Title: Using neutral theory to reveal the contribution of dispersal to community assembly in complex landscapes

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Abstract

The metacommunity perspective appears naturally as the appropriate conceptual framework to make ecology more predictive, integrating elements of theoretical ecology. 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 a useful tool to understand the impact of dispersal on community organization in landscapes of various complexities. Our main objective is to use neutral theory to stress the importance of complex landscape network 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 simple 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 centrality-species richness relationship was observed for the patch dynamics, a model without any interactions. On the other hand, strong and unequal competitive interactions minimized the effect of centrality. We conclude that the neutral model is thus a useful tool to understand the joint effects of dispersal and community interactions. Our analysis shows that ecologists must now integrate more realistic landscapes when analyzing community assembly from a metacommunity perspective.

Introduction

Ecology needs to move toward a more predictive approach, integrating elements of theoretical ecology ("A road map for integrating eco-evolutionary processes into biodiversity models"). The metacommunity perspective (**Leibold2004a**) 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 & Blasius 2011)) to the regional (e.g. connection of lakes (**Leibold2004b**; Gravel et al. 2010) scales. It 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. Neutral theory of biodiversity makes the provocative assumption that species are ecologically equivalent (**Hubbell2001**; Bell 2000). Neutral ecological communities are driven only by demographic stochasticity and dispersa and thus, variation in the environment has no impact on demography. Neutral theory sparked an historical debate still lasting after more than a decade (**Etienne2011**; Chave 2004; Clark 2012; 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 (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 & 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 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 (**Wennekes2011**). Because every ecological model is a simplification of reality, scientists have to subjectively decide the level of details they put in, leaving out some elements they consider unimportant. The realism perspective requires that all assumptions of the theory must 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 **Schmueli2010**). Obviously neutral theory could only be instrumental. The question then is if such a 'general, large-scale, but vague' theory (**Wennekes2011**) is a satisfying approximation.

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 eco-

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logical drift (**Gravel2011a**). Much has been said the existence of demographic stochasticity (Clark 2012), and we therefore will let this discussion for other papers. A second answer is that dispersal and historical contingencies might have a much more profound impact on species distribution (Bahn & McGill 2007; Boulangeat et al. 2012) and ecological dynamics. The debate over the equivalence assumption and demographic stochasticity has perhaps overlook 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 (**Peterson2013**). 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-Neto2013**) that could potentially affect the coexistence mechanisms at play. We will therefore move from a perspective where dispersal is either global or spatially explicit (e.g. over a lattice), and spatial constant, to a perspective focusing on the variance of dispersal. A second generation of neutral models (e.g. **Desjardins2012a**; **Desjardins2012b**; Economo (2011); Economo & Keitt (2008), and even experiments (**Altermat2012**), recently introduced more realis-

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tic 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 operationally of the 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 **new10** The term "graph" is often preferred in computer science and mathematics **gro06** with graph algorithms being an important and active area of research **sed01** 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 **wri21; new10** We are especially interested in spatial networks, a special kind of network mixing the combinatorial properties of networks with a topological space **kob94** Thus, the vertices 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 vertices 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 **dij59** 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 for its ability to model complex structures while allowing us to extract useful metrics (Table 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 lake. 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.

For simulations, spatial networks can easily be generated with the random geometric graph algorithm **sed01** 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 **app97a**; **app97 b**; **app02a**; **app02b**; **pen03** and we provide a 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.

We also provide the code for a second structure that we call a random geometric

tree. The algorithm first builds a random geometric graph, then select a node from which to start the tree. It then calculaes the the shortest path tree **dij59** from this node to all other ones. Edges that are not located along this tree are pruned. This random geometric tree does not exactly represent dendritic landscapes but is a convenient model to simulate lake connected by rivers to a series of smaller lakes.

Spatial graphs are increasingly popular in spatial ecology and conservation biology, where patterns of connections can be used to study and influence the flow of organisms **min07**; **fal07**; **min08**; **gar08**; **urb09**; **dal10** In the neutral theory, networks were pioneered by Economo and Keitt **eco08**; **eco10** They used networks to study how different spatial structures influenced diversity. They were also used to study how the spatial structure influenced nonsympatric speciation **des12**; **des12b**

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 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 (Table 2 summarizes the parameters and variables that are 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 a S species extension of traditional metapopulation models (()Hanski1999). The standard Levins metapopulation model (()Levins1969) 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 an 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 (()Hanski1997). There are no interactions in this simple model, which means there is no limit to local species richness and no carrying capacity. Competitive, mutualistic and predator-prey interactions have been added to this framework (e.g. **Holt1996**; **Klausmeier1998**; Gravel et al. (2011); 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

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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 (**Hanski1998**). 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 is $I_i x = 1 - \prod d_x (1 - C_{ixy})$. This equation basically 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 $p_i x = I_x (I_i x + e)^{-1}$. The feedback between local and regional dynamics arises because all $p_i x$ 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, $s_x = \sum p_i$. 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). Multi-species 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 & Gyllenberg 1997), and proved to be useful in conservation ecology with predictions of extinctions following habitat destruction (**Nee1994**; **Rybicki2013**).

