

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

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1 Introduction

Ecologists are required to move toward a predictive ecology, integrating elements of theoretical ecology (**Thuiller2013**), and the metacommunity perspective appears naturally as the appropriate conceptual framework to develop the new modeling techniques required 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 **Leibold2004a**. This perspective is particularly relevant to limnology, where exchanges of organisms and nutrients affect community and ecosystem properties from the local (e.g. vertical mixing (**Ryabov2011**)) to the regional (e.g. connection of lakes (**Leibold2004b**)) scales. It emphasizes the importance of dispersal relative to pairwise interactions in the organization of ecological communities.

The development of neutral theory has been quite provocative in that respect, as one could see it as a step back in time. Neutral theory makes the provocative assumption that species are ecologically equivalent and thereby any variation in the environment has no impact on demography (**Bell2000; Hubbell2001**). Only demographic stochasticity and dispersal drive the structure of neutral ecological communities. It therefore appears that, on first sight, neutral theory is useless. We will develop in this paper the argument that neutral theory could be a useful tool to understand the impact of dispersal on community organization in landscapes of various complexities.

Neutral theory sparked an historical debate that is still lasting after more than a decade (**Chave2004; Etiennee2011; Rosindell2012; Clark2012**). It was stimulated by the surprising ability of neutral models to fit several well studied empirical observations such as species abundance distributions and distance-decay relationships. A remarkable strength of neutral 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” (**Bell2001**). Even if new studies rejecting neutral theory are consistently published (e.g. **Ricklefs2012**), there is now almost a consensus 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. **Bell2001** 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 is still useful when used as a null hypothesis (**Gotelli2006**). It is considered as an improvement over traditional null hypotheses based on randomization (**Gotelli2000**) because it readily integrates dispersal. The strong version on the other hand 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, any scientist has to subjectively decide the level of details he puts in, leaving out some elements judged unimportant. The realism perspective requires that all assumptions of 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 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? We see two

potential answers to this question. A first answer might be that stochasticity of various origins can blur the deterministic differences among species and promote ecological drift (**Gravel2011**). Much has been said the existence of demographic stochasticity, some ecologists even arguing that neutral models impede progress in community ecology by hiding niche differences (**Clark2012**), and we therefore will let this discussion for other papers. The second answer is that dispersal and historical contingencies might have a much more profound impact on species distribution (**Bahn2007**; **Boulangeat2012**) 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 is useful both to understand and predict the impact of dispersal on community organization. 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 a their discrete nature and spatially complex arrangements (**Peterson2013**). We will also reveal the relative contribution of ecological interaction and niche differentiation by contrasting predictions of a neutral model to other metacommunity perspectives.

Our main objective in this paper 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,

97 to a perspective focusing on the variance of dispersal. A second generation of neutral
 98 models (e.g. **Economo2008; Economo2011; Desjardins2012a; Desjardins2012b** and
 99 even experiments (**Altermat2012**), recently introduced more realistic landscapes and
 100 found surprising contributions of spatial contingencies. We will start with a short re-
 101 view of the main approaches to describe spatial networks and the studies investigating
 102 them. Then we will describe three simple toy models of metacommunity dynamics,
 103 taking this opportunity to review their assumptions and main predictions. We provide
 104 as Supplementary Material the R scripts for the toy models and all simulations con-
 105 ducted for this paper. We then conduct simple simulations of these models to reveal
 106 with simple examples the impact of spatial network structure on diversity distribu-
 107 tion. We conclude with a discussion on the operationality of the framework.

