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Using neutral theory to reveal the contribution of meta-community processes to assembly in complex landscapes

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ABSTRACT

*The metacommunity perspective appears as an appropriate conceptual framework to make ecology more predictive. It is particularly relevant to limnology, where exchanges of organisms and nutrients affect community and ecosystem properties from the local to the regional scales. The recent development of neutral theory appears as a step back in that direction because of the assumption of ecological equivalence and the absence of any effect of the environment on community organization. A remarkable strength of neutral theory is nonetheless to provide a general theory of diversity that accounts for a wide range of empirical observations. In this paper, we argue that neutral theory can be useful to understand the impact of dispersal on community assembly in landscapes of various complexities. Our analysis focus on spatially explicit landscapes conceptualized as networks of local communities (*e.g.*, lakes) connected to each other by dispersal channels (*e.g.*, rivers). The main objective of the paper is to use neutral theory to stress the importance of landscape structure on the distribution of diversity. We refer to the landscape organization as a* spatial contingency *that could potentially affect the coexistence mechanisms at play. We briefly review the main approaches to describe spatial networks and describe three simple toy models of metacommunity dynamics. We take this opportunity to review their assumptions and main predictions. We then conduct simulations of these models to reveal with simple examples the impact of spatial network structure on diversity distribution. The simulation results show that competitive interactions buffer the potential impact of landscape structure. The strongest relationship between node position in the landscape and species richness was observed for the patch dynamics model without any interactions. On the other hand, strong and unequal competitive interactions minimized the effect of node position. We conclude that the neutral model is a useful tool to understand the joint effects of dispersal and ecological interactions. Our analysis shows that limnologists must now integrate more realistic landscapes when analyzing community assembly from a metacommunity perspective.*

Key words: metacommunity, neutral theory, species sorting, metapopulation, spatial network, centrality.

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INTRODUCTION

Ecology needs to move toward a more predictive approach, integrating elements of theoretical ecology (Thuiller *et al.*, 2013). The metacommunity perspective (Leibold *et al*., 2004) appears naturally as the appropriate conceptual framework to fill this challenge. The metacommunity concept builds on feedbacks between local scale processes, such as competitive interactions and local adaptation, and regional scale processes such as dispersal, gene flow and speciation. It is particularly relevant to limnology, where exchanges of organisms and nutrients affect community and ecosystem properties from the local (*e.g*., vertical mixing, Ryabov and Blasius, 2011) to the regional (*e.g*., connections of lakes, Gravel *et al*., 2010; Leibold and Norberg, 2004; Muneepeerakul *et al*., 2008) scales. The metacommunity perspective emphasizes the importance of dispersal relative to pairwise interactions in the organization of ecological communities.

At first sight, the development of neutral theory appears as a step back. The neutral theory of biodiversity makes the provocative assumption that species are ecologically equivalent (Bell, 2000; Hubbell, 2001). Neutral community dynamics are driven only by demographic stochasticity and dispersal and thus, variation in the environment has no impact on demography. Neutral theory sparked a historical debate still lasting after more than a decade (Chave, 2004; Clark, 2012; Etienne and Rosindell, 2011; Rosindell *et al*., 2012). It was stimulated by the surprising ability of neutral models to fit some well studied empirical observations such as species abundance distributions and distance-decay relationships. A remarkable strength of the theory is to provide a *formal general theory of abundance and diversity that will account, in a simple and economical fashion, for the many patterns that ecologists have documented* (Bell, 2001). Even if new studies rejecting neutral theory are consistently published [*e.g*., Ricklefs and Renner, 2012; but see the comments associated with this study (Chen, 2012)], a consensus is forming that neutral theory is a well-developed null hypothesis for niche theory and could even be used as

an adequate approximation of ecological dynamics in some situations. Bell (2001) nicely envisioned two perspectives to neutral theory that are still standing today. Under the weak perspective, neutral theory provides a set of realistic predictions of community organization despite false assumptions. Even if being fundamentally wrong, neutral theory would still useful when used as a null hypothesis (Gotelli and McGill, 2006). It is considered as an improvement over traditional null hypotheses based on randomization (Gotelli, 2000) because it readily integrates dispersal. On the other had, the strong version posits that neutral theory is a satisfying approximation to community dynamics and an appropriate theory to explain the distribution of biodiversity. It implies that the right mechanisms have been identified and that the consistently observed differences among species do not strongly impact community organization. Neutral theory has also been proposed as a useful tool to understand and predict some aspects of community dynamics. It links to an old philosophical debate between realism and instrumentalism (Wennekes *et al*., 2012). Because every ecological model is a simplification of reality, scientists have to subjectively decide the level of detail they put in, leaving out some elements they consider unimportant. The realist perspective requires all assumptions of the theory to be true, while the utility of the theory is more important to instrumentalism. The utilitarian value of a theory could either be for understanding or for prediction (another old philosophical debate; see Shmueli, 2010). Obviously neutral theory could only be instrumental. The question then is if such a *general, large-scale, but vague* theory is a satisfying approximation (Wennekes *et al*., 2012). The instrumentalist view of neutral theory raises the question of why it should be a satisfying approximation despite knowing the pieces are wrong? Perhaps stochasticity of various origins blur the deterministic differences among species and promote ecological drift (Gravel *et al*., 2011a). Much has been said about the existence of demographic stochasticity (Clark, 2012), and we will therefore leave this discussion for other papers. A second explanation is that dispersal and historical contingencies might have a much more profound impact on species distribution (Bahn and McGill, 2007; Boulangeat *et al*., 2012) and ecological dynamics. The debate over the equivalence assumption and demographic stochasticity might have overlooked the recognition of how much dispersal influence community assembly.