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* (**Hubbell2001**; Bell 2000), 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 tracts the local abundance of all species N_{ix} in each local patch. At each time step an individidual 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 possible the coupling with the metacommunity and neighbouring patches. We adopt a simple formulation based on (**Gravel2006**). 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 (**Gravel2006**). 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 neigbouring patches 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 $P_{ix} = \frac{\sum P_{iy}d_y^{-1}}{\sum d_y^{-1}}$. We assume for simplicity (and without loss of generality, (Bell 2000)) that the relative

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abundance in the metacommunity is uniform, i.-e. equal to S^{-1}. 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 **Hubbell2001**). The local recruitment probability is consequently

$Pr_{ix} = MS^{-1} + mP_{ix} + (1 - m - M)N_{ix}J_x^{-1}$.

The model is neutral because it assumes that the probabilities of local recruitment, immigration and mortality events are all equal across species. Demographic stochasticity is the source of variations in abundance, but larger disturbances could be simulated as well, as long as they hit all species with the same probability, independently of their abundance. The fundamental feature of neutral dynamics is therefore the ecological drift, defined as population changes emerging from neutraly stable population dynamics. It can be measured as the variance between replicated time series of community dynamics (**Gravel2011a**). **Hubbell2001** 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 **Hubbell2001** 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 aspect of neutral models is the realism of the speciation process and the required speciation rates to sustain species richness (**Ricklefs2003**; **Etienne2007**). Recent neutral models with more credible speciation models (**Rosindell2009**; **Desjardins2012a**) revealed the difficulty to maintain diversity in neutral models over macro-evolutionary time scales. These models nonetheless

proposed interesting predictions on endemic species richness and island biogeography (**Desjardins2012b**; Rosindell & 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 (**Leibold2004a**). There are various ways to simulate such dynamics and we picked the lottery model, in line with tradition (**Mouquet2002**) 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 offsprings that are candidate for recruitment but only one will survive and develop to the adult stage. The effect of a differentiation 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 (**Mouquet2003**; **Tilman2004**; **Gravel2006**)). 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 local 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

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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 $Pr_{ix} = \frac{\lambda_{inx}Z_{ix}}{\sum \lambda_{jnx}Z_{jx}}$. 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 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 shown that predictions are extremely variables and depend on the frequency distributions of environmental conditions, niche optimums and 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 (**Tilman2004**; **Gravel2006**). The main prediction is nonetheless that stable and predictable (meaning which species will coexist) 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 dissimilaritya mong species (**Schwilk2005**). 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 homogenizes environmental conditions. This is one of the main result 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

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(α) diversity, with a peak at intermediate dispersal. On the other hand, we expect a monotonic decrease of beta (β) and γ diversity with dispersal (**Mouquet2003**). This prediction has been validated in some experiments (**Venail2008**; Logue et al. 2011).

Results

In this section we provide simple simulation results to illustrate the impact of saptial 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 (e.g. spatial sampling sites), but both different number of edges (e.g. dispersal routes between sampling sites) and patterns of connectivity between nodes. We ask how these differences in connectivity 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 geographical and tree graph, 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 far less clear-cut result, which can

probably be attributed to the fact that our networks are relatively small in size. 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. 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 model, 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 enveloppe 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 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

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distribution of environmental conditions) and dispersal.

To a vast extent, these relationships are preserved when looking at the geodesic distances (Fiig. 4), i.e. along how many edges should one travel to connect two patchs. 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

Our objective in 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 both to understand and predict the impact of dispersal on community organization. The review of the different models shows that the fundamental difference between a neutral model and the patch dynamics model is the effect of competitive interactions on distribution, while the difference between the neutral and the 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 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 (**Gilarranz2012**). For field ecologists, and particularly limnologists,

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our review emphasizes that we need to go beyond geographic based analysis of β diversity (e.g. (**Legendre2005**)) to topological based analyses (**Peterson2013**).