108 **2 Network representation of landscapes**

109 A network is a discrete mathematical object made of two sets: a set of vertices (or
 110 nodes) V and a set of edges E connecting the vertices **new10** The term “graph” is often
 111 preferred in computer science and mathematics **gro06** with graph algorithms being an
 112 important and active area of research **sed01** A network is a combinatorial object: it is
 113 used to study how discrete entities are connected and how they combine together to
 114 create complex structures. They are used to study molecules, food webs, social net-
 115 works, or even the relationship between variables in statistics **wri21; new10** We are
 116 especially interested in spatial networks, a special kind of network mixing the com-
 117 binatorial properties of networks with a topological space **kob94** Thus, the vertices in
 118 a spatial graph are embedded in some other space, most often the two or three- di-
 119 mensional Euclidean space. This object brings a rich representation to spatial ecology
 120 and is particularly suited for systems of lakes and rivers, which can easily be repre-

121 sented by vertices and edges. There are two notions of distance in spatial networks.
 122 Euclidean distance represents the geographical distance between the vertices (i, j) , i.e.:
 123 $\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$. Geodesic distance is the distance in the graph space, i.e.: the
 124 length of the shortest path **dij59** For example, two lakes could be very close on a map
 125 (short Euclidean distance) but if they are not directly linked by a river the geodesic
 126 distance could be great.

127 For simulations, spatial networks can easily be generated with the random geomet-
 128 ric graph algorithm **sed01** In this algorithm, all vertices are assigned to a position in
 129 some two-dimensional space, most often the unit square. Then, all pairs of vertices
 130 within some threshold Euclidean distance r are connected with an edge. The resulting
 131 networks have the desirable property of locality: if a vertex A is connected to two ver-
 132 tices B and C . then B and C are more likely to be connected than two random vertices.
 133 Random geometric networks have been extensively studied **app97a; app97 b; app02a;**
 134 **app02b; pen03** and we provide a R function to generate them. The position of vertices
 135 is typically random, but we could also imagine alterations where they are either more
 136 aggregated or segregated than expected by chance alone.

137 We also provide the code for a second structure that we call a random geometric
 138 tree. It builds a tree from the shortest path tree **dij59** of a vertex in a random geometric
 139 network. This random geometric tree does not exactly represent dendritic landscapes
 140 but is a convenient model to simulate lake connected by rivers to a series of smaller
 141 lakes.

142 Spatial graphs are increasingly popular in spatial ecology and conservation biol-
 143 ogy, where patterns of connections can be used to study and influence the flow of
 144 organisms **min07; fal07; min08; gar08; urb09; dal10** In the neutral theory, networks
 145 were pioneered by Economo and Keitt **eco08; eco10** They used networks to study how
 146 different spatial structures influenced diversity. They were also used to study how the

147 spatial structure influenced nonsympatric speciation **des12; des12b**

148 Concepts Path A sequence of edges forming a sequence of vertices. Connection Two
149 vertices are connected iff there is a path between them. Geodesic distance Length of
150 the shortest path between two vertices. Network-level metrics Order Total number of
151 vertices. Size Total number of edges. Connectivity A measure of robustness: the min-
152 imum number of elements to remove to isolate the vertices. Components The number
153 of connected subsets. Vertex-level metrics Degree The number of edges of a vertex.
154 Closeness centrality Average geodesic distance between a vertex and all other vertex.
155 Eigenvector centrality A measure of centrality based on the concept that connection to
156 highly connected vertices are more important. Betweenness centrality The number of
157 shortest paths from all vertices to all others that pass through that vertex.

158 **Model description**

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

	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
\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 1: List of variables, indices and parameters from the three models

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 population over a homogeneous landscape. The basic unit is the population. The Levins 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. 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 (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. Tilman1994; Klausmeier1998; Holt1996) 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 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 (Hanski1997), 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

221 simulate this *zero-sum rule* (Bell2000; Hubbell2001), but they all result in the same
 222 constraint that the increase in abundance of a species could only occur after an equiv-
 223 alent decrease by another species. One important change in the formulation of most
 224 neutral models relative the patch dynamics model presented above is therefore that it
 225 is individual-based, not population based. We therefore considered in our toy model
 226 of neutral dynamics that each local patch holds J_x individuals. The model tracts the
 227 local abundance of all species N_{ix} in each local patch. At each time step an individid-
 228 ual dies with probability k . Recruitment only occurs in vacant sites, similarly to a tree
 229 by tree replacement process in a closed canopy forest.

