β - and γ -diversity in a chain graph of 20 nodes, as local community size is varied between a range of 2000–60 000 individuals. α -, β - and γ -diversity all grow linearly with metacommunity size.

Figure 5b shows how diversity scales as local communities are added to a network. Interestingly, overall γ -diversity scales linearly while there is a nonlinear tradeoff between α - and β -diversity. This occurs as the average distance between pairs of nodes in the network is increased.

DISCUSSION

Our results highlight the importance of spatial structure and the biological parameters of the neutral model in determining species diversity of a local community, among spatially

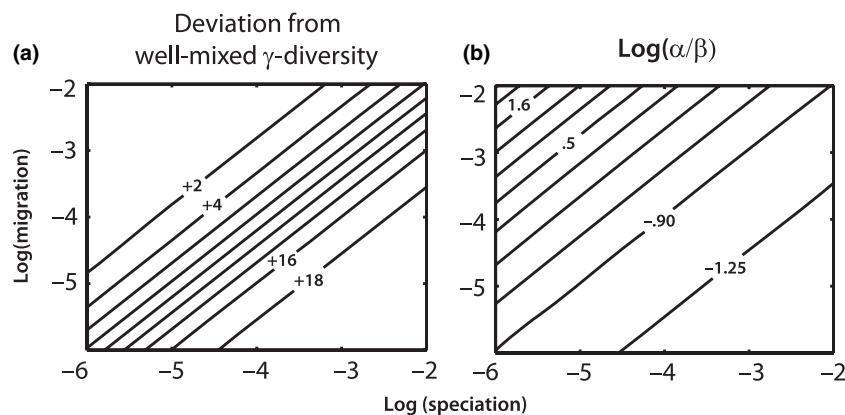


Figure 4 Contour plots showing diversity calculated in a range of migration and speciation rates on a chain graph with 20 nodes, and local population sizes set to 20 000. (a) The deviation of the equilibrium γ -diversity in a spatially explicit metacommunity from a well-mixed metacommunity of the same size. The units are effective number of species, isoclines depicted in increments of two. The maximum is expected to be 19 ($n - 1$, see text). (b) $\log(\alpha/\beta)$, an index of the allocation of diversity into within and between components, isoclines are in increments of 0.35. Both plots have parallel, linear isoclines, indicating the ratio of m/v is the important driver of these patterns.

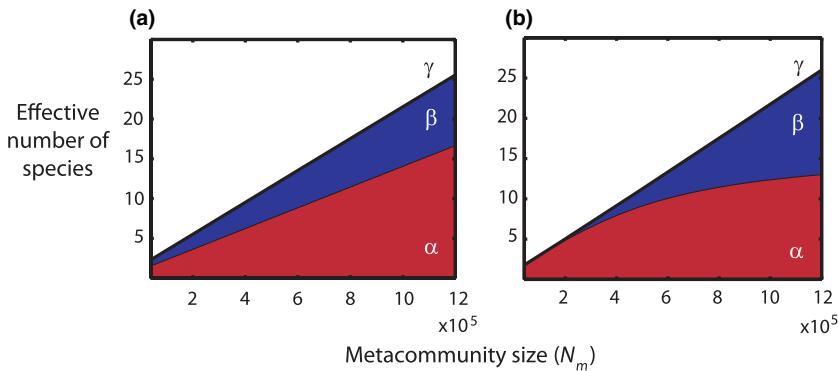


Figure 5 Diversity as a function of meta-community size. (a) diversity of a chain graph of length 20, ($m = 1 \times 10^{-3}$) as local community sizes are increased such that total metacommunity size varies between 40 000 and 1.2 million. (b) Diversity in a chain graph as nodes are added, so length varies between 1 and 30 local communities of 40 000 individuals each.

separated communities, and on the scale of the entire metacommunity. As the results presented in the previous section are in terms of a rather abstract parameter space, it is instructive to discuss how they may relate to natural systems. We find spatially structured metacommunities to have elevated γ -diversity compared with a well-mixed metacommunity if connectivity is low (Fig. 2,3) relative to speciation rate (Fig. 4a). The magnitude of this effect is, at most, $n - 1$ effective species in a network of n patches and the relative effect on metacommunity diversity is determined by the relative magnitude of the number of patches to the fundamental diversity number, the latter a function of speciation rate and metacommunity size. For metacommunities with high diversity relative to the number of patches ($\theta + 1 \gg n - 1$), because speciation rate is high or metacommunity size is large (because, for example, the areas involved are large) or both, metacommunity structure has little effect on overall diversity even if migration is highly restricted. An example of this situation would be a set of large but isolated mountain ranges distributed on a continent. In these cases, α - and β -diversity, but not γ -diversity, would be highly dependent on the connectivity of such patches.

