

Title: 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

47 shows that limnologists must now integrate more realistic landscapes when analyzing
48 community assembly from a metacommunity perspective.

49 Introduction

50 Ecology needs to move toward a more predictive approach, integrating elements of
51 theoretical ecology (Thuiller et al. 2013). The metacommunity perspective (Leibold et
52 al. 2004) appears naturally as the appropriate conceptual framework to fill this chal-
53 lenge. The metacommunity concept builds on feedbacks between local scale processes,
54 such as competitive interactions and local adaptation, and regional scale processes
55 such as dispersal, gene flow and speciation. It is particularly relevant to limnology,
56 where exchanges of organisms and nutrients affect community and ecosystem proper-
57 ties from the local (e.g. vertical mixing (Ryabov & Blasius 2011)) to the regional (e.g.
58 connections of lakes (Gravel et al. 2010; Leibold & Norberg 2004; Muneeppeerakul et al.
59 2008) scales. The metacommunity perspective emphasizes the importance of dispersal
60 relative to pairwise interactions in the organization of ecological communities.

61 At first sight, the development of neutral theory appears as a step back. The neutral
62 theory of biodiversity makes the provocative assumption that species are ecologically
63 equivalent (Bell 2000; Hubbell 2001). Neutral community dynamics are driven only
64 by demographic stochasticity and dispersal and thus, variation in the environment has
65 no impact on demography. Neutral theory sparked a historical debate still lasting after
66 more than a decade (Chave 2004; Clark 2012; Etienne & Rosindell 2011; Rosindell et
67 al. 2012). It was stimulated by the surprising ability of neutral models to fit some well
68 studied empirical observations such as species abundance distributions and distance-
69 decay relationships.

70 A remarkable strength of the theory is to provide a *"formal general theory of abun-*
71 *dance and diversity that will account, in a simple and economical fashion, for the many*
72 *patterns that ecologists have documented"* (Bell 2001). Even if new studies rejecting neu-
73 tral theory are consistently published (e.g. Ricklefs & Renner (2012), but see the com-
74 ments associated with this study, e.g. Etienne & Rosindell (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 be 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 hand, 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 (Wennekes et al. 2012) 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 stochas-

101 ticity of various origins blur the deterministic differences among species and promote
102 ecological drift (Gravel et al. 2011). Much has been said about the existence of demo-
103 graphic stochasticity (Clark 2012), and we will therefore leave this discussion for other
104 papers. A second explanation is that dispersal and historical contingencies might
105 have a much more profound impact on species distribution (Bahn & McGill 2007;
106 Boulangeat et al. 2012) and ecological dynamics. The debate over the equivalence
107 assumption and demographic stochasticity might have overlooked the recognition of
108 how much dispersal influence community assembly.

109 In this paper, we argue that neutral theory can be a useful tool to understand the
110 impact of dispersal on community organization in landscapes of various complexities.
111 Even for purely theoretical analyses, we need a benchmark without niche differences
112 to reveal the role of dispersal in structuring communities and understand how it in-
113 teracts with niche differentiation. We will explore recent applications of neutral the-
114 ory, at the crossroad of network theory, to better represent the impact of landscape
115 structure on biodiversity distribution. This analysis will prove particularly relevant
116 to limnology, where most riverine and lacustre habitats are characterized by their dis-
117 crete nature and spatially complex arrangements (Peterson et al. 2013). We will also
118 explore the relative contribution of ecological interaction and niche differentiation by
119 contrasting predictions of a neutral model to other metacommunity perspectives.

120 Our main objective is to use neutral theory to stress the importance of landscape
121 network structure on the distribution of diversity. We refer to the landscape organi-
122 zation as a *spatial contingency* (Peres-Neto et al. 2012) that could potentially affect the
123 coexistence mechanisms at play. We will therefore move from a perspective where dis-
124 persal is either global or constant over space (e.g. a lattice), to a perspective focusing
125 on the variance of dispersal. A second generation of neutral models (e.g. Desjardins-
126 Proulx & Gravel (2012a,b); Economo (2011); Economo & 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 & 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.

151 There are two notions of distance in spatial networks. Euclidean distance represents
152 the geographical distance between the nodes (i, j) , i.e.: $\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$. Geodesic
153 distance is the distance in the graph space, i.e.: the length of the shortest path (Dijkstra
154 1959). For example, two lakes could be very close on a map (short Euclidean distance)
155 but the geodesic distance could be great if they are not directly linked by a river.