230 The formulation of the recruitment probability is the central piece of all neutral
 231 models, making possible the coupling with the metacommunity and neighbouring
 232 patches. We adopt a simple formulation in our model based on (Gravel2006). The
 233 approach is conceptually similar to placing a seed trap in a canopy gap and pick-
 234 ing a seed at random among the ones falling in to determine the identity of the re-
 235 cruited species. The composition of the seed pool in that trap will be a mixture of
 236 local dispersal and immigrants from the metacommunity. For simplicity, we consider
 237 three spatial scales of dispersal but it would be easy to generalize the approach to
 238 a continuous seed dispersal kernel (Gravel2006). The parameter m is the probab-
 239 ity that the recruit is a migrant from neighbouring patches, M is the probability it
 240 comes from a larger (and fixed) metacommunity, and consequently, by substraction,
 241 $1 - m - M$ is the probability it comes from local dispersal. The fraction $N_{ix}J_x^{-1}$ is the
 242 local relative abundance and P_{ix} is the relative abundance of species i in the seed pool
 243 coming from neighbouring patches x . The relative abundance in the neighborhood is
 244 weighted by the degree of the connected nodes because some nodes will spread their
 245 seeds across a higher number of nodes and thus contribute less to the seed pool. We
 246 consider simply $P_{ix} = \frac{\sum_y d_y^{-1} P_{iy}}{\sum_y d_y^{-1}}$. We assume for simplicity (and without loss of gener-

ality, (**Bell2000**)) that the relative abundance in the metacommunity is uniform, i.-e. equal to S^{-1} . This immigration prevents the collapse of the metacommunity because 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 a local recruitment, an immigration and a mortality event 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 density. The fundamental feature of neutral dynamics is therefore the ecological drift, defined as population changes emerging from neutrally stable population dynamics. It can be measured as the variance between replicated time series of community dynamics (**Gravel2011**). **Hubbell2001** provides a very comprehensive analysis of the model, with specific attention to the effect of the different parameters on the drift (and consequently variance in abundance) and time to extinction. Despite its simplicity, the neutral model is surprisingly rich in the predictions it makes. **Bell2001** and **Hubbell2001** analyzed the performance of neutral models to predict species abundance distributions, range-abundance relationship, spatial variation in abundance, species-area relationship, community turnover (beta-diversity) and co-occurrence. Recent trophic neutral models also predicted realistic ecological networks (**Canard2012**). 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 however also generated interesting novel predictions on en-

273 demic species richness (**Rosindell2011; Desjardins2012b**).

274 **Species-sorting and mass effect**

275 The species-sorting and the mass effect perspectives build on the notion of species-
276 specific responses to a spatially varying environment (**Leibold2004a**). There are var-
277 ious ways to simulate such dynamics and we picked the lottery model, in line with
278 tradition (**Mouquet2002**) and for its proximity to the neutral model described above.
279 Competition for space occurs during recruitment after the death of an adult. The re-
280 cruitment is a lottery among potential candidates as in the neutral model. The recruit-
281 ment probability is however biased by species specific response to local environmental
282 conditions.

283 The lottery dynamics described above for the neutral model assume there is a very
284 large number of offsprings that are candidate for recruitment but only one will sur-
285 vive and develop to the adult stage. The effect of a differentiation to local environ-
286 mental conditions could be implemented at this stage with a biased survival proba-
287 bility. The J_x individuals all experience a unique environmental condition E_{nx} called
288 a microsite n . We considered a patch average $\overline{E_x}$, with a within-patch variance σ_x .
289 The regional average is $\overline{E_R}$ and the regional variance σ_R (for simplicity we considered
290 normal distributions, but different distributions will lead to different regional similar-
291 ity constraints (**Mouquet2003; Tilman2004; Gravel2006**)). We consider that a frac-
292 tion λ_{inx} of offsprings reaching the microsite where recruitment occurs will survive.
293 The recruitment probability is therefore biased in favour of the species with highest
294 survival because only some species will be able to cope with the local environmen-
295 tal conditions. For tractability we define the relative abundance in the seed rain as
296 $Z_{ix} = MS^{-1} + mP_{ix} + (1 - m - M)N_{ix}J_x^{-1}$. The calculation of the relative abundance in
297 the seed rain is the same as the neutral model but the recruitment probability dif-