In this paper, we argue that neutral theory can be a useful tool to understand the impact of dispersal on community organization in landscapes of various complexities. Even for purely theoretical analyses, we need a benchmark without niche differences to reveal the role of dispersal in structuring communities and understand how it interacts with niche differentiation. We will explore recent applications of neutral theory, at the crossroad of network theory, to better represent the impact of landscape structure on biodiversity distribution. This analysis will prove particularly relevant to limnology, where most riverine and lacustre habitats are characterized by their discrete nature and spatially complex arrangements (Peterson *et al*., 2013). We will also explore the relative contribution of ecological interaction and niche differentiation by contrasting predictions of a neutral model to other metacommunity perspectives. Our main objective is to use neutral theory to stress the importance of landscape network structure on the distribution of diversity. We refer to the landscape organization as a *spatial contingency* (Peres-Neto *et al*., 2012) that could potentially affect the coexistence mechanisms at play. We will therefore move from a perspective where dispersal is either global or constant over space (*e.g*., a lattice), to a perspective focusing on the variance of dispersal. A second generation of neutral models (Desjardins-Proulx and Gravel, 2012a, 2012b; Economo, 2011; Economo and Keitt, 2008), field surveys (Muneepeerakul *et al*., 2008) and even experiments (Carrara *et al*., 2012), recently introduced more realistic landscapes and found surprising contributions of spatial contingencies. We start with a short review of the main approaches to describe spatial networks. Then we describe three simple toy models of metacommunity dynamics, using this opportunity to review their assumptions and main predictions. We provide as Supplementary Material the R scripts for the toy models and all simulations conducted for this paper. We then conduct simple simulations of these models to reveal with simple examples the impact of spatial network structure on diversity distribution. We conclude with a discussion on the operationality of the metacommunity framework.

NETWORK REPRESENTATION OF LANDSCAPES

A network is a discrete mathematical object made of two sets: a set of nodes (or vertices) and a set of edges connecting the nodes (Newman, 2010). The term *graph* is often preferred in computer science and mathematics (Gross and Yellen, 2006), with graph algorithms being an important and active area of research (Sedgewick, 2001). A network is a combinatorial object: it is used to study how discrete entities are connected and how they combine together to create complex structures. They are used to study molecules, food webs, social networks, or even the relationship between variables in statistics (Newman, 2010; Wright, 1921). We are especially interested in spatial networks, a special kind of network mixing the combinatorial properties of networks with a topological space (Kobayashi, 1994). Thus, the nodes in a spatial graph are embedded in some other space, most often the two or three- dimensional Euclidean space. This object brings a rich representation to spatial ecology and is particularly

suited for systems of lakes and rivers, which can easily be represented by nodes and edges. There are two notions of distance in spatial networks. Euclidean distance represents the geographical distance between the nodes *(i,j)*, *i.e.*: $\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$.

Geodesic distance is the distance in the graph space*, i.e.*: the length of the shortest path (Dijkstra, 1959). For example, two lakes could be very close on a map (short Euclidean distance) but the geodesic distance could be great if they are not directly linked by a river.

The popularity of network theory stems from its ability to model complex structures while allowing us to extract useful metrics (Tab. 1). At a very high level, a network can be described by its number of nodes (the order) and edges (the size). Looking more closely, the relationship between nodes is influenced by paths, which are ordered series of nodes. Centrality is a *central* concept in network theory, where it can be seen to as a measure of *importance*. The simplest measure of the centrality of a node is its degree, which is the number of nodes directly connected to it. Of course, this is a very rough description of centrality. For example, two lakes can have the same degree, with one being connected to a small isolated cluster, while the other one is part of one of the biggest network of lakes. In this case, measures of centrality like eigen-centrality will weight the importance of the connection, so a node connected to well-connected nodes will have higher centrality than a node connected to isolated nodes.

In this paper, we study four types of networks (Fig. 1). First, for the sake of comparisons, we study a complete network where dispersal is global. Then, we consider a lattice, which is the most regular type of spatially explicit network. Thereafter, we simulated two types of random spatial networks. We considered random geometric graphs. In this algorithm, all nodes are assigned to a position in some two-dimensional space, most often the unit square. Then, all pairs of nodes within some threshold Euclidean distance *r* are connected with an edge. The resulting networks have the desirable property of locality: if a node *A* is connected to two vertices *B* and *C,* then *B* and *C* are more likely to be connected than two random vertices. Random geometric networks have been extensively studied (Appel and Russo 1997a, 1997b, 2002; Appel *et al*., 2002; Penrose, 2003) and we provide an R function to generate them. The position of nodes is typically random, but we could also imagine alterations where they are either more aggregated or segregated than expected by chance alone. Finally, we also provided the code for a second structure that we call a random geometric tree. The algorithm first builds a random geometric graph, and then selects a node from which to start the tree. It then calculates the the shortest path tree (Dijkstra, 1959) from this node to all other ones and remove edges not located along this tree. This random geometric tree does not exactly represent dendritic landscapes but is a convenient model to simulate a lake connected by rivers to a series of smaller lakes.

Spatial graphs are increasingly popular in spatial ecology and conservation biology, where the structure of connections can be used to study and influence the flow of organisms (Dale and Fortin, 2010; Fall *et al*., 2007; Garroway *et al*., 2008; Minor and Urban, 2007, 2008; Urban *et al*., 2009). In the neutral theory, networks were pioneered by Economo and Keitt (2008, 2010); they used networks to study how different spatial structures influenced diversity and were also used to study how the spa-

Tab. 1. Main descriptors of spatial networks used in this study. In the case of spatial networks describing dispersal, nodes refer to local communities and edges to a connexion by dispersal between them.

Concept	Definition
Path	A sequence of edges forming a sequence of nodes
Connection	Two nodes are connected if there is a path between them
Euclidean distance	Geographical distance between two nodes
Geodesic distance	Length of the shortest path between two nodes
Network-level metrics	
Order	Total number of nodes
Size	Total number of edges
Connectivity	A measure of robustness: the minimum number of elements to remove to isolate the nodes
Components	The number of connected subsets
Node-level metrics	
Degree	The number of edges of a node
Closeness centrality	Average geodesic distance between a node and all other vertices
Eigenvector centrality	A measure of centrality based on the concept that connection to highly connected nodes are more important
Betweenness centrality	The number of shortest paths from all nodes to all others that pass through that node

tial structure influenced nonsympatric speciation (Desjardins-Proulx and Gravel 2012a, 2012b).

