Neutral metacommunity clustering and SAR: River basin vs. 2-D landscape biodiversity patterns

M. Convertino [a,b,∗]

[a] Department of Agricultural and Biological Engineering-IFAS, University of Florida, Gainesville, FL, USA
[b] USACE Engineer Research and Development Center (ERDC), Risk Modeling and Decision Science Area, Concord, MA, USA

ABSTRACT

Moving from the analysis of the spatial distribution of fishes and big/small trees of the Mississippi Missouri River System, I evidenced and modeled with a neutral metacommunity model the power-law exceedence probability of the cluster-size of species and the species–area relationship (SAR). The slopes of the power-law distribution of the cluster-size $P(CS \geq c)$ and of the SAR vary for each taxa and life-stages underlying different spatial organization. A clear relationship exists between the slope z of the SAR and the slope ϵ of $P(CS \geq c)$, that is dependent on the ecosystem topology and shape, and on the dispersal kernel function. The heterogeneity of the environmental features leads to the formation of smaller clusters than in the ideal homogeneous scenario. $P(CS \geq cs)$ declines to an exponential distribution in dispersal-limited scenarios for which the effect of the environmental heterogeneities is stronger, the probability distribution of the local and pairwise species richness similarity is a lognormal function and the occupancy-rank is concave upward. The clustering of species has been studied on other real and artificial river networks and on 2-D non-fragmented landscapes. River networks have smaller clusters than 2-D landscapes for the same ecological dispersal scenario however the range in which $P(CS \geq c)$ holds is larger. The higher the elongation of the ecosystem the bigger the LSR, and the smaller the mean cluster-size. River networks due to the larger link-diameter than 2-D landscapes with the same domain are potentially more robust ecosystems, for example against invasion of invasive/exotic species and pathogens. The ecological ratio between the mean dispersal parameter and the average diameter is introduced as useful tool to compare biodiversity patterns. The influence of the dendritic structure of the river network has been reinforced. Nonetheless $P(CS \geq c)$, is found not invariant across different scales, and coarse-graining levels of the ecosystems. The study enhances the robustness of the stochastic birth-depth process in shaping biodiversity patterns, however I underline the strong influence of the dispersal parameter in the assemblage of species. The understanding of the relative influence of exogenous and endogenous variables is important to detect climatic and anthropic effects on the cluster-size distribution of species.

1. Introduction

The factors that determine species distributions in ecosystems are many and debated and their relative importance is difficult to quantify (Liza et al., 2010). Some studies have successfully detected the influence of the stochastic birth–death and dispersal processes and of the environmental heterogeneities on some biodiversity patterns (Legendre et al., 2009; Convertino et al., in review). The Poisson and the negative binomial distribution are the most widely used to respectively model random and aggregated distributions of species in infinitely large areas, however

new models for finite populations have been recently developed (Zillio and He, 2010). Understanding the aggregation properties of species is necessary for detecting the importance of neutral and niche factors (Niu et al., 2009) and their response to climate change (Kéfi et al., 2007; Konar et al., 2010; Convertino et al., in review; Kefi et al., 2011). The finding of distinctive fractal and scaling signatures of long-distance dispersal in the spatial patterns in ecosystems at different scales (Scanlon et al., 2007b; Rodriguez-Iturbe et al., 2009) represents a significant step in understanding the ubiquity of long-range dispersal in apparently diverse natural systems (Convertino et al., in review; Muneepeerakul et al., 2011).

Power-law distributions of the cluster-size of patches have been analyzed diffusely in previous studies, both numerically and by using empirical data (Convertino et al., in review). In savannah ecosystems Scanlon et al. (2007b) found a power-law of the cluster-size whose slope decreases with the average annual rain-

∗ Correspondence address: Department of Agricultural and Biological Engineering-IFAS, Frazier Rogers Hall, Museum Road, PO box 110570, FL 32611-0570, USA. Tel.: +1 352 392 1864x218; fax: +1 352 392 4092.
E-mail address: mconvertino@ufl.edu

fall decrease, Kéfi et al. (2007) found power-laws for the number of patches in Mediterranean arid ecosystems as a function of the grazing pressures and aridity, Wu (2004) described the qualitative trend of the power-law of the cluster-size as a function of the scale of analysis, and He et al. (2003) characterized the distribution of species in the Barro Colorado island using the percolation theory. In general clustering is a widespread characteristic phenomena of many biotic and abiotic systems (Convertino et al., in review), for example Boer et al. (2008) found aggregation in clusters of forest-fires confirming the model of Bak et al. (1990) and Zinck and Grimm (2009), Vandermeer et al. (2008) found clusters of ant colonies in tropical agrosystems, Marco et al. (2009) detected a power-law of the cluster-size of cancer cells with analogy to the species distribution in ecosystems, (Gamarra and He, 2008) detected scale-invariant clustered patterns of pine-beetle infestations, and (Decker et al., 2007) studied the nighttime light clustered patterns of cities.