fers 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, $\lambda_{inx} = \exp -\frac{(E_{inx}-u_i)^2}{2\pi b_i^2}$, 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 distribution 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. Local species richness will first depend on the joint effects of local heterogeneity and niche breadth because coexistence requires a sufficient dissimilarity among 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 diversity, with a peak at intermediate dispersal. On the other hand, we expect a monotonic decrease of beta and gamma diversity with

dispersal (Mouquet2003). This prediction has been validated in some experiments (Venail2008; Logue2011).

3 Results

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 (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 meta-community model. Our analysis is not exhaustive, it is provided simply to illustrate the interaction between metacommunity perspectives and landscape structures on alpha, beta and gamma diversity.

In Fig. 2, we present the species richness of each node of the network (alpha diversity), as a function of the centrality of the node, under different assumptions of meta-community dynamics and network structure. We scaled the species richness by the maximal local species richness to facilitate comparison between models. The model parameterization is responsible for differences in both alpha and gamma diversity and thus prevents meaningful absolute comparisons. It appears that both in the geographical and random tree graphs, the path dynamics model has a much more considerable variation in local species richness. However, in all cases the alpha diversity increases with the node degree centrality and not so much with eigencentality. There are some clear differences among metacommunity perspectives. First, the relationship between degree centrality and species richness is strongest for patch dynamics, followed by

348 neutral dynamics and then species sorting. Second, there is apparently much more
349 scatter in the species sorting scenario. Thirdly, the richness-centrality relationship
350 appears weaker for the random tree graph.

351 Finally, Figs. 3 and 4 present, respectively, the between patch β diversity as a func-
352 tion of the shape of the network, under the three dynamic models. We simply used
353 Bray-Curtis measure of dissimilarity between patches. In Fig. 3, the distance is ex-
354 pressed as the euclidean (geographic) distance between two patches. Although this
355 neglects how dispersal connects the different patches, there is already a clear signal
356 of geographic distance on β diversity. In both the neutral and patch dynamics model,
357 local communities become increasingly dissimilar when the distance between them
358 increases. In other words, two communities which are close to each other will share a
359 large proportion of their species, whereas two communities which are afar will share
360 a small proportion. In the species-sorting model, the relationship between distance
361 and dissimilarity is similar, Nonetheless, it forms an envelope of points (with most
362 points lying in the upper-left part of the graph). While two distant communities will
363 be dissimilar, there is no telling how dissimilar two close communities will be. Note
364 this relationship for SS varies significantly with the spatial distribution of microsites
365 (not shown). At one extreme, if all patches hold the same average conditions, then
366 we should expect no relationship between dissimilarity and distance. On the other
367 hand, if the average conditions are highly variable among localities (as in here), then
368 we should expect two communities close to be potentially dissimilar (if conditions are
369 different) or similar (if they are the same). The variance should thus be larger. A
370 distance-dissimilarity relationship arises in the situation where dispersal promotes a
371 mass effect (as in here). Such results emphasize the interaction between spatial con-
372 tingencies (here connectivity and distribution of environmental conditions).

373 To a vast extent, these relationships are preseved when looking at the topological

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

4 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 alpha 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 (Gillarranz2012). For field ecologists, and particularly limnologists, our review emphasizes that we need to go beyond geographic based analysis of beta-diversity (e.g. (Legendre2005)) to topological based analyses (Peterson2013).