The network approach to the study of spatially explicit landscapes is 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 makes a significant departure to simple island-mainland or global dispersal approaches used previously (e.g. (**Hubbell2001**; **Mouquet2002**; 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 the consideration of spatial heterogeneity of dispersal. In agreement with previous theoretical (**Desjardins2012**; Economo 2011) and experimemental studies (**Altermat2012**), the simulations show that the degree centrality has a significant impact on α diversity. Central nodes might also contribute more to maintain γ diversity, as they are essential for species to spread throughout the landscape. The nodes could be potentially quantified as keystone for the metacommunity (**Mouquet2013**). Interestingly, but not surprisingly, this effect is weaker with species sorting dynamics. We could even hypothesize it will vanish in the extreme case of niche differentiation (with low 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 reveal there could be spatial variation in coexistence mechanisms. If we take the species-sorting perspective for instance, we find that α diversity is higher in more central nodes. Since the environment is on average the same from one patch to another, 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

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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 to parametrize them and simulate real landscapes. The recruitment probabilities defined above could 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 **Hanski1998** and recently extended to species distribution models including both species sorting and dispersal limitations (Boulangeat et al. 2012). Given the parametrization, 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 (**Gotelli1996**) in which there are no interactions and no dispersal limitations.

The multivariate variance partitioning framework originally proposed by **Borcard1992** and further developed by **Borcard2002** 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 (**Leduc1992**; **Borcard1992**; **Legendre1993**). This methodology has been widely used over the last decade as a test of the neutral theory, its underlying assumption and a quantification of dispersal limitations (e.g. **Svenning2004**; **Hardy2004**;

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Gilbert2004; Cottenie2005 One problem of this approach is however that it makes a weak test of neutrality (**McGill200**), 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 more useful if used to predict biodiversity under different global change scenarios. For instance, neutral models could be used to predict the consequences of habitat destruction, fragmentation or a change in the connectivity matrix (**Hubbell2008**). 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 diverse. This diverse structure has long been recognized as a key component of diversity. In the 19th century, Moritz Wagner noted that patterns of rivers **coy04** 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 the relationship between community assembly and spatial structures. For example, the neutral theory predict less diversity in isolated communities and constant speciation (regardless of isolation) **eco08** Adding the effect of gene flow changes the predictions, but the neutral theory do not predict adaptive radiation and might thus face problems for predicting many long-term ecological processes.

Finally, our analyses emphasize the need to expand on the canonial neutral theory. As pointed out by **Wootoon2005** most of the unexplained deviation of empirical community from the prediction 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 theoreticians' 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 relevés of species richness and community structure ought to be compared, and coming up with realistic parameters to calibrate these models calls for a closer cooperation and dialogue between theoreticians and empiricists.

Acknowledgements

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References

Bahn, V. & McGill, B. J. (2007) *Can niche-based distribution models outperform spatial interpolation?* Global Ecology and Biogeography, **16**, 733–742.

Bell, G (2000) *The Distribution of Abundance in Neutral Communities.* The American naturalist, **155**, 606–617.

Bell, G (2001) *Neutral macroecology.* Science (New York, N.Y.), **293**, 2413–8.

Boulangeat, I., Gravel, D. & Thuiller, W. (2012) *Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances.* Ecology letters, 1–10.

Canard, E. et al. (2012) *Emergence of Structural Patterns in Neutral Trophic Networks.* PLoS ONE, **7**. Ed. by Ravasi, T., e38295.

Chave, J. (2004) *Neutral theory and community ecology.* Ecology Letters, **7**, 241–253.

Clark, J. S. (2012) *The coherence problem with the Unified Neutral Theory of Biodiversity.* Trends in Ecology & Evolution, **27**, 199–203.

Economo, E. P. (2011) *Biodiversity conservation in metacommunity networks: linking pattern and persistence.* The American naturalist, **177**, E167–80.

Economo, E. P. & Keitt, T. H. (2008) *Species diversity in neutral metacommunities: a network approach.* Ecology letters, **11**, 52–62.

Gotelli, N. J. & McGill, B. J. (2006) *Null Versus Neutral Models: What's The Difference?* Ecography, **29**, 793–800.

Gotelli, N. J. (2000) *Null Model Analysis of Species Co-Occurrence Patterns.* Ecology, **81**, 2606.

Gravel, D., Beaudet, M. & Messier, C. (2008) *Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species.* Ecology, **89**, 2879–88.

Gravel, D. et al. (2010) *Shade tolerance, canopy gaps and mechanisms of coexistence of forest trees.* Oikos, **119**, 475–484.

Gravel, D. et al. (2011) *Trophic theory of island biogeography.* Ecology letters, **14**, 1010–6.

Hanski, I & Gyllenberg, M (1997) *Uniting Two General Patterns in the Distribution of Species.* Science (New York, N.Y.), **275**, 397–400.