Aggregation patterns of vegetation and animals usually have benefited of a separate large-tree/small-tree treatment (Condit et al., 1996; Plotkin et al., 2000, 2002; Simini et al., 2010), that permitted also to test the aggregation theories of Janzen (1970) and Connellz (1971). Self-similarity and scaling have been observed in tropical forest for the trees' crown and the diameter (Simini et al., 2010) and patterns of plant height have been correlated to climatic variables (Moles et al., 2009). Recent observations have shown that at microscales, microbes tend to cluster-size according a neutral dynamic (Houchmandzadeh, 2002, 2008; Convertino et al., in review). Various theories and models have been proposed for the clustering phenomena. Pascual et al. (2002) used lattice-based models with antagonist ecological interactions concluding that the clustering is a self-organized process arising from the interaction of species (confirmed also by data of mussels and simulation results by Wootton (2001)), He et al. (2003) provided an elegant formulation using the percolation theory at different scale however without specifying any determinant mechanism for the phenomena, Plotkin and Muller-Landau (2002) modeled the clustering of conspecific and individuals with a negative binomial distribution (that implies a lognormal species-abundance distribution) in place of the Poisson distribution. Other studies in literature motivate the ubiquity and emergence of clustered patterns to niche features, e.g. soil specialization and species traits (Russo et al., 2007). Liza et al. (2010) found a strong negative density dependence effect of the conspecific neighbors for the survival of tropical trees that is stronger for rare species. Thus, apparently the aggregation of tropical forest patterns is reached through an optimization of individual interactions of different species. The clustering in forests has been categorized by many studies as a self-organized critical phenomena (Manrubia and Sol, 1996; Scanlon et al., 2007b; Manor and Shnerb, 2008). Recently Convertino et al. (in review) provided a method and an elegant mathematical formulation for characterizing the cluster-size distribution for animate and inanimate organisms regardless the drivers determining the spatial aggregation.

However Houchmandzadeh (2002), Houchmandzadeh and Vallade (2003), Houchmandzadeh (2008) and Marco et al. (2009) found that ecological systems display considerable patchiness and this is caused solely by the birth, death and dispersal dynamics of individuals (neutral hypothesis). These causes seem to be common to all aggregation phenomena (Marco et al., 2009; Convertino et al., in review). It is not realistic to neglect the importance of the environmental heterogeneities on the spatial distribution of species (Young et al., 2001; Houchmandzadeh, 2002) nonetheless their roles seems deeply relevant only in particular conditions of the ecosystems. This is in agreement with Etienne and Alonso (2007) and partially with Manor and Shnerb (2008) and Kefi et al. (2011) which claims that the stochasticity produced by the neutral drift

and dispersal can explain species coexistence. The unified neutral theory of biodiversity (Hubbell, 2001, 2006) is a robust ecological theory that allows at the macroecological scale the prediction of real patterns without assuming interaction between species. Marco et al. (2009) evidenced the central role of local speciation in each local community and dispersal of species to other local communities. Moreover Martín and Goldenfeld (2006) tried to link the species–area relationship (SAR, i.e. the relationship between the number of species and their habitat area) to the aggregation features of species, arguing that the power-law structure of the SAR is a robust consequence of a skewed species-abundance distribution with higher rarity, together with the observation that individuals of a given species tend to cluster. The long-distance dispersal seems to enhance the aggregation of species (Rosindell and Cornell, 2008; Muneepeerakul et al., 2011). Qualitative studies that used different types of null models (Hausdorf and Henning, 2007) exist, despite there is some consensus in considering the neutral model different than standard null models (Gotelli, 2006). Houchmandzadeh and Vallade (2003) elegantly provide also the analytical solution for the neutral clustering problem in 1-D (that can be for example the case of a river bed or of a shoreline), in 2-D and in 3-D. Emphasis about the importance of dendritic ecosystems has been reported, among the others, by Fagan (2002); Goldberg et al. (2010) and Labonne et al. (2008) for the population demogenetics in river basins, Morrissey and Kerckhove (2009) for the maintenance of gene flow, Gastner et al. (2009) studying the transition from connected to fragmented vegetation patterns due to external changes, and by Lowe et al. (2006); Lowe (2008) and Grant et al. (2007) for linking animal dynamics and traits to the dispersal in riverine ecosystems.

The clustering phenomena has been studied in this paper with a model based on a neutral metacommunity model (NMM) originally developed by Muneepeerakul et al. (2008) for the study of fishes in the Mississippi-Missouri River System (MMRS), extended by Convertino et al. (2009) for the study of biodiversity patterns at different scale of aggregations, and modified by Konar et al. (2010) for the study of big-trees patterns in the same basin. The biodiversity patterns have been simulated and compared with data at different scales (extent) and coarse-graining levels following the approach of Convertino et al. (2009). The patterns of species are studied also as a function of the topology of the ecosystem and in particular comparing the dissected ecosystem of river networks (RNs) vs. the open structure of 2-D landscapes with the same domain. The comparison between ecosystems with the same boundaries performed in this paper seems more valid than what Muneepeerakul et al. (2007a,b) proposed in which the study was performed using ecosystems with different shape and different number of local communities. The effect of the branching structure of river networks has also been analyzed. The behavior of the cluster-size probability distribution has been investigated as a function of the parameters of the model. The clustering analysis is performed for:

1. different ecosystem topology, that are river networks with different elongation ratio (OCN, Cordevole, Tanaro, and MMRS) to study the effect of the shape of the network, and 2-D non-dissected landscapes;
2. different dispersal kernels, namely the exponential and exponential-Cauchy kernels, varying also the speciation rate;
3. homogeneous and heterogeneous conditions that are modeled using a constant and variable habitat capacity respectively;
4. different coarse-graining levels and scales of analysis.

Moreover, for the first time, the species–area relationship has been quantitatively linked to the probability distribution of the cluster-size for different ecosystem topologies and dispersal kernel scenarios. The paper is organized as follows. Section 2 describes our