398 The network approach to the study of spatially explicit landscapes is a major ad-
399 vancement in metacommunity ecology. It is a first step to make the concept opera-
400 tional because it accounts for more realistic landscape structures and dispersal ker-
401 nels. It makes a significant departure to simple island-mainland or global dispersal
402 approaches used previously (e.g. (Tilman1994; Mouquet2002; Hubbell2001)). But
403 dispersal is also spatially explicit in a lattice model and it does not make the landscape
404 more realistic. We believe the fundamental contribution of this approach is the consid-
405 eration of spatial heterogeneity of dispersal. In agreement with previous theoretical
406 (Economo2011; Desjardins2012) and experimental studies (Altermat2012), the
407 simulations show that the degree centrality has a significant impact on local species
408 richness. Central nodes might also contribute more to maintain regional diversity, as
409 they are essential for species to spread throughout the landscape. The nodes could
410 be potentially quantified as keystone for the metacommunity (Mouquet2013). In-
411 terestingly, but not surprisingly, this effect is weaker with species sorting dynamics.
412 We could even hypothesize it will vanish in the extreme case of niche differentiation
413 (with low overlap for instance) and low mass effect. The neutral versus niche com-
414 parison therefore illustrates that very strong unequal competitive interactions could
415 overwhelm the impact of dispersal.

416 The network approach and the comparison between metacommunity perspectives
417 reveal there could be spatial variation in coexistence mechanisms. If we take the
418 species-sorting perspective for instance, we find that alpha diversity is higher in more
419 central nodes. Since the environment is constant, it implies that diversity in these
420 communities is maintained by a stronger mass effect. It results in spatial variation in
421 the relative importance of species-sorting, the mass effect and to a certain extent the
422 neutral drift. Because the degree centrality was the best variable explaining diversity,
423 we should expect the degree distribution to strongly impact the relative importance

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 parameterize 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 **Gravel2008**. 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 (**Boulangeat2012**). Given the parameterization, one could run neutral models to generate null hypotheses that could be eventually compared to observed distribution. This would make a significant improvement over traditional null models in ecology (Gotelli1996) where there are no interactions and no dispersal limitations.

The multivariate variance partitioning framework originally proposed by Borcard et al. (1992) and further developed by Borcard and Legendre (2002) has been widely used to quantify the relative importance of species sorting and dispersal limitations in species distribution. This framework was originally proposed to model species distribution as a function of environmental variables, taking into account the spatial autocorrelation of species distribution (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; Gilbert2004; Cottenie2005). One problem of this approach is however that it makes a weak test of neutrality (McGill2003), 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 expectations based on different hypotheses and then compare them. But most of all, parameterized spatially explicit neutral models could be more useful if used to generate expectations. 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 realistic landscapes

How to add other types of interactions - Wootton: variation arises from unaccounted interactions

5 Acknowledgements

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465 **Figure legends**

466 **Figure 1**

467 **Illustration of the four simulated landscapes.** The color code represents the local
468 species richness simulated with a neutral model, ranked from the poorest (red) to the
469 richest (blue). Parameters are: $P = 100$, $N = 25$, $m = 0.2$, $M = 0.01$, $k = 0.1$, $J_x = 100$.

470 **Figure 2**

471 **Relationship between local species richness and metrics of node centrality.** The
472 upper two panels are simulation results conducted with the random geometric graph
473 illustrated at Fig. 1 and the lower two panels are runs with the random tree graph.

474 **Figure 3**

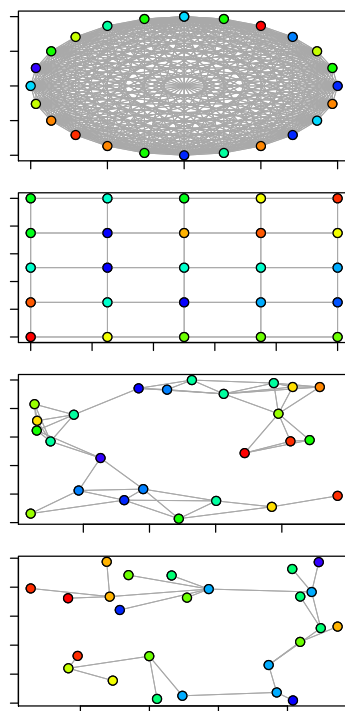
475 **Bray curtis dissimilarity as a function of geographic distance.**