MODEL DESCRIPTION

In this section, we describe three toy models representing different perspectives of metacommunity ecology: patch dynamics, neutral dynamics and species sorting. While the neutral model is interesting in itself, it is by its comparison with a model without any interactions (patch dynamics) and with niche differentiation (species sorting) that we will be able to fully understand the interaction between these processes and landscape structure. Despite being neutral, competitive interactions in neutral models are very strong because of the zero-sum assumption (the community is always at carrying capacity). We will first review the fundamental assumptions of each model with their description (Tab. 2 summarizes the parameters and variables used), and then briefly discuss their main predictions. Simulation results are presented in the next section, with the corresponding R code provided in the Supplementary Material.

Patch dynamics

The simplest metacommunity model is an S species extension of traditional metapopulation models (Hanski, 1999). The standard Levins metapopulation model (Levins, 1969) describes the stochastic colonizations and extinctions of a single species over a homogenous landscape. The basic unit is the population. The model tracts the dynamics of occupancy (the fraction of the landscape that is occupied) with an ordinary differential equation and therefore assumes an infinite landscape. The simulation model we run is more realistic as it simulates a finite number N of discrete patches (or nodes in network terminology). The rules described in the previous section were used to generate connectivity matrices along four scenarios (Fig. 1): global dispersal (connected graph), a lattice, a random geometric graph and a random tree graph. A patch x shares d_x links with neigbhouring patches (its degree). At each time step (the simulation model is discrete in time), the probability that a colonist coming from an occupied patch y arrives at patch x is cd_y^{-1}, where c is the probability a colonization event takes place if all connected patches are occupied. The expected probability that a colonist arrives to patch x from patch y is then $C_{ixy}=cp_{iy}d_y^{-1}$, where p_iy is the probability that patch y is occupied by species i. The probability that extinction occurs in a given patch is e. The Levins model is for a single species, but a basic metacommunity patch dynamics model could be run by aggregating S independent metapopulation models (Hanski and Gyllenberg, 1997). There are no interactions in this simple model, which means there are no limits to local species richness and no carrying capacity. Competitive, mutualistic and predator-

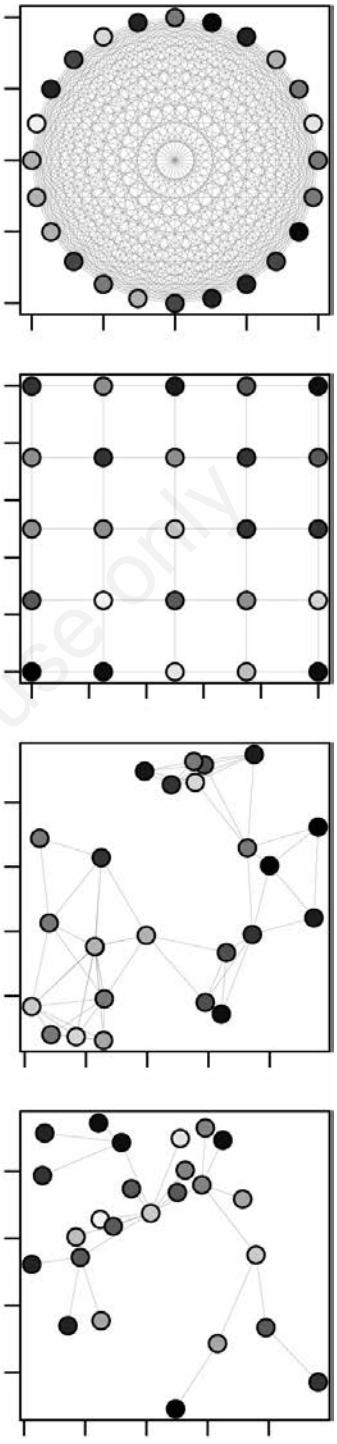

Fig. 1. Illustration of the four simulated landscapes. The colour code represents the α diversity simulated with a neutral model, ranked from the poorest (black) to the richest (white). Parameters: N=25, r=0.3, S=100, m=0.2, M=0.01, k=0.1, J_x=100. Simulations run 1000 time steps. Note that over replicated runs the global dispersal and the lattice scenarios would have a very regular distribution of diversity (spatially uniform, with declining diversity at the edges for the lattice), while the structure should be maintained for the two random networks.

Tab. 2. List of variables, indices and parameters from the three models.

	Definition	Patch dynamics	Neutral	Species-sorting
Variables				
p	Occupancy	X		
N	Local population size		X	X
Z	Local relative abundance		X	X
P	Relative abundance in the neighborhood		X	X
s	Local species richness	X	X	X
d	Node degree	X	X	X
C	Colonization probability from patch y to patch x	X		
I	Colonization probability at patch x given neighbours	X		
Pr	Recruitment probability		X	X
λ	Survival probability			X
Indices				
x,y	Node location	X	X	X
i,j	Species	X	X	X
n	Microsite			X
Parameters				
r	Number of patches	X	X	X
S	Size of regional species pool	X	X	X
c	Colonization probability	X		
e	Extinction probability	X		
J	Local carrying capacity		X	X
m	Immigration probability from neighborhood		X	X
M	Immigration probability from metacolonization		X	X
k	Death probability		X	X
u	Niche optimum			X
b	Niche breadth			X
E	Microsite environment conditions			X
$\overline{E}$	Local environment average			X
σ	Local environment variance			X
$\overline{E_R}$	Regional environment average			X
σ_R	Regional environment variance			X

prey interactions have been added to this framework (Gravel *et al*., 2011b; Holt, 1996; Klausmeier, 1998; Tilman, 1994) but we will keep this model minimal for the sake of comparison with the neutral model.

Predictions of the patch dynamics metacommunity model are quite straightforward. First, a fundamental result of metapopulation ecology is that persistence will occur if colonization probability is larger than extinction probability ($c>e$). Given that all species are the same, then we should expect the regional diversity (γ) to be S if this condition is satisfied and 0 if not. The situation is however more complex in spatially explicit landscapes with complex connectivity matrices (Hanski 1998). Spatially explicit dispersal usually reduces the occupancy and thereby the likelihood of persistence. The second prediction is that, given spatial variation in connectivity, there will be spatial variation in occurrence probability. Given the above formulation of a colonization event to occur, the probability that an empty location is colonized by an offspring coming from a least one of the r neighbouring patches is $I_{ix} = 1 - \prod_{y=1}^{r} d_x(1 - C_{ixy})$. This equation tells us that the colonization probability will increase asymptotically with the degree of a patch (because of the product). It is easy to show from metapopulation theory that the occurrence probability in a patch is then $p_{ix}=I_{ix}(I_{ix}+e)^{-1}$. The feedback between local and regional dynamics arises because all p_{ix} from the landscape are dependent from each other. Simulations are usually conducted to solve the model for a large landscape, but numerical solutions are theoretically possible. The aggregation across the S species of the regional species pool is obtained by taking the summation of occurrence probabilities over all species, $s_x=\Sigma p_i$. Because in this model all species are equal, we expect the local species richness to be a linear function of the patch degree (number of edges). Multispecies analysis of metapopulation models also reveals interesting predictions on other aspects of community organization at various spatial scales such as the species-area relationship (Hanski and Gyllenberg, 1997), and proved to be useful in conservation ecology with predictions of extinctions following habitat destruction (Rybicki and Hanski, 2013; Tilman *et al*., 1994).