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

168 In this paper we study four types of networks (Fig. 1). First, for the sake of com-
169 parisons, we study a complete network where dispersal is global. Then we consider
170 a lattice, which is the most regular type of spatially explicit network. Then after we
171 simulated two types of random spatial networks. We considered random geometric
172 graphs (Sedgewick 2001). In this algorithm, all nodes are assigned to a position in
173 some two-dimensional space, most often the unit square. Then, all pairs of nodes
174 within some threshold Euclidean distance r are connected with an edge. The resulting
175 networks have the desirable property of locality: if a node A is connected to two ver-
176 tices B and C . then B and C are more likely to be connected than two random vertices.

177 Random geometric networks have been extensively studied (Appel et al. 2002; Appel
178 & Russo 1997a,b, 2002; Penrose 2003) and we provide a R function to generate them.
179 The position of nodes is typically random, but we could also imagine alterations where
180 they are either more aggregated or segregated than expected by chance alone. Finally,
181 we also provided the code for a second structure that we call a random geometric tree.
182 The algorithm first builds a random geometric graph, then selects a node from which
183 to start the tree. It then calculates the the shortest path tree (Dijkstra 1959) from this
184 node to all other ones and remove edges not located along this tree. This random geo-
185 metric tree does not exactly represent dendritic landscapes but is a convenient model
186 to simulate a lake connected by rivers to a series of smaller lakes.

187 Spatial graphs are increasingly popular in spatial ecology and conservation bi-
188 ology, where the structure of connections can be used to study and influence the
189 flow of organisms (Dale & Fortin 2010; Fall et al. 2007; Garroway et al. 2008; Minor
190 & Urban 2007, 2008; Urban et al. 2009). In the neutral theory, networks were pio-
191 neered by Economo and Keitt (Economo & Keitt 2010; Economo & Keitt 2008). They
192 used networks to study how different spatial structures influenced diversity. They
193 were also used to study how the spatial structure influenced nonsympatric speciation
194 (Desjardins-Proulx & Gravel 2012a,b).

195 **Model description**

196 In this section we describe three toy models representing different perspectives of
197 metacommunity ecology: patch dynamics, neutral dynamics and species sorting. While
198 the neutral model is interesting in itself, it is by its comparison with a model without
199 any interactions (patch dynamics) and with niche differentiation (species sorting) that
200 we will be able to fully understand the interaction between these processes and land-

scape 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 (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 (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 neighbouring 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

(Hanski & Gyllenberg 1997). 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. Gravel et al. (2011); 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 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 $p_{ix} = I_{ix}(I_{ix} + e)^{-1}$. 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, $s_x = \sum p_i$. 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 anal-

252 ysis of metapopulation models also reveals interesting predictions on other aspects of
253 community organization at various spatial scales such as the species-area relationship
254 (Hanski & Gyllenberg 1997), and proved to be useful in conservation ecology with pre-
255 dictions of extinctions following habitat destruction (Rybicki & Hanski 2013; Tilman
256 et al. 1994).

257 **Neutral dynamics**

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

269 The formulation of the recruitment probability is the central piece of all neutral
270 models, making the coupling with the metacommunity and neighbouring patches pos-
271 sible. We adopt a simple formulation based on (Gravel et al. 2006). The approach is
272 conceptually similar to placing a trap in a canopy gap and picking a seed at random
273 among the ones falling in to determine the identity of the recruited species. The com-
274 position of the seed pool in that trap will be a mixture of local dispersal and immi-
275 grants from the metacommunity. For simplicity, we consider three spatial scales of
276 dispersal but it would be easy to generalize the approach to a continuous seed disper-