Logue, J. et al. (2011) *Empirical approaches to metacommunities: a review and comparison with theory.* Trends in ecology & evolution, **26**, 482–491.

Ricklefs, R. E. (2012) *Naturalists, natural history, and the nature of biological diversity (american society of naturalists address) *.* The American naturalist, **179**, 423–35.

Rosindell, J. & Phillimore, A. B. (2011) *A unified model of island biogeography sheds light on the zone of radiation.* Ecology letters, **14**, 552–60.

Rosindell, J. et al. (2012) *The case for ecological neutral theory.* Trends in ecology & evolution, **27**, 204–209.

Ryabov, A. B. & Blasius, B. (2011) *A graphical theory of competition on spatial resource gradients.* Ecology letters, **14**, 220–8.

Thuiller, W. et al. *A road map for integrating eco-evolutionary processes into biodiversity models.* Ecology Letters,

Tilman, D. (1994) *Competition and Biodiversity in Spatially Structured Habitats.* Ecology, **75**, 2–16.

Figure legends

Figure 1

Illustration of the four simulated landscapes. The color code represents the α diversity simulated with a neutral model, ranked from the poorest (red) to the richest (blue). 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.

Figure 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:$S = 100$, $c = 0.4$, $e = 0.1$, $J_x = 100$, $m = 0.2$, $M = 0.01$, $k = 0.1$, $u \epsilon [0, 100]$, $b = 15$, $E_x \epsilon [0, 100]$, $\overline{E_R} = 50$, $\sigma E_R = 5$. Simulations run 1000 time steps
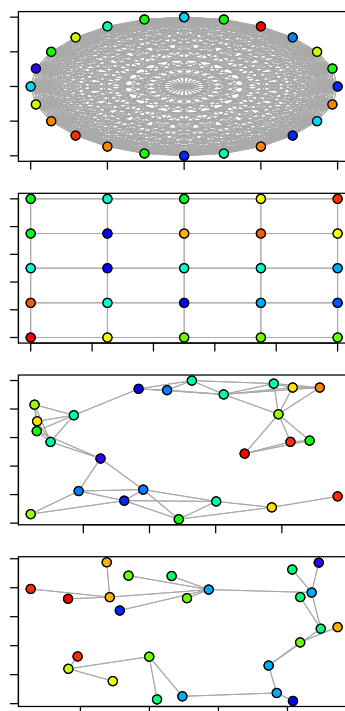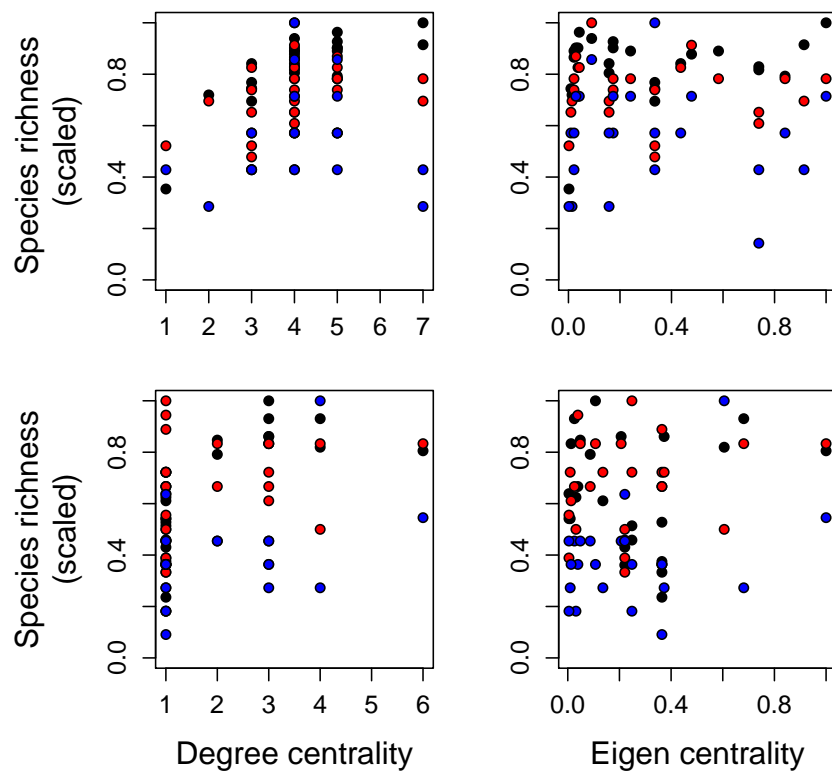
Figure 3