Neutral dynamics

Neutral theory introduces strong competitive interactions by assuming there is a finite number of individuals that could occupy a patch. There are different ways to simulate this *zero-sum rule* (Bell, 2000; Hubbell, 2001), but they all result in the same constraint that the increase in abundance of a species could only occur after an equivalent decrease by another species. One important change in the formulation of most neutral models relative the patch dynamics model presented above is therefore that it is individual-based, not population based. We therefore considered in our toy model of neutral dynamics that each local patch holds J_x individuals. The model tracks the local abundance of all species N_{ix} in each local patch. At each time step an individual dies with probability k. Recruitment only occurs in vacant sites, similarly to a tree-by-tree replacement process in a closed canopy forest.

The formulation of the recruitment probability is the central piece of all neutral models, making the coupling with the metacommunity and neighbouring patches possible. We adopt a simple formulation based on Gravel *et al*. (2006). The approach is conceptually similar to placing a trap in a canopy gap and picking a seed at random among the ones falling in to determine the identity of the recruited species. The composition of the seed pool in that trap will be a mixture of local dispersal and immigrants from the metacommunity. For simplicity, we consider three spatial scales of dispersal but it would be easy to generalize the approach to a continuous seed dispersal kernel (Gravel *et al*., 2006). The parameter m is the probability that the recruit is a migrant from neighbouring patches, M is the probability it comes from a larger (and fixed) metacommunity, and consequently, by substraction, $1–m–M$ is the probability it comes from local dispersal. The fraction $N_{ix}J_x^{-1}$ is the local relative abundance and P_{ix} is the relative abundance of species i in the seed pool coming from patches connected to patch x. The relative abundance in the neighborhood is weighted by the degree of the connected nodes because some nodes will spread their seeds across a higher number of nodes and thus contribute less to the seed pool. We thus consider $P_{ix} = \sum P_{iy} d_y^{-1} / \sum d_y^{-1}$. We assume for simplicity that the relative abundance in the metacommunity is uniform, *i.e.* equal to S^{-1}, but other distributions could be used. The metacommunity is usually modelled with a log-series (*e.g*., Hubbell, 2001), but it has been shown that for a range of realistic dispersal rates a uniform distribution does not have distinguishable impacts relative to a log-series (Bell, 2000). This immigration prevents the collapse of the metacommunity to a single species; since otherwise all species except one will face extinction by ecological drift (speciation prevents this phenomenon to occur in Hubbell, 2001). The local recruitment probability Pr_{ix} is consequently $Pr_{ix}=MS^{-1}+mP_{ix}+(1–m–M)N_{ix}J_x^{-1}$. Self-replacement occurs when an individual of species i is replaced by an offspring of the same species coming either from the remaining local individuals or from the metacommunity.

The model is neutral because it assumes that the probabilities of local recruitment, immigration and mortality events are equal across species. Demographic stochasticity is the source of variation in abundance, but larger disturbances could be simulated as well, as long as they hit all species with the same probability, independently of their identity. The fundamental feature of neutral dynamics is therefore the ecological drift, defined as population changes emerging from neutrally stable population dynamics. It can be measured as the variance between replicated time series of community dynamics (Gravel *et al*., 2011b). Hubbell (2001) provides a very comprehensive analysis of the model, with specific attention to the effect of the different parameters on drift (and consequently variance in abundance) and time to extinction. Despite its simplicity, the neutral model is surprisingly rich in the predictions it makes. Bell (2001) and Hubbell (2001) analyzed the performance of neutral models to predict species abundance distributions, the range-abundance relationship, spatial variation in abundance, the species-area relationship, community turnover (beta-diversity) and co-occurrence. Recent trophic neutral models were also found to predict realistic ecological network structures (Canard *et al*., 2012). Other than the ecological equivalence assumption, one of the most criticized aspects of neutral models is the realism of the speciation process and the required speciation rates to sustain species richness (Etienne *et al*., 2007; Ricklefs, 2003). Recent neutral models with more credible speciation models (Desjardins-Proulx and Gravel, 2012b; Rosindell *et al*., 2010) revealed the difficulty to maintain diversity over macro-evolutionary time scales. These models nonetheless proposed interesting predictions on endemic species richness and island biogeography (Desjardins-Proulx and Gravel, 2012a; Rosindell and Phillimore, 2011).

Species sorting and mass effect

The species sorting and the mass effect perspectives build on the notion of species-specific responses to a spatially varying environment (Leibold *et al*., 2004). There are various ways to simulate such dynamics and we picked the lottery model, in line with tradition (Mouquet and Loreau, 2002) and for its proximity to the neutral model described above. Competition for space occurs during recruitment after the death of an adult. The recruitment is a lottery among potential candidates as in the neutral model. The recruitment probability is however biased by species-specific responses to local environmental conditions.