277 sal kernel (Gravel et al. 2006). The parameter m is the probability that the recruit is a
 278 migrant from neighbouring patches, M is the probability it comes from a larger (and
 279 fixed) metacommunity, and consequently, by subtraction, $1 - m - M$ is the probab-
 280 ity it comes from local dispersal. The fraction $N_{ix}J_x^{-1}$ is the local relative abundance
 281 and P_{ix} is the relative abundance of species i in the seed pool coming from patches
 282 connected to patch x . The relative abundance in the neighborhood is weighted by the
 283 degree of the connected nodes because some nodes will spread their seeds across a
 284 higher number of nodes and thus contribute less to the seed pool. We thus consider
 285 $P_{ix} = \sum P_{iy}d_y^{-1} / \sum d_y^{-1}$. We assume for simplicity that the relative abundance in the
 286 metacommunity is uniform, i.e. equal to S^{-1} , but other distributions could be used.
 287 The metacommunity is usually modelled with a log-series (e.g. Hubbell (2001)), but it
 288 has been shown that for a range of realistic dispersal rates a uniform distribution does
 289 not have distinguishable impacts relative to a log-series (Bell 2000). This immigra-
 290 tion prevents the collapse of the metacommunity to a single species, since otherwise
 291 all species except one will face extinction by ecological drift (speciation prevents this
 292 phenomenon to occur in Hubbell (2001)). The local recruitment probability Pr_{ix} is
 293 consequently $Pr_{ix} = MS^{-1} + mP_{ix} + (1 - m - M)N_{ix}J_x^{-1}$. Self-replacement occurs when
 294 an individual of species i is replaced by an offspring of the same species coming either
 295 from the remaining local individuals or from the metacommunity.

296 The model is neutral because it assumes that the probabilities of local recruitment,
 297 immigration and mortality events are all equal across species. Demographic stochas-
 298 ticity is the source of variations in abundance, but larger disturbances could be simu-
 299 lated as well, as long as they hit all species with the same probability, independently
 300 of their identity. The fundamental feature of neutral dynamics is therefore the eco-
 301 logical drift, defined as population changes emerging from neutrally stable population
 302 dynamics. It can be measured as the variance between replicated time series of com-

303 munity dynamics (Gravel et al. 2011). Hubbell (2001) provides a very comprehensive
304 analysis of the model, with specific attention to the effect of the different parame-
305 ters on drift (and consequently variance in abundance) and time to extinction. De-
306 spite its simplicity, the neutral model is surprisingly rich in the predictions it makes.
307 Bell (2001) and Hubbell (2001) analyzed the performance of neutral models to pre-
308 dict species abundance distributions, the range-abundance relationship, spatial varia-
309 tion in abundance, the species-area relationship, community turnover (beta-diversity)
310 and co-occurrence. Recent trophic neutral models were also found to predict real-
311 istic ecological network structures (Canard et al. 2012). Other than the ecological
312 equivalence assumption, one of the most criticized aspect of neutral models is the
313 realism of the speciation process and the required speciation rates to sustain species
314 richness (Etienne et al. 2007; Ricklefs 2003). Recent neutral models with more cred-
315 ible speciation models (Desjardins-Proulx & Gravel 2012b; Rosindell et al. 2010) re-
316 vealed the difficulty to maintain diversity in neutral models over macro-evolutionary
317 time scales. These models nonetheless proposed interesting predictions on endemic
318 species richness and island biogeography (Desjardins-Proulx & Gravel 2012a; Rosin-
319 dell & Phillimore 2011).

320 **Species sorting and mass effect**

321 The species sorting and the mass effect perspectives build on the notion of species-
322 specific responses to a spatially varying environment (Leibold et al. 2004). There are
323 various ways to simulate such dynamics and we picked the lottery model, in line with
324 tradition (Mouquet & Loreau 2002) and for its proximity to the neutral model de-
325 scribed above. Competition for space occurs during recruitment after the death of
326 an adult. The recruitment is a lottery among potential candidates as in the neutral
327 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 & 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 $Pr_{ix} = \lambda_{inx}Z_{ix} / \sum \lambda_{jnx}Z_{jx}$. The function describing the relationship between a microsite condition and survival could take various forms; we used the traditional gaussian curve describing the niche, $\lambda_{inx} = \exp\left(-\frac{(E_{nx}-u_i)^2}{2\pi b_i^2}\right)$, 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 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 & 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 homogenizes 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 & 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 both in num-

ber 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 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. 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

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

423 To a vast extent, these relationships are preserved when looking at the geodesic
424 distances (Fig. 4), i.e. along how many edges should one travel to connect two patches.
425 Interestingly enough, the distance-dissimilarity relationship for the neutral model is
426 markedly hump-shaped, with sites being at a medium distance having the maximal
427 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 both to 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 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 & Bascompte 2012). For field ecologists, and particularly limnologists, our review emphasizes that we need to go beyond geographic based analysis of β diversity (e.g. (Legendre et al. 2005)) to topological based analyses (Dale & 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 (e.g. Hubbell (2001); Mouquet & 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 & Gravel 2012a; Economo 2011) and experimental 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 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 instru-

ment 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 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 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 (Gotelli & 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 & 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 (e.g. Cottenie (2005); Gilbert & 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

