



Spatial patterns in the tropical forest reveal connections between negative feedback, aggregation and abundance



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HIGHLIGHTS

- Variance–mean ratio (VMR) analysis is applied to spatial patterns on different scales.
- Reveals the relative importance of aggregating vs. repulsive mechanism per scale.
- Tropical forest aggregation is dominant at large scales, characterized by power law.
- Negative feedback is dominant at short scales, negatively correlated with abundance.
- Suggests an extension of the neutral theory to include multiple dispersal syndromes.

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ABSTRACT

The spatial arrangement of trees in a tropical forest reflects the interplay between aggregating processes, like dispersal limitation, and negative feedback that induces effective repulsion among individuals. Monitoring the variance–mean ratio for conspecific individuals along length-scales, we show that the effect of negative feedback is dominant at short scales, while aggregation characterizes the large-scale patterns. A comparison of different species indicates, surprisingly, that both aggregation and negative feedback scales are related to the overall abundance of the species. This suggests a bottom-up control mechanism, in which the negative feedback dictates the dispersal kernel and the overall abundance.

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1. Introduction

One of the main characteristics of natural populations, and in particular of sessile species, is their spatial structure. In many cases conspecific individuals are aggregated in space, a phenomena that may be attributed to various mechanisms like dispersal limitation (Borda de Agua et al., 2007; Seri et al., 2012), positive feedback (Kéfi et al., 2007; Scanlon et al., 2007; von Hardenberg et al., 2001) or habitat association. Negative feedback mechanisms, on the other hand, lead to an effective “repulsion” between individuals or clusters (Fort and Inchausti, 2013; Manor and Shnerb, 2008); the excess competition between same-species individuals may induce self-thinning, and the presence of species-specific parasites or predators around an adult tree may decrease the chance of recruitment in its neighborhood.

Turning from populations to communities, the dynamics of ultra-diverse systems like the tropical forest have attracted a lot of interest, as these systems appear to violate a fundamental assumption of natural selection theory, the competitive exclusion principle (Ricklefs and Miller, 2000). Many mechanistic solutions were suggested to this puzzle (Clark et al., 2010; Connell, 1970; Hubbell, 2001; Huisman and Weissing, 1999; Janzen, 1970; McGill, 2003; Tilman, 1994), and almost all of them have to do with some features of these spatial patterns. For example, a competition–colonization tradeoff (Tilman, 1994) implies that the better competitors are more clustered in space. Unfortunately, it is quite difficult to relate directly the spatial patterns to the underlying process, since the details of the dynamics (like the recruitment kernel, or the identity of the best competitor) are usually unknown. Still, by pointing out some generic features of the spatial structure of the forest, an analysis may put severe constraints on the suggested models and may serve as a guide for the establishment and refinement of more realistic hypotheses.

A long-standing hypothesis, aimed to explain the apparent excess biodiversity of the tropical forest, was suggested by Janzen and Connell (Connell, 1970; Janzen, 1970). Basically, the idea is that

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host-specific enemies (like pathogens or herbivores) are attracted to an adult tree, making its neighborhood hostile to seeds and seedlings of the same species. Accordingly, conspecific individuals effectively repel each other, implying that inferior species may survive in the forest by filling the gaps between superior competitors.

Recently, the Janzen–Connell hypothesis has gained a renewed popularity and attracted a lot of attention, following a few empirical studies that monitor conspecific negative density dependence and tracked its origin. In particular, a substantial decrease of seed efficiency close to a conspecific adult tree was demonstrated (Comita et al., 2010; Swamy et al., 2011), and the reduction in the chance of establishment was attributed to the negative effect of soil biota (Mangan et al., 2010). Moreover, the analysis suggests that the strength of this negative feedback is a good predictor of the commonness/rarity of a species in the tropical forest (Comita et al., 2010; Mangan et al., 2010). Similar results (that locally rare species suffer most from the proximity of relatives) were obtained in subtropical (Liu et al., 2012) and temperate (Johnson et al., 2012) forests.

These new results pose a few interesting questions. The first has to do with the range of the effect. For the Janzen–Connell mechanism to work the negative feedback has to be localized around the adult tree (Nathan and Casagrandi, 2005). How such a localized interaction, with a range of, say, a few meters, can affect the community-wide pattern in tree composition (Hubbell et al., 2001)? What is the mechanism that allows the negative feedback to dictate features of the forest on a much larger scale? One can easily imagine a counter example, where the effect of negative feedback is balanced by another feature. For example, if the seedlings of the “fittest” species (the one that will select out all other species in the absence of negative-feedback mechanisms) cannot establish at all in a radius of 4 m around an adult tree, this may be the strongest repulsive effect among all species, still the fittest will be one of the most common species in a 500,000 m² forest (like the 50-ha plot in Barro-Colorado Island considered below), with more than 10,000 trees, since its offspring win the competition once they are out of the 4 m radius.