The lottery dynamics described above for the neutral

model assume there is a very large number of offspring that are candidate for recruitment but only one will survive and develop to the adult stage. The effect of a specific response to local environmental conditions could be implemented at this stage with a biased survival probability. The J_x individuals all experience a unique environmental condition E_{nx} called a microsite n. We considered a patch average $\overline{E_x}$, with a within-patch variance σ_x. The regional average is $\overline{E_R}$ and the regional variance σ_R (for simplicity we considered normal distributions of environmental conditions, but different distributions will lead to different regional similarity constraints; Gravel *et al*., 2006; Mouquet and Loreau, 2003; Tilman, 2004). We consider that a fraction λ_{inx} of offsprings reaching the microsite where recruitment occurs will survive. The recruitment probability is therefore biased in favour of the species with highest survival because only some species will be able to cope with the microsite environmental conditions. We define the relative abundance in the seed rain as $Z_{ix}=MS^{-1}+mP_{ix}+(1-m-M)N_{ix}J_x^{-1}$. The calculation of the relative abundance in the seed rain is the same as the neutral model but the recruitment probability differs because only a fraction of offspring survive. It is formulated as $Pr_{ix}=\lambda_{inx}Z_{ix}/\Sigma\lambda_{jnx}Z_{jx}$. The function describing the relationship between a microsite condition and survival could take various forms; we used the traditional gaussian curve describing the niche, $\lambda_{inx} = \exp-\frac{(E_{nx}-u_i)^2}{2\Pi b_i^2}$, where u_i is the niche optimum and b_i is the niche breadth. Note that the model will converge to a neutral model when the niche breadth tends to infinity (which is in fact how we simulated neutral dynamics in the Supplementary Material to minimize the complexity of the code).

Analyses of similar models with a combination of dispersal and species sorting shows that predictions are extremely variables and depend on the frequency distributions of environmental conditions, niche optimums and niche breadth. For instance, a well-studied prediction of neutral models is the species abundance distribution. It was shown that niche models can predict similar distributions given appropriate parameters (Gravel *et al*., 2006; Tilman, 2004). The main prediction is nonetheless that stable and predictable coexistence is possible if species are sufficiently dissimilar, which differs from neutral models. Local species richness will first depend on the joint effects of local heterogeneity and niche breadth because coexistence requires a sufficient dissimilarity among species (Schwilk and Ackerly, 2005). Local species richness could be increased by a mass effect when dispersal is consistently supplying individuals coming from more favorable locations (refuges). The limiting similarity required to maintain regional coexistence depends on the amount of dispersal because exchanges among communities homogenize environmental conditions. This is one of the main results from the species sorting theory and a clever example of local-regional feedbacks: increasing dispersal promotes local coexistence, but on the other hand, it diminishes regional coexistence. Only the best average competitors will remain at very high dispersal. We therefore expect a hump-shaped relationship between dispersal and alpha (α) diversity, with a peak at intermediate dispersal. On the other hand, we expect a monotonic decrease of β and γ diversity with increasing dispersal (Mouquet and Loreau, 2003). This prediction has been validated in some experiments (Logue *et al.*, 2011; Venail *et al*., 2008).

ILLUSTRATIVE EXAMPLES

In this section, we provide simple simulation results to illustrate the impact of spatial contingencies on species distribution and coexistence. We consider four different landscapes, illustrated at Fig. 1 with the outcome of simulations using the neutral model. All of these networks have the same number of nodes, but differ in both number of edges (*e.g*., dispersal routes between sampling sites) and connectivity between nodes. We ask how these differences in topological structures will shape the emerging properties of the community under the scenarios represented by each metacommunity model. Our analysis is not exhaustive, it is provided simply to illustrate the interaction between metacommunity perspectives and landscape structures on α, β and γ diversity.

In Fig. 2, we present the species richness of each node of the network (α diversity), as a function of the centrality of the node, under different assumptions of metacommunity dynamics and network structure. We scaled the species richness by the maximal α diversity to facilitate comparison between models. The model parameterization is responsible for differences in both α and γ diversity, meaning that only the shape of the relationship between centrality and richness ought to be looked at. It appears that both in the random geographical and tree networks, the path dynamics model has a much more considerable variation in α diversity. However, in all cases the α diversity increases with the node degree centrality, meaning that nodes with more connections also host a more diverse community. Eigen-centrality gave a less clear-cut result, which can probably be attributed to the fact that our networks are relatively small. Eigen-centrality reports how well your neighbors are connected, and in graphs with a short diameter (*i.e*., the two farthest points are not extremely far apart), this measure might hold less information.

Finally, Figs. 3 and 4 present, respectively, the between patch β diversity as a function of the shape of the network, under the three dynamic models. The connected graph was not considered because there is no variation in path length. We used Bray-Curtis measure of dissimilarity between patches. In Fig. 3, the distance is expressed as the Euclidean (geographic) distance between two patches.

Although this neglects how dispersal connects the different patches, there is already a clear signal of geographic distance on β diversity, indicating the importance of dispersal under the three scenarios. In both the neutral and patch dynamics models, local communities become increasingly dissimilar when the distance between them increases. In other words, two communities, which are close to each other, will share a large proportion of their species pool, whereas two communities, which are afar, will share a small proportion. The relationship between distance and dissimilarity is similar for species sorting. Nonetheless, it forms an envelope of points (with most points lying in the upper-left part of the graph). While two distant communities will be dissimilar, there is no telling how dissimilar two close communities will be. Note this relationship for species sorting varies significantly with the spatial distribution of microsites (*not shown*). At one extreme, if all patches hold the same average and variance in microsite conditions, then we should expect no relationship between dissimilarity and distance. On the other hand, if the average conditions are highly variable among localities (as in here), then we should expect two communities close to be potentially dissimilar (if conditions are different) or similar (if they are the same). The variance should thus be larger. A distance-dissimilarity relationship arises in the situation where dispersal promotes a mass effect (as in here). Such results emphasize the interaction between spatial contingencies (here connectivity and distribution of environmental conditions) and dispersal.