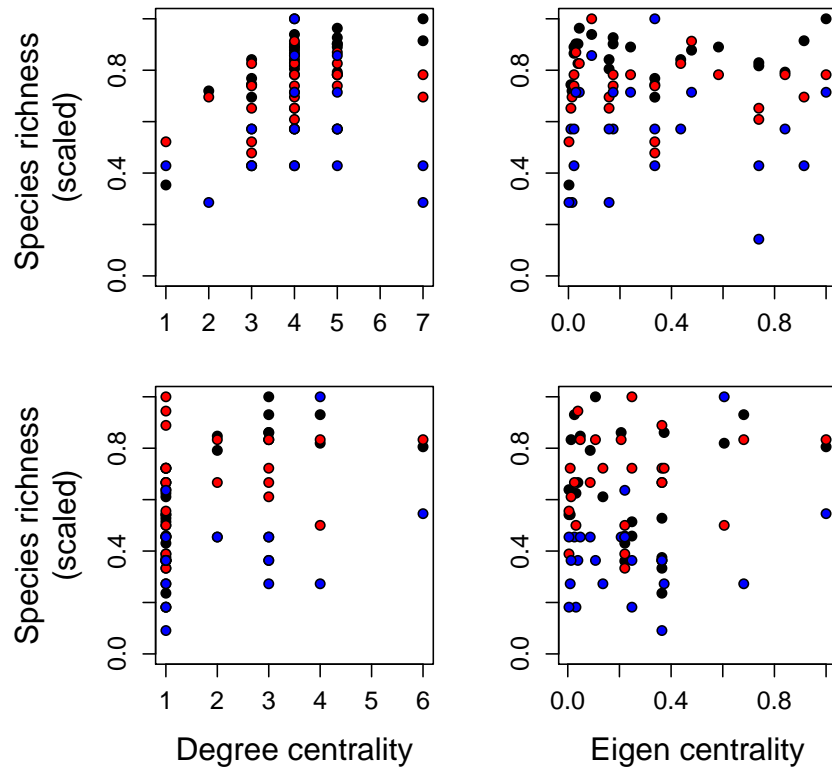
476 **Figure 4**

477 **Bray curtis dissimilarity as a function of topological distance.**

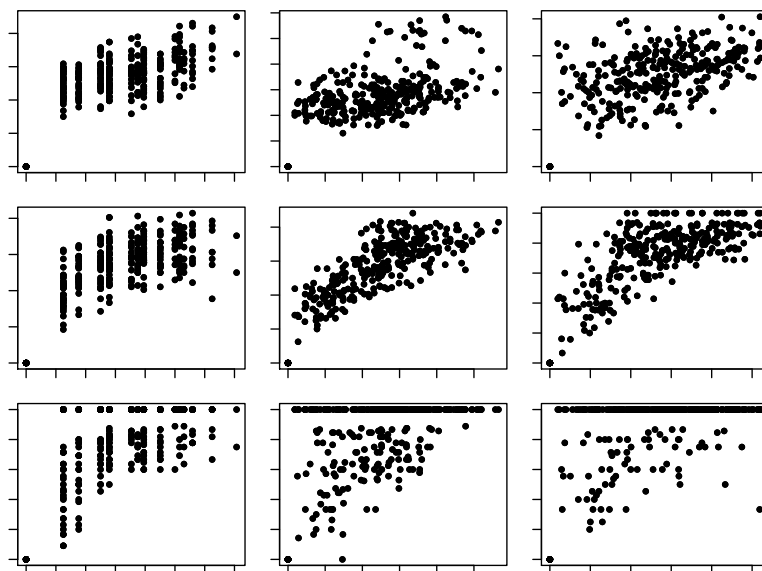
478 **Figures**

479 **Figure 1**





481 **Figure 3**



482 **Figure 4**