If diversity is low compared with the number of patches ($\theta + 1 \ll n - 1$), the spatial effect can be of consequence to overall diversity. Hypothetical examples of this situation would be an isolated network of many small oceanic islands, or other numerous but isolated habitat types such as caves or mountain peaks. The total size of the metacommunity (N_m) may be unable to support much diversity if it were one well-mixed unit, but the isolation inhibits one or a few species from numerically dominating and thus enables species persistence. In this situation, the connectivity of the system has important consequences for α -, β - and γ -diversity.

These results demonstrate that under certain conditions, fragmentation promotes γ -diversity as subcommunities maintain uniqueness. It should be noted that the zero-sum assumption implies the indefinite persistence of subcommunities. In highly fragmented metacommunities with many small subcommunities, one might expect occasional extinc-

tion of those subcommunities because of environmental stochasticity, which may depress overall metacommunity diversity. An interesting extension would be to examine neutral community dynamics in a network with dynamic structure.

Topological differences in metacommunity structure reflect different spatial arrangements of habitat. Some communities are arranged in long chains, such as riverine or coastal systems. Other metacommunities may be hierarchically clustered reflecting patchy habitat distributions on multiple scales, or characterized by asymmetric flows because of wind or water currents. Given the diversity of organisms in variables such as body size, life history and habitat affinities, and the complexity of landscapes and environmental gradients, the structures of real metacommunities can be expected to be highly variable in nature.

The transition from β - to α -dominated metacommunities as m/v increases highlights the neutral hypothesis for global patterns of provincialism (Hubbell 2001). When migration is too weak to overcome the differentiating effects of speciation, provinces with distinct biotas form in the subcommunities. When migration is relatively strong, communities embedded in large networks can have similar compositions. We have shown how the geometry of such networks also contributes to this transition. The linear scaling of γ -diversity with metacommunity size is consistent with the linearity of interprovincial species–area curves (Rosenzweig 1995), although it remains to be seen if species number has the same behaviour as the effective richness predicted by our model.

The main strength of the neutral theory is testability. The model's transparent parameters allow for empirical tests, and quantitative tools for fitting the model to data have blossomed (Etienne 2005, 2007; Etienne *et al.* 2007b). Aside from several notable exceptions (Condit *et al.* 2002; Rosindell & Cornell 2007), these efforts are based on fitting data to the spatially implicit model, some going so far as to use a spatially implicit model to generate predictions for community similarity (Dornelas *et al.* 2006). Given that spatial structure is a pervasive feature of real metacommunities, and

thus migration rates among pairs of communities are often variable, neutral processes in nature could produce more complex diversity and similarity patterns than can be generated with spatially implicit models.

The challenges are formidable: a spatially explicit metacommunity requires more parameters to describe than a spatially implicit version, when one considers the large number of m_{ij} and local community sizes. Increasing the complexity of that structure increases the number of parameters to be fit to data. However, simplifying assumptions can be made about relations of distance with dispersal rates, and area with community size. From this perspective, the model presented here is not significantly more complex than metapopulation models (Hanski 1999), which are commonly fit to data by making such simplifying assumptions. An exploration of that potential is left for future work.

Our analytic method permits the exploration of regions of parameter space that are inaccessible to simulation because of computational limits. This is because long transients are not an issue and speciation rates and numbers of individuals (but not number of subcommunities) can take on any finite values. However, a disadvantage of our method is the focus on diversity indices as opposed to species abundance curves, which contain information on richness and all higher order diversity metrics. We expect this limitation will prove to be temporary, as recursive techniques similar to the Malécot equation can generate more detailed information about the coalescent process than is captured in probabilities of identity (Hudson 1991; Nagylaki 2000; Laporte & Charlesworth 2002; Etienne & Olf 2004). In addition, our method follows many other neutral models by assuming point speciation, the frequency of which in nature is uncertain. Under allopatric or other speciation mechanisms, it is possible diversity patterns will have a different relationship with spatial structure, and initial steps have been taken in this direction (Moullot & Gaston 2007).

The questions addressed here mostly pertain to global properties of the metacommunity, but there are many questions outstanding regarding how the internal network structure of a metacommunity determines neutral pattern. The position of a node in a network has consequences for both local diversity and uniqueness, and similarity with other nodes at a given location in the network (Economo & Keitt, unpublished results). A rich tradition of quantitative methods developed to quantify the local and global structure of networks (Albert & Barabási 2002) may prove useful for these ends.

The possibility that relatively simple stochastic ecological and evolutionary processes may underlie biodiversity patterns is an idea that traces back at least to MacArthur–Wilson island biogeography (MacArthur & Wilson 1967). Neutral theory shows us again that spatial pattern can arise in the absence of environmental species sorting, niche

partitioning, complex interactions, and historical contingencies. As complexity continues to be added to the theory highlighting different biological and geographical realities, we will eventually gain the ability to produce ever more specific and discriminating predictions. The future is promising for a rigorous assessment of the importance of stochastic processes in biodiversity dynamics in space and time, and across the tree of life.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 The effect of variable N_m , holding m/v constant.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01126.x>.

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