To a vast extent, these relationships are preserved

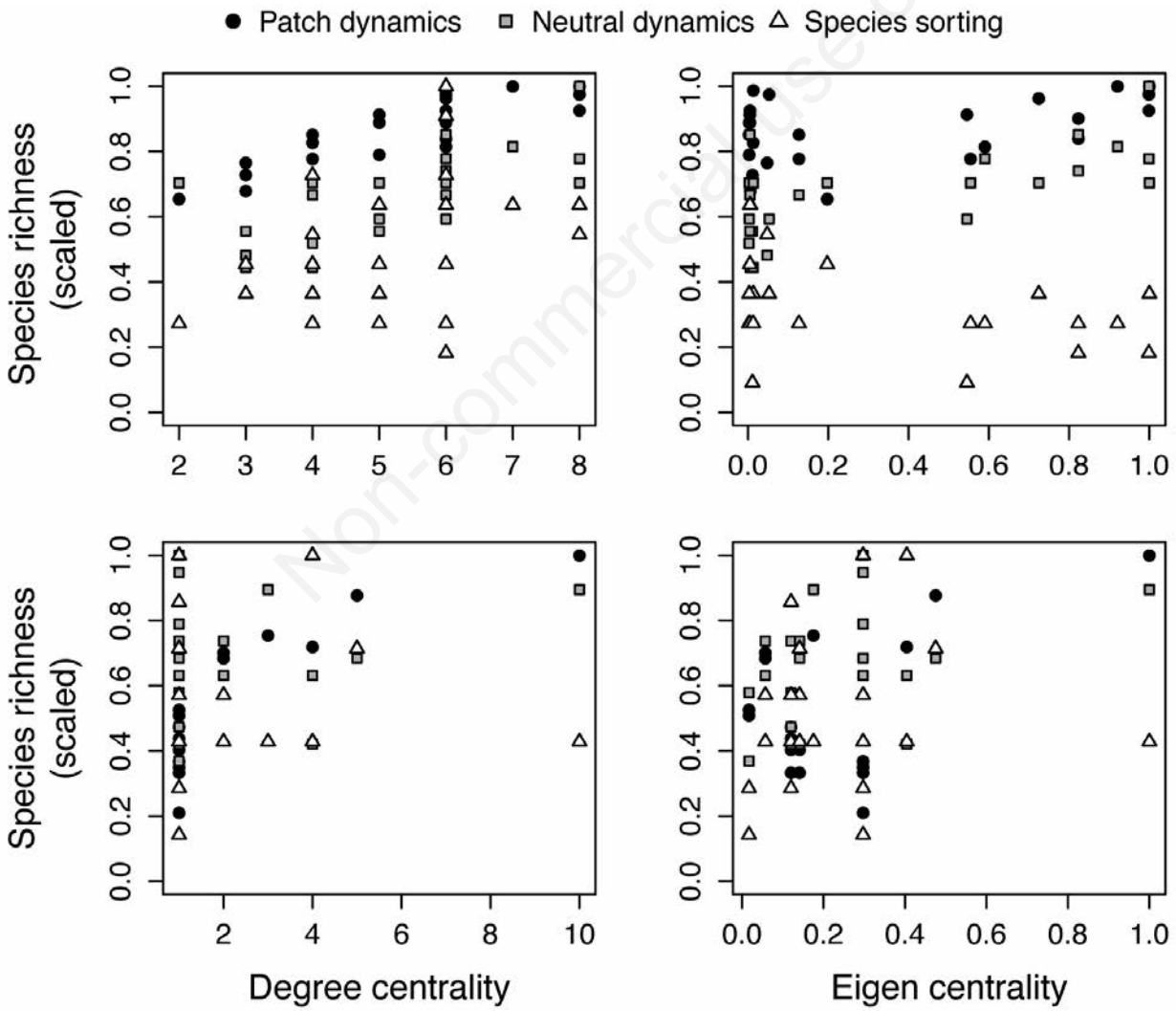

Fig. 2. Relationship between α diversity and node centrality. The upper two panels are simulation results conducted with the random geometric graph illustrated at Fig. 1 and the lower two panels are runs with the random tree graph. Parameters: S=100, c=0.4, e=0.1, J_x=100, m=0.2, M=0.01, k=0.1, $u \sim \varepsilon[0,100]$, b=15, $E_x \sim \varepsilon[0,100]$, $\overline{E_R}$=50, σ_R=5. Simulations were run 1000 time steps.

when looking at the geodesic distances (Fig. 4), *i.e.,* along how many edges should one travel to connect two patches. Interestingly enough, the distance-dissimilarity relationship for the neutral model is markedly hump-shaped, with sites being at a medium distance having the maximal dissimilarity.

DISCUSSION

The main objective of this paper was to review the main assumptions of three metacommunity models and illustrate how the implementation of more realistic landscapes could reveal the importance of dispersal on community structure. We argued in the introduction that neutral theory is useful to both understand and predict the impact of dispersal on community organization. The review of the different models shows that the fundamental difference between the neutral model and the patch dynamics model is the effect of competitive interactions on distribution, while the difference between neutral and species sorting models is the effect of unequal competitive interactions. The neutral model is thus a useful tool to understand the joint effects of dispersal and community interactions. Our comparison of the distribution of α diversity was particularly meaningful in that respect. The simulation results show that competitive interactions buffer the potential impact of landscape structure. The strongest centrality-species richness relationship was observed for the patch dynamics, a model without any interactions. On the other hand, strong and unequal

