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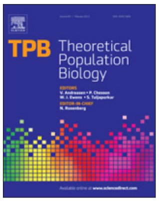

# The distance decay of similarity in tropical rainforests. A spatial point processes analytical formulation

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A R T I C L E I N F O

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In this paper we are concerned with the analytical description of the change in floristic composition (species turnover) with the distance between two plots of a tropical rainforest due to the clustering of the individuals of the different species. We describe the plant arrangement by a superposition of spatial point processes and in this framework we introduce an analytical function which represents the average spatial density of the Sørensen similarity between two infinitesimal plots at distance $r$. We see that the decay in similarity with the distance is essentially described by the pair correlation function of the superposed process and that it is governed by the most abundant species. We test our analytical model with empirical data obtained for the Barro Colorado Island and Pasoh rainforests. To this end we adopt the statistical estimator for the pair correlation function in Shimatani (2001) and we design a novel one for the Sørensen similarity. Furthermore, we test our analytical formula by modeling the forest study area with Neyman–Scott point processes. We conclude comparing the advantages of our approach with other ones existing in literature.

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## 0. Introduction

Estimating biodiversity of forests is a central issue in modern conservation ecology. Both from the theoretical and field application point of view it represents a daunting challenge. Since the pioneering work of Whittaker (1972) and Preston (1962a, b) a number of diversity indices have been introduced in literature and their effectiveness has been tested against field data, with various degrees of success. In this paper we are concerned with a single aspect of this broad issue, namely the study of the decay of similarity between two regions of a landscape as a function of the distance between them. To specify the intuitive concept of similarity we will adopt the widely used Sørensen[1] similarity index (Sørensen, 1948; Chao et al., 2005) (see Eq. (2)) and its associated spatial density Eq. (3). Equally used in literature is the notion, complementary to the concept of similarity, of species turnover or $\beta$-diversity, that is the change in species composition between two plots as a function of the distance between them. Even stated in these terms, this more restricted problem is hard to reduce to a mathematical model since on real landscapes many drivers of diversity are acting at the same time and may contribute with different intensity depending on the spatial scales (Soininen et al., 2007): at a continental scale climatic factor may dominate whereas at a smaller scale orographic factors may create specific environmental gradients due to the change in altitude or to the orientation of valleys. At any scale, the effect of past transformations of the environment may have shaped the territory with dispersal barriers or niches. The heterogeneity of these factors may have hampered the construction of a all-compassing mathematical model and, effectively, a relatively small (compared the huge number of articles dedicated to biodiversity issues) number of works are available on the specific problem of finding the function that best describes the change in species composition with the distance. In chronological order, important contributions to this central problem of estimating biodiversity of forests are the seminal works of Leigh et al. (1993), Nekola and White (1999) and the neutral theory approach of Hubbell (1997, 2001) (see e.g. the comprehensive book Magurran and McGill (2011)).

In this paper we focus on a single driver of diversity, that is the tendency of plants to form clusters of individuals. The shape and extent of the cluster may vary from species to species depending on seed dispersal limiting factors, or other effects, e.g Janzen–Connell effect (Janzen, 1970; Connell, 1971), which may be inter or intra specific. We aim at reducing this multiplicity of biotic factors to a single statistical descriptor. Stated in more mathematical terms, we wish to study the effect of spatial correlations between the

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[1] We are aware that each diversity index has its own field of application and it is more or less biased. Our analytical treatment of a decay of similarity function based on a specific index will hence necessarily suffer from the same limitations of the index itself, but we are confident that our procedure can be applied to other indices.

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individuals' (plants) positions on the change in the species' composition of two small plots at a given distance. The mathematical tool adapted to this task is the spatial point process theory (see Stoyan and Stoyan, 1994; Baddeley et al., 2007). The main sources of inspiration for our approach are the works of Shimatani (2001), Shimatani and Kubota (2004), Plotkin and Muller-Landau (2002), Morlon et al. (2008) (based on Plotkin and Muller-Landau, 2002), and also Chave and Leigh (2002). Using the language of point processes we derive in Sect. 1 an analytical formula for $\chi(r)$, the (spatial density of) Sørensen similarity between two small plots distance $r$ apart. This gives the form of the decay of similarity as a function of the distance:

$$\chi(r) = \lambda(g_X(r) - 1) + \chi_\infty \tag{1}$$

where the first term $g_X(\cdot)$ is the pair correlation function of the superposed process having intensity $\lambda$ and $\chi_\infty$ is a constant depending solely on the species' abundances and representing the similarity at a scale where the clustering of individuals has no effect. Thus, essentially, the decay in similarity is described by the pair correlation function of the whole forest plot. This latter in turn depends on the clustering of each species *weighted by their relative abundance* (see Eq. (15)). Therefore in our model the similarity decay function is dominated by the most abundant species, a feature previously recognized in other studies (Morlon et al., 2008), but still debated (Chao et al., 2005, 2006).

Apart from presenting a novel analytical approach to the definition of a decay of similarity function using point processes, the main aim of this paper is to test the proposed formula against field data. In our study we use the BCI (Barro Colorado Island) and Pasoh forest databases, which register the spatial position of respectively 222 602 and 310 520 plants belonging to 301 and 927 species covering an area of 50 ha each. In Section 2 we introduce the statistical estimators for the similarity decay, $\hat{\chi}$, and for the pair correlation function, $\hat{g}_X$. The former, based directly on Sørensen similarity formula (2), as far as we know is a novel one, whereas the latter has been used in Shimatani (2001) and it is derived from the general theory of point processes even if it *does not need any hypothesis on the type of stochastic point process* that we should associate to the species of the forest under study. They therefore provide a test of the formula (1) above at a very general level.