506 useful if used to predict biodiversity under different global change scenarios. For in-
507 stance in freshwater systems, neutral models combined with a dendritic network anal-
508 ysis were shown to predict well the distribution of diversity in central United-States
509 (Muneepeerakul et al. 2008). Fitted neutral models could be used to predict the conse-
510 quences of habitat destruction, fragmentation or a change in the connectivity matrix
511 (Hubbell et al. 2008). The spatially explicit description of the landscape is a major im-
512 provement toward that end, providing much flexibility in the scenarios that could be
513 explored.

514 Working with more complex representations on landscapes has several advantages.
515 Real landscapes are not flat geometric objects, they are highly structured and divers-
516 fied. This structure has long been recognized as a key component of biological diver-
517 sity. In the 19th century, Moritz Wagner noted that patterns of rivers (Coyne & Orr
518 2004) could explain how beetles diversified. Yet, to this day, the relationship between
519 spatial structures and biodiversity is not resolved, but networks provide powerful
520 tools to analyze landscapes and generate testable predictions on community assem-
521 bly. For example, the neutral theory predicts less diversity in isolated communities
522 and constant speciation (regardless of isolation – (Economo & Keitt 2008). Adding the
523 effect of gene flow changes the predictions (Desjardins-Proulx & Gravel 2012a), but
524 the neutral theory does not predict adaptive radiation and might thus face problems
525 for predicting many long-term evolutionary processes.

526 Finally, our analyses emphasize the need to expand on the canonical neutral the-
527 ory. As pointed out by Wootton (2005), most of the unexplained deviation of empirical
528 communities from the predictions of accurately calibrated neutral models can be at-
529 tributed to non-competitive interactions. Canard et al. (2012) proposed that neutral
530 processes can explain the network structure of trophic interactions with a good accu-
531 racy. Incorporating reasonable complexity in the mechanisms addressed by neutral

models is not a theoretical 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 coming up with realistic parameters to calibrate these models calls for a closer cooperation and dialogue between theoreticians and empiricists.

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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. 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.