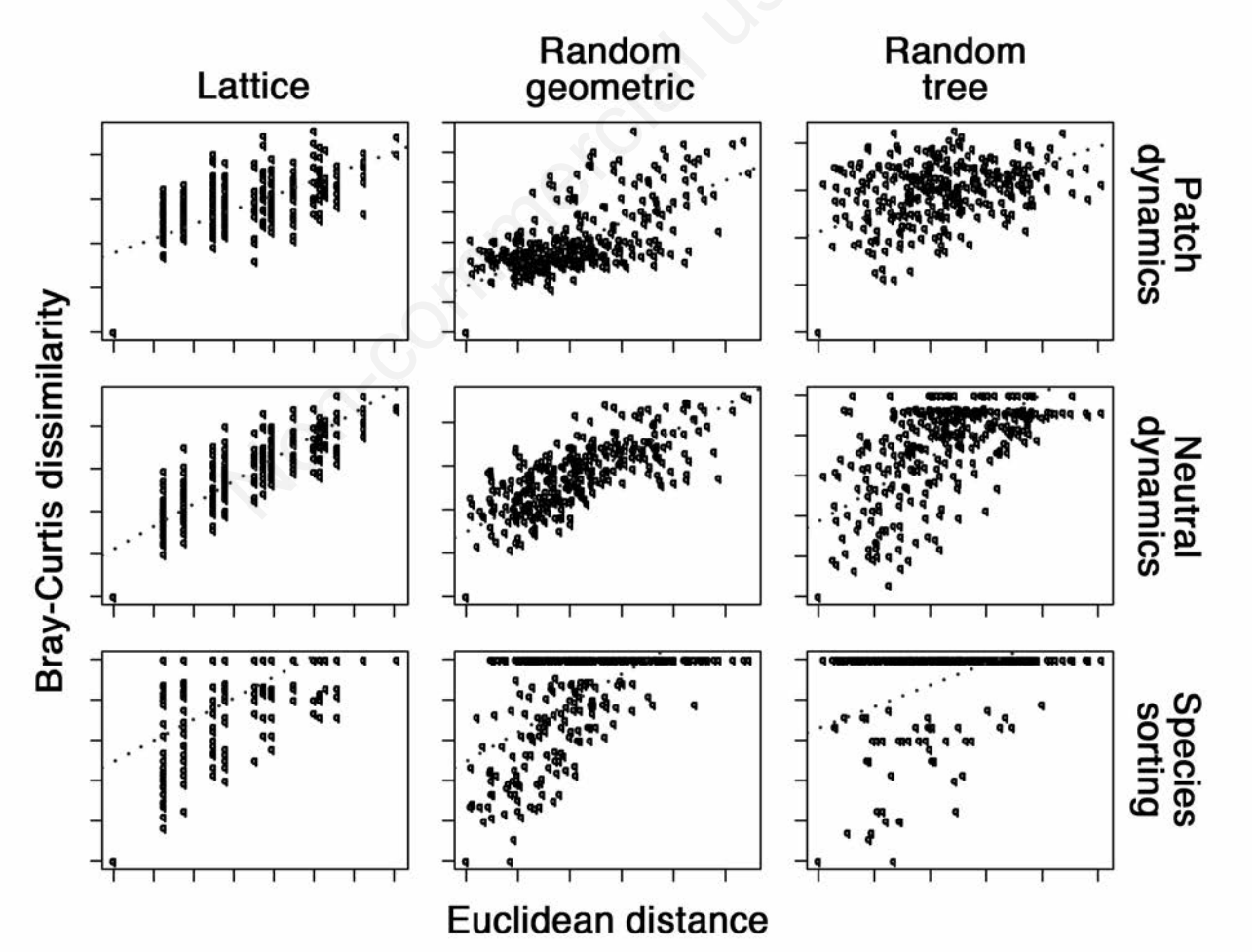

Fig. 3. Bray-Curtis dissimilarity as a function of Euclidean distance. The dissimilarity among all pairs of local communities is illustrated as a function of the distance for three types of spatial networks and three metacommunity perspectives. Parameters as in Fig. 2.

competitive interactions minimized the effect of centrality. Our model analysis greatly illustrates the growing recognition in metacommunity ecology that we must move toward more realistic landscapes (Gilarranz and Bascompte, 2012). For field ecologists, and particularly limnologists, our review emphasizes that we need to go beyond geographic based analysis of β diversity (Legendre *et al*., 2005) to topological based analyses (Dale and Fortin, 2010; Peterson *et al.,* 2013).

The network approach to the study of spatially explicit landscapes was a major advancement in metacommunity ecology. It is a first step to make the concept operational because it accounts for more realistic landscape structures and dispersal kernels. It is a significant departure to island-mainland or global dispersal approaches used previously (Hubbell, 2001; Mouquet and Loreau, 2002; Tilman, 1994). But dispersal is also spatially explicit in a lattice model and it does not make the landscape more realistic. We believe the fundamental contribution of this approach is accounting for spatial heterogeneity of dispersal. In agreement with previous theoretical (Desjardins-Proulx and Gravel, 2012a; Economo, 2011) and experimemental studies (Carrara *et al*., 2012), the simulations show that the degree centrality has a significant impact on α diversity. Central nodes might also be important to maintain γ diversity, as they promote spreading throughout the landscape. Such nodes could be potentially quantified as keystone for the metacommunity (Mouquet *et al*., 2013). Interestingly, but not surprisingly, this effect is weaker with species sorting dynamics. We could even