This brings us to a second question: the relative strength of this negative feedback mechanism, as opposed to well-known processes that lead to aggregation of conspecific individuals, like dispersal limitation (Manor and Shnerb, 2008). While the chance of a seed to germinate, or of a seedling to establish as an adult, may be smaller close to a conspecific tree, the number of attempts (i.e., the number of seed and seedlings in the vicinity of a reproductive individual) is much larger, and the overall pattern will depend on the interplay between these factors. In particular, very strong negative feedback will lead to a lattice-like forest, while strong aggregating forces yield clumped patterns. In fact, it is well known that a pronounced feature of these spatial patterns is aggregation and clustering (Condit et al., 2000; Plotkin et al., 2002; Seri et al., 2012; Zhu et al., 2013), while a direct identification of negative feedback effects from the overall spatial structure of the population has proved itself as quite a difficult task (Zhu et al., 2013). Given that, one may wonder again about the relevance of conspecific local density dependence to the composition of the community.

In this paper we are trying to shed some light on these problems. Analyzing the spatial patterns that emerge from a few generic models and comparing them to the empirical data, we show that local negative effects and “repulsion” between conspecific individuals indeed dominate the spatial pattern on very short length scales, while aggregation mechanism take over at larger distances.

A more surprising outcome of our analysis emerges when we compare the results for different tree species. It turns out that both

the aggregation and the negative feedback are related to the overall abundance of the species in the plot. This phenomenon suggests that the local negative feedback cascades upscales (perhaps by controlling the typical recruitment length) to yield the global pattern. While we cannot suggest a specific mechanistic explanation for these features, we can extract some severe constraints on the possible models of forest dynamics.

This paper is organized as follows. In the methods section we explain the usage of variance–mean ratio and present the results of our analysis for point patterns obtained from a few well-known mechanistic models. The results section is devoted to the analysis of empirical data from the Barro-Colorado island plot (BCI) (Condit, 1998; Hubbell and Foster, 1983; Hubbell et al., 2005; Hubbell et al., 1999), in comparison with the patterns surveyed in the methods, emphasizing the universality of the empirical patterns. Finally, we discuss our result in the general context of variance–mean ratio (Taylor’s law) and analyze the apparent insights.

2. Methods

The method we implement in this paper is a multiscale analysis of the variance–mean ratio (VMR, also known as index of dispersion, Fano factor). As we shall see, the VMR technique allows for a direct demonstration of both negative feedback and aggregation on different scales.

An analysis of the spatial deployment of a single population, or a comparison between two or many populations in a community, may be done using either objective scales (like meters) or by using a species specific length scale, like the average distance between neighboring trees. In a recent work (Seri et al., 2015), we have suggested that the second method (intrinsic scales) provides a better insight, at least for the tropical forest we have examined. Using other methods of point pattern distribution analysis (nearest neighbor distance distribution, correlation length and cluster statistics), we discovered that spatial patterns of different species obey a universal scaling law once the length is normalized by the typical distance between conspecific trees $\ell_{0i} = \sqrt{A/N_i}$, where A is the area of the plot and N_i is the abundance of the i th species in the area A . Following these results we implemented here two versions of the VMR analysis: one is based on objective scales, the other utilizes the species specific scale ℓ_{0i} . As seen in the results section, the VMR analysis seems to support the conclusions of (Seri et al., 2015), suggesting that spatial patterns of different species are becoming similar once the distances are normalized (for every species) by ℓ_{0i} .

The index of dispersion is defined, in general, as the ratio between the variance and the mean of a random variable. Here we are looking at a population, i.e., all the individuals of the focal species i in the BCI 50-ha plot. We start by covering the plot area by a rectangular mesh of lattice constant ℓ (so that the area of each cell is $\ell \times \ell$), and counting the number of individuals in any box. The mean number of individuals of the i th species in one of those grid cells will be $N_i \ell^2 / A$ and the variance (calculated between the number of individuals in all grid cells) depends on the spatial arrangement of the population. The variance mean ratio (VMR) will be a small number if each box contains, more or less, the same number of individuals and will be large when some boxes are almost empty and others are densely occupied so the population is clustered. The degree of clustering may depend on the length scale; accordingly, by plotting the VMR over scales one obtains a summary of the aggregation properties of the system.

Throughout this paper we present two types of plots. One is a plot of VMR versus the box area $s = \ell^2$, the other is a plot of VMR versus the normalized area $\tilde{s} = (\ell / \ell_{0i})^2$. In the last case length is

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