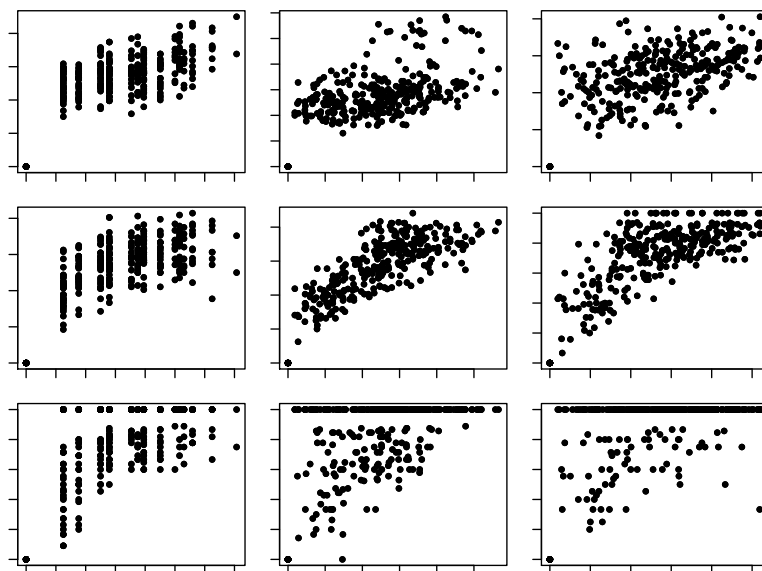**Bray curtis dissimilarity as a function of Euclidean distance**. Parameters as in Fig. 2.

Figure 4

Bray curtis dissimilarity as a function of geodesic distance. Parameters as in Fig. 2.

Figure 1

Figure 2

Figure 3

Figure 4
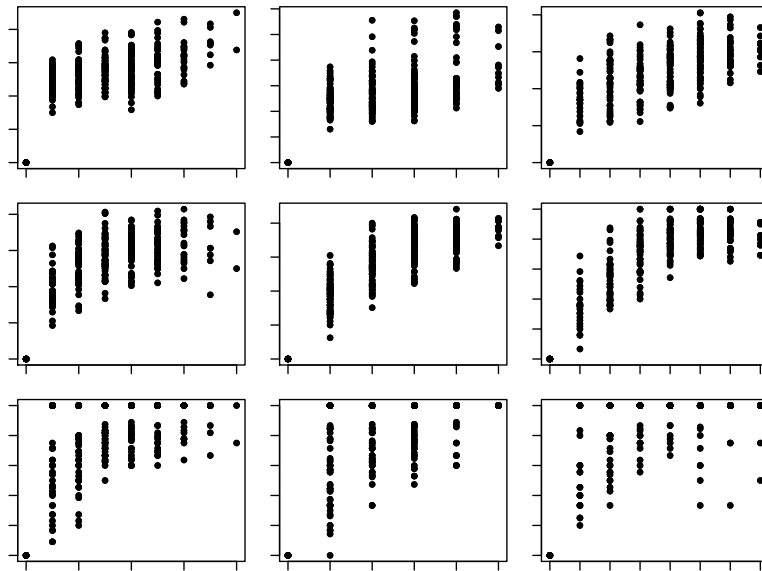
Concept	Definition
Path	A sequence of edges forming a sequence of nodes
Connection	Two nodes are connected if there is a path between them
Euclidean distance	Geographical distance between two nodes
Geodesic distance	Length of the shortest path between two nodes
Network-level metrics	
Order	Total number 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 vertex
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 note

Table 1: Main descriptors of spatial networks used in this study.

	Definition	Patch dynamics	Neutral	Species-sorting
Variables				
p	Occupancy	X		
N	Local population size		X	X
Z	Local rel. abund.		X	X
P	Rel. abund. in the neighborhood		X	X
s	Local species richness	X	X	X
d	Node degree	X	X	X
C	Prob. of a colonization event	X		
I	Prob. of a colonization event	X		
Pr	Recruitment prob.		X	X
λ	Survival prob.			X
Indices				
x, y	Node location	X	X	X
i, j	Species	X	X	X
n	Microsite			X
Parameters				
S	Size of regional species pool	X	X	X
c	Colonization prob.	X		
e	Extinction prob.	X		
J	Local carrying capacity		X	X
m	immigration prob. from neigh.		X	X
M	immigration prob. from metaco.		X	X
k	Death prob.		X	X
u	Niche optimum			X
b	Niche breadth			X
E	Microsite env. conditions			X
$\overline{E}$	Local env. average			X
σ	Local env. variance			X
$\overline{E_R}$	Regioal env. average			X
σ_R	Regional env. variance			X

Table 2: List of variables, indices and parameters from the three models