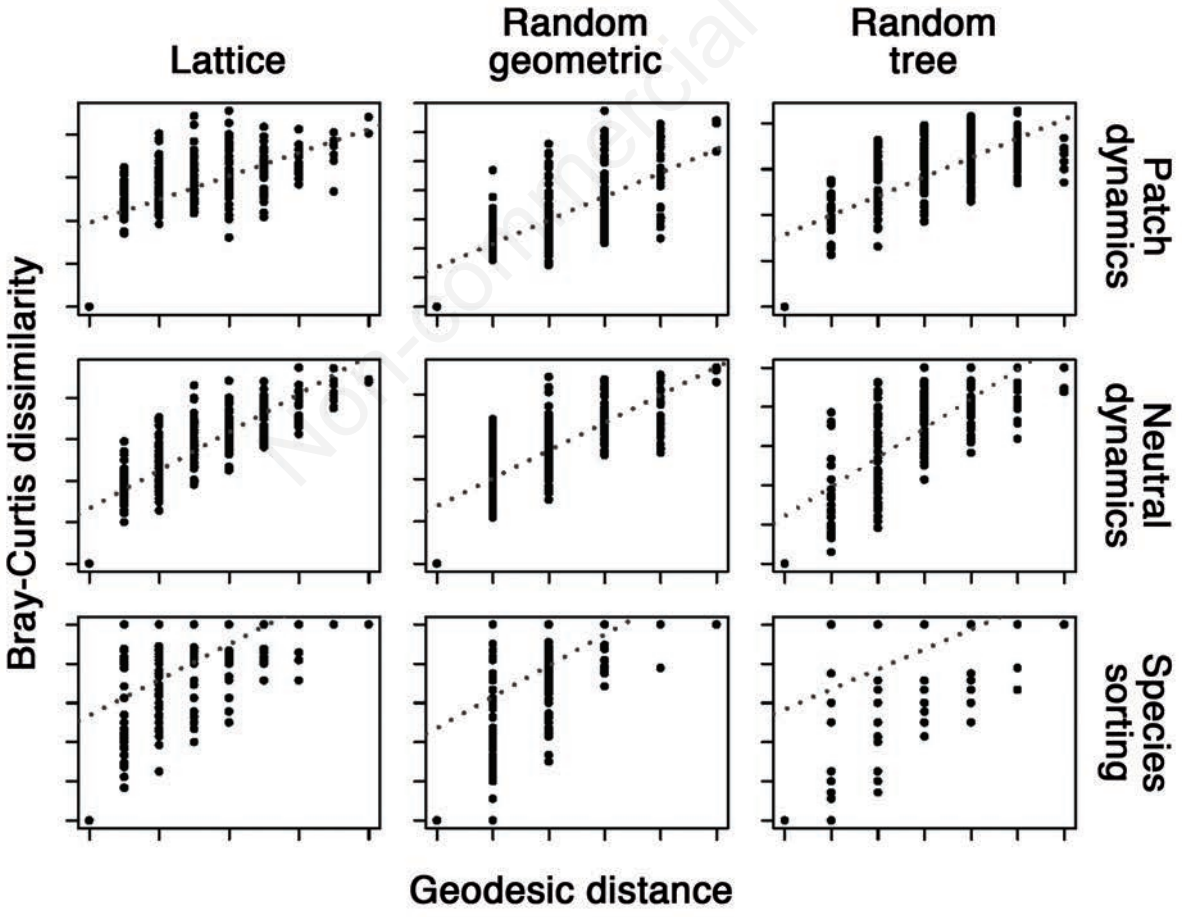

Fig. 4. Bray-Curtis dissimilarity as a function of geodesic distance. The dissimilarity among all pairs of local communities is illustrated as a function of the distance for three types of spatial networks and three metacommunity perspectives. Parameters as in Fig. 2.

hypothesize it will vanish with very strong niche differentiation (which would occur with low niche overlap for instance) and low mass effect. In this particular case, the neutral *versus* niche comparison therefore illustrates that very strong unequal competitive interactions could overwhelm the impact of dispersal. The network approach and the comparison between metacommunity perspectives reveals there could be spatial variation in coexistence mechanisms. If we take the species-sorting perspective for instance, we find that α diversity could be higher in more central nodes under some dispersal rates. Since the environment is on average the same from one patch to another, and thus should hold a similar number of species, it implies that diversity in these communities is maintained by a stronger mass effect. It results in spatial variation in the relative importance of species sorting, the mass effect and to a certain extent the neutral drift. Because the degree centrality was the best variable explaining diversity, we should expect the degree distribution to strongly impact the relative contribution of these coexistence mechanisms. For a given set of ecological processes and distribution of species traits, we might expect the coexistence mechanisms to differ from one landscape to another.

We introduced this article arguing that neutral theory could be used as an instrument to predict species distribution in spatially heterogeneous landscapes. So far, we have treated only theoretical models, but we could also envision parameterizing them and simulating real landscapes. The recruitment probabilities defined above could all be used as statistical models (likelihood functions) to fit to empirical data. Prior information could be used to define apriori dispersal kernels and then fit the model as in Gravel *et al.* (2008). The fit of metapopulation models to spatially explicit landscapes was pioneered by Hanski (1998) and recently extended to species distribution models including both species sorting and dispersal limitations (Boulangeat *et al.,* 2012). Given the parameterization, one could run neutral models to generate null hypotheses that could be eventually compared to observed distribution. This would make a significant improvement over traditional null models in ecology (Gotelli and Graves, 1996) in which there are no interactions and no dispersal limitations.

The multivariate variance partitioning framework originally proposed by Borcard *et al.* (1992) and further developed by Borcard and Legendre (2002) has been widely used to quantify the relative importance of species sorting and dispersal limitations in species distribution. This framework was originally proposed to model species distribution as a function of environmental variables, taking into account the spatial autocorrelation of species distribution (Borcard *et al*., 1992; Leduc *et al*., 1992; Legendre 1993). This methodology has been widely used over the last decade as a test of the neutral theory, its underlying assumption and to quantify dispersal limitations (Cottenie, 2005; Gilbert and Lechowicz, 2004; Hardy, 2004; Svenning *et al.,* 2004). This approach is however only a weak test of neutrality (McGill, 2003), based on the description of spatial community structure, rather than hypothesis testing. The different models we reviewed in this article could be better employed if used to generate null expectations of species distribution based on different hypotheses and then compare them. But most of all, parametrized spatially explicit neutral models could be useful if used to predict biodiversity under different global change scenarios. For instance in freshwater systems, neutral models combined with a dendritic network analysis were shown to predict well the distribution of diversity in central U.S. (Muneepeerakul *et al*., 2008). Fitted neutral models could be used to predict the consequences of habitat destruction, fragmentation or a change in the connectivity matrix (Hubbell *et al*., 2008). The spatially explicit description of the landscape is a major improvement toward that end, providing much flexibility in the scenarios that could be explored. Working with more complex representations on landscapes has several advantages. Real landscapes are not flat geometric objects; they are highly structured and diversified. This structure has long been recognized as a key component of biological diversity. In the 19th century, Moritz Wagner noted that patterns of rivers (Coyne and Orr, 2004) could explain how beetles diversified. Yet, to this day, the relationship between spatial structures and biodiversity is not resolved, but networks provide powerful tools to analyze landscapes and generate testable predictions on community assembly. For example, the neutral theory predicts less diversity in isolated communities and constant speciation (regardless of isolation; Economo and Keitt, 2008). Adding the effect of gene flow changes the predictions (Desjardins-Proulx and Gravel, 2012a), but the neutral theory does not predict adaptive radiation and might thus face problems for predicting many long-term evolutionary processes.

Finally, our analyses emphasize the need to expand on the canonical neutral theory. As pointed out by Wootton (2005), most of the unexplained deviation of empirical communities from the predictions of accurately calibrated neutral models can be attributed to non-competitive interactions. Canard *et al.* (2012) proposed that neutral processes can explain the network structure of trophic interactions with a good accuracy. Incorporating reasonable complexity in the mechanisms addressed by neutral models is not a theoreticial exercise: it will re-enforce the usefulness of the neutral theory as an operational concept, specifically one that can be used to derive baseline predictions about i) the expected local species richness, and ii) the expected species pool dissimilarity at the between-site and regional scales. These predictions are the benchmark against which empirical surveys of species richness and community structure ought to be compared and com-

ing up with realistic parameters to calibrate these models calls for a closer cooperation and dialogue between theoreticians and empiricists.

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