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

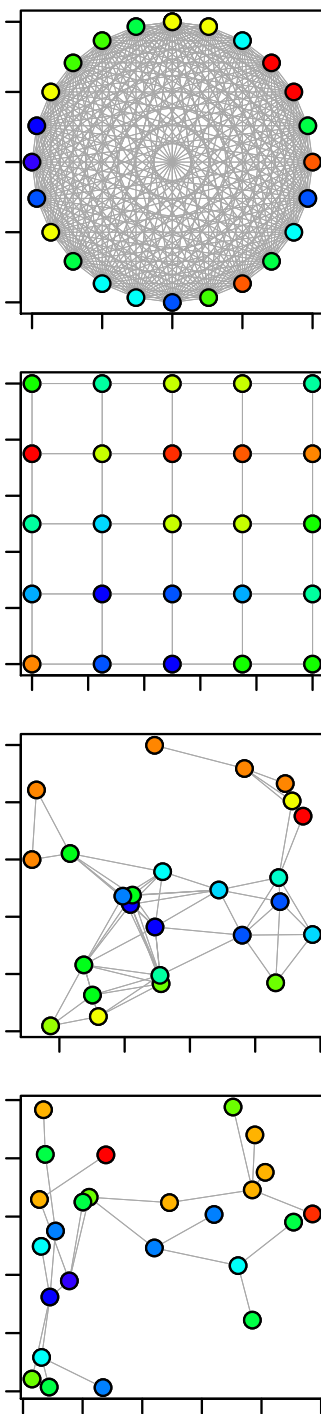
Figure 3

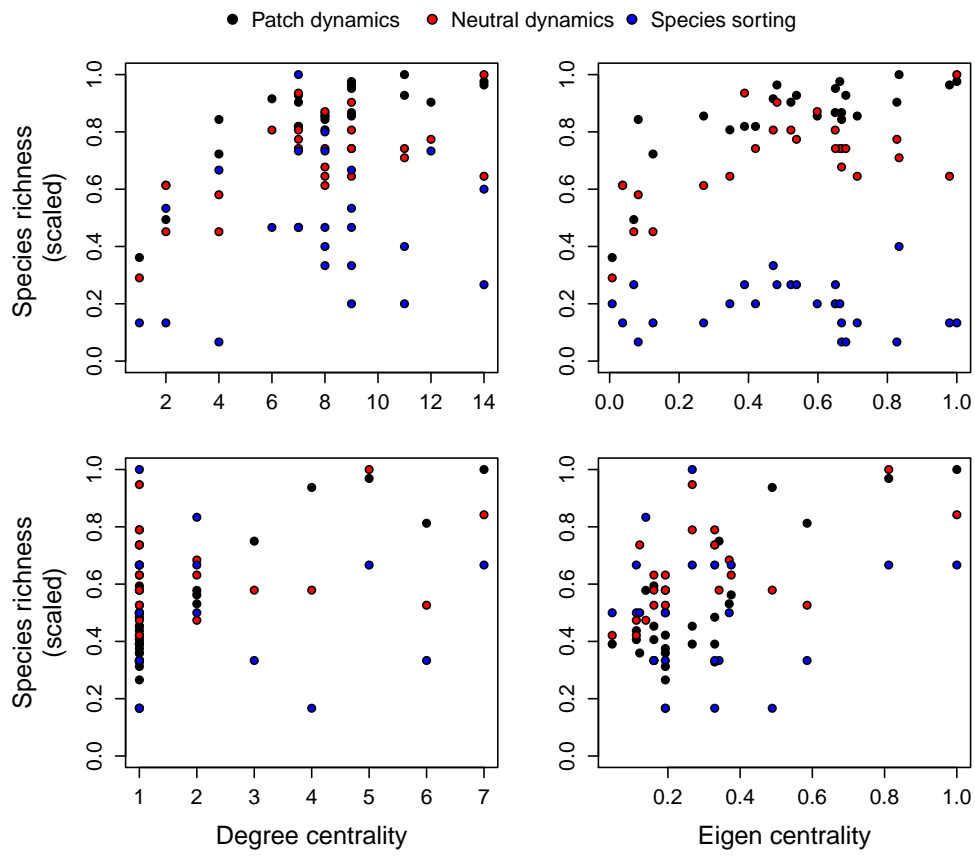
Bray curtis dissimilarity as a function of Euclidean distance. The dissimilarity among all pairs of local communities is illustrated as a function of the distance for three types of spatial networks and three metacommunity perspectives. Parameters as in Fig. 2.

