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

Authors: Dominique Gravel[1,2,*], Timothée Poisot[1,2], Philippe Desjardins-Proulx[1,2]

1: Canada Research Chair on Terrestrial Ecosystems. Département de biologie, chimie et géographique, Université du Québec à Rimouski, 300 Allée des Ursulines, Québec, Canada. G5L 3A1.

2: Québec Centre for Biodiversity Sciences, Stewart Biological Sciences Building, 1205 Dr. Penfield Avenue, Montréal (QC), H3A 1B1, Canada

Words in the abstract:
Words in the main text:
Words in the legends:
References:
Table:

1   Introduction

Community assembly is concerned by patterns and processes occurring at various spatial scales (**Levin1992**). Until the development of metacommunity ecology, studies on community assembly were often restricted to local populations, with a strong focus on pairwise interactions (e.g. **MacArthur1972**; **May1973**; **Pimm1982**; **DeAngelis1992**). The emphasis on local communities has been vigorously criticized by **Ricklefs2008** who has long recognized that local dynamics and community structure are strongly contingent on processes occurring at much larger spatial scales (**Ricklefs1987**). 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 metacommunity concept has been proposed by **Leibold2004a** as a novel approach to link different spatial scales in ecology. It 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. Ecologists are now 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 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 in community ecology that is still lasting after more than a decade (**Chave2004**; **Etiennee2011**; **Rosindell2012**; **Clark2012**). It was stimulated by the impressive ability of neutral models to fit several well studied empirical observations such as species abundance distributions and distance-decay relationships. A remarkable strenght 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 envisionned 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

3

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 the 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 hidding niche differences (**Clark2012**), and we therefore will keep 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**) 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 biodiversitity 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. 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, to a perspective focusing on the variance of dispersal. A second generation of neutral models (e.g. **Economo2008**; **Economo2011**; **Desjardins2012a**; **Desjardins2012b** and even experiments (**Altermat2012**), recently introduced more realistic lanscapes and found surprising contributions of spatial contingencies. We will start with a short review of the main approaches to describe spatial networks and the studies investigating them. Then we will describe three simple toy models of metacommunity dynamics, taking 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 the impact of spatial network structure on diversity distribution. We conclude with a discussion on the operationally of the framework.

2 Network representation of landscapes

Entités discrètes –¿ réseaux

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 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 1 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 population over a homogenous 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 neigbhouring patches (its degree). At each time step (the simulation model is discrete in time), the

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

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 in-

teractions 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 straightfor-

ward. 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 spa-

tially explicit landscapes with complex connectivity matrices (**Hanski1998**). Spatially

explicit dispersal usually reduces the occupancy and thereby the likelihood of per-

sistence. 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

$I_ix = 1 - \prod d_x(1 - C_{ixy})$. This equation basically tells us that the colonization probabil-

ity 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 $p_ix = I_x(I_ix + e)^{-1}$. The feedback between local and regional dynamics

arises because all $p_i x$ from the landscape are dependent from each other. Simulation 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. Multi-species analysis of metapopulation models also reveals interesting predictions on other aspects of community organization at various spatial scales such as 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 simulate this *zero-sum rule* (**Bell2000**; **Hubbell2001**), 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 is made of 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 in our model based on (**Gravel2006**). The

approach is conceptually similar to placing a seed trap in a gap in a forest and picking a seed at random among the one that fall 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 $P_i x$ 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 consider simply $P_{ix} = \frac{\sum d_y^{-1} P_{iy}}{\sum d y^{-1}}$. We assume for simplicity (and without loss of generality, (**Bell2000**)) that the relative abundance in the metacommunity is uniform, ie 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. 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 neutraly stable population dynamics. It can be measured as the variance between replicated time series of commu-

nity 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 ability 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. 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 endemic species richness (**Rosindell2011**; **Desjardins2012b**).

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 models, 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 against potential candidates. The recruitment probability is however biased by species specific response 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 environ-

mental conditions could be implemented at this stage. The J_x individuals all experience unique environmental conditions 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, 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 because only some species will be able to cope with the local environmental conditions. For tractability 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 $Pr_{ix} = \frac{\lambda_{inx}Z_{ix}}{\sum \lambda_{jnx}Z_{jx}}$. The function describing the relationship between microsite conditions and survival could take various forms and 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 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 (**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

12

a limiting similarity (**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 co-existence 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 fig. 1, we illustrate the outcome of simulations using the neutral model on the four different network shapes considered in this article. 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.

In fig. 2, we present the richness of each node of the network, as a function of the centrality of the node, under different assumptions of meta-community dynamics and network structure. It appears that both in the goeographical and tree graph, the path dynamics model allows more diversity to persist overall. However, the local diversity

13

increases with the node centrality, whether it is measured by the degree or the eigen-centrality. All situations examined give a remarkably congruent signal. The patch dynamics model, *i.e.* when there are no interactions between species, allows more α diversity. The neutral model allowed the maintenance of slightly more diversity than the species-sorting model. In all cases however, it is clear that the richness maintained tend to increase with the node centrality.

4 Discussion

Contrasting the three perspectives: what do we learn?

New questions

Making the theory operational - how to parameterize neutral models - making predictions for specific landscapes -

Distribution attendue des espèces dans un paysage: utiliser la théorie neutre pour avoir un attendu (différents de la méthode classique de permutation)

- Utiliser les déviations locales pour comprendre le rôle de la sélection

- Approche par réseau: vers une approche qui intègre la variance des mécanismes de coexistence

Our results point to an important, although often overlooked, consequence of neutral dynamics. Emerging properties of a community (i.e. the number of species, but also their spatial distribution and co-occurence in different local patches), are affected by the dispersal structure.

- Importance de la structure du paysage sur les propriétés émergentes - importance relative de species sorting et drift va dépendre de l'organisation du paysage - prédiction - rôle de la distribution de degrés -

14

5 Acknowledgements

Figure legends

Figure 1

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

Figure 2

Relationship between local species richness and metrics of 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.

Figure 3

Bray curtis dissimilarity as a function of geographic distance.

Figure 4

Bray curtis dissimilarity as a function of topological distance.

336 **Figure 1**

Figure 2

Figure 3

Figure 4