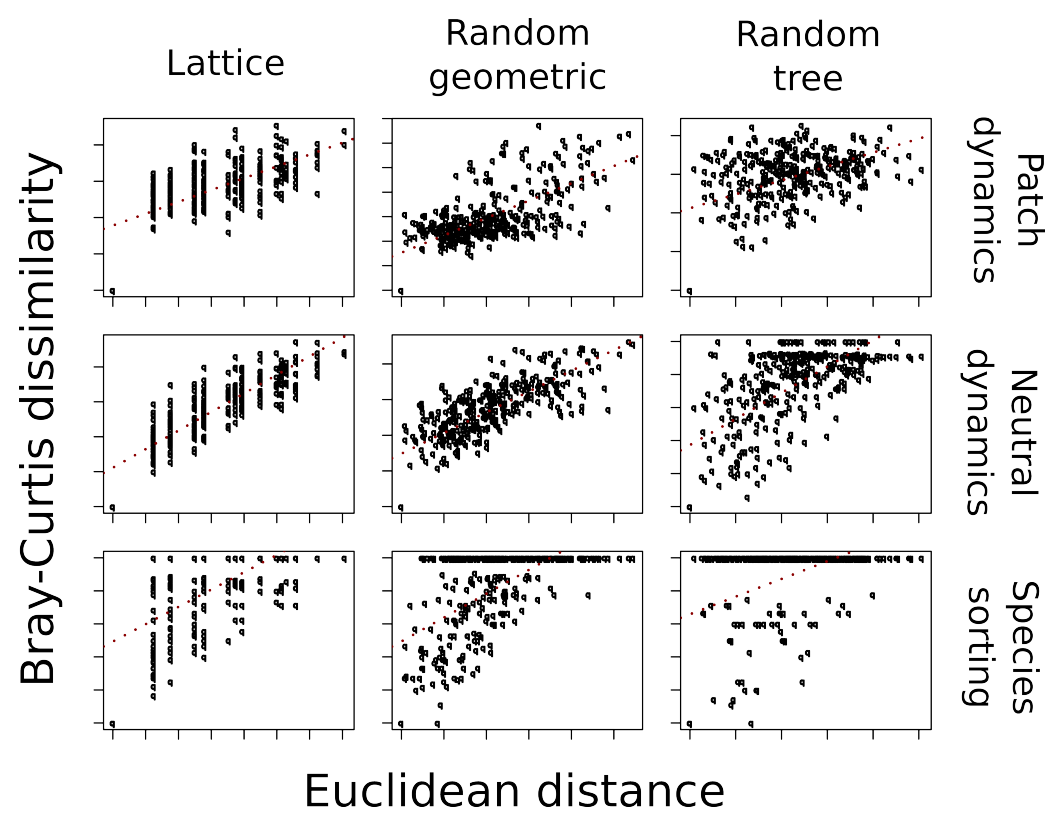
Figure 4

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.

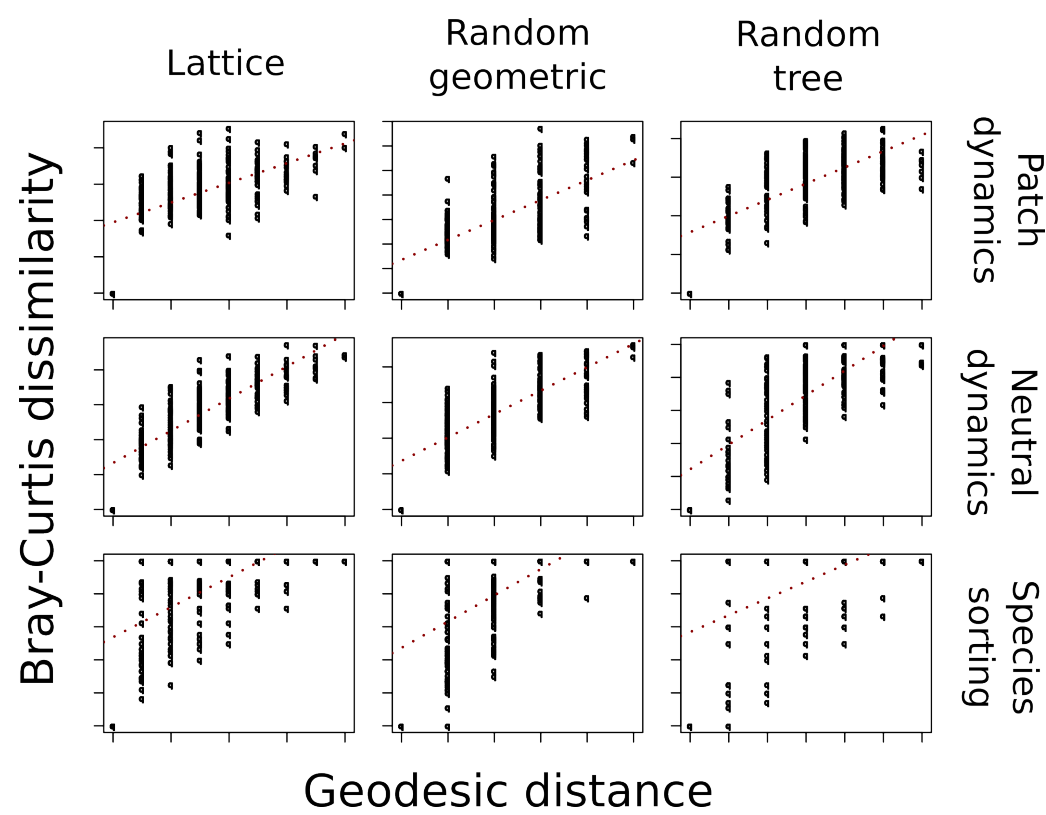
737 **Figure 1**







740 **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 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

Table 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.

	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	Col. prob. from patch y to patch x	X		
I	Col. prob. at patch x given neighbours	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				
r	Number of patches	X	X	X
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
\bar{E}	Local env. average			X
σ	Local env. variance			X
\bar{E}_R	Regional env. average			X
σ_R	Regional env. variance			X

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