A second goal of this work is to select the class of spatial point process that best describes the plants' arrangement in the study area and test its effectiveness in reproducing the decay of similarity function. This is done in Section 3. The clustering of each species $\alpha$ is described by a univariate (if we assume rotational symmetry of the two-dimensional cluster) probability density $d_\alpha(r)$, the so-called dispersal kernel, which gives the probability that an individual of the cluster will establish at distance $r$ from its parent, located at the cluster's center. The dispersal kernel features of each species are thus the essential informations for our model that have to be drawn from experimental data (by the minimum contrast method in this work). We test the effectiveness of three dispersal kernels (exponential, Gaussian, Cauchy) at describing the species' clustering. Once we determine the cluster parameters for each species, we compute the analytical form of the pair correlation function $g_X$ and of the similarity index $\chi(r)$. These are compared with their statistical estimates in Section 5.2.

## 1. Similarity decay functions

### 1.1. Sørensen index for point processes

We begin by recalling the definition of Sørensen similarity index. We consider a flat region $W$ with no environmental gradients. Given two disjoint ($A \cap B = \emptyset$) subregions $A$ and $B$, let $s(A)$ and $s(B)$ be the number of different species present, respectively, in $A$ and $B$ and let $s(A, B)$ be the number of co-present species in $A$ and $B$. Provided that $s(A) + s(B) > 0$, the Sørensen similarity between regions $A$ and $B$ is the symmetric function $0 \leq \sigma(A, B) \leq 1$

$$\sigma(A, B) = \frac{s(A, B)}{\frac{1}{2}(s(A) + s(B))}. \tag{2}$$

When $s(A) = s(B)$, $\sigma(A, B)$ gives the number of co-present species per species. As it is well known, the number of present or co-present species depends on the size of the regions $A$ and $B$. Therefore we assume, as it is generally the case, that $A$ and $B$ have the same size $a$ and we denote with

$$\chi(A, B) = a^{-1}\sigma(A, B) \tag{3}$$

the number of co-present species per species and per unit of survey area, i.e. the spatial density of Sørensen similarity.

In the same spirit of Shimatani (2001), we wish now to reformulate the notion of Sørensen similarity in the language of spatial point processes. We model the presence of $S$ species by a spatial point process $X = \cup_\alpha X_\alpha$, which is the superposition of $S$ mutually independent, homogeneous and isotropic spatial point processes $X_\alpha$, $\alpha \in \{1, \ldots, S\}$. In this way we model a community of $S$ independent species where intra-specific interactions are allowed. Let us denote with $n_\alpha(x)$ and $n_\alpha(y)$ the random number of points of the process $X_\alpha$ contained in two infinitesimal disks centered at $x$ and $y$, having equal area $dx = dy$ and being disjoint. Therefore $n(x) = \sum_\alpha n_\alpha(x)$ is the total number of individuals in $dx$, regardless of their species.

Let us now introduce some basic notions on point process theory. Let $\lambda_\alpha(x)$ be the intensity (spatial density of points) of $X_\alpha$, $\lambda(x) = \sum_\alpha \lambda_\alpha(x)$ be the intensity of the superposed process $X$, $\rho_\alpha(x, y)$ be the associated second order product density (second moment density, see Baddeley et al. (2007) or Diggle (2013)) and set for simplicity' sake $\rho(x, y) = \sum_\alpha \rho_\alpha(x, y)$. The following interpretations are standard

$$\lambda_\alpha(x)dx = P(n_\alpha(x) = 1), \quad P(n_\alpha(x) > 1) = o(dx) \tag{4}$$

and

$$\rho_\alpha(x, y)dxdy = P(n_\alpha(x) = 1, n_\alpha(y) = 1), \tag{5}$$

$$P(\{n_\alpha(x) > 1\} \cup \{n_\alpha(y) > 1\}) = o(dxdy).$$

Denoting with $s(x)$, $s(y)$ and $s(x, y)$ the number of species (point processes) present in $dx$, $dy$ and in both $dx$ and $dy$ respectively, and neglecting higher order terms in $dx$ or $dxdy$, we have that the *expected number* of species found in $dx$ around $x$ can be expressed as

$$\mathbb{E}[s(x)] = \sum_\alpha P(n_\alpha(dx) = 1) = \lambda(x)dx, \tag{6}$$

while the average number of co-present species in the infinitesimal regions $dx$ and $dy$ around $x$ and $y$ is

$$\mathbb{E}[s(x, y)] = \sum_\alpha P(n_\alpha(x) = 1, n_\alpha(y) = 1) = \rho(x, y)dxdy. \tag{7}$$

The number $s(x)$ of species at $x$ and the number $s(x, y)$ of shared species at $x$ and $y$ are discrete random variables whose expected values can be described by the above formulas (6) and (7). Apart from their averages, their distribution is assumed to be unknown. The equivalent of the Sørensen similarity index for infinitesimal regions is thus given by the random variable

$$\sigma(x, y) = \frac{2s(x, y)}{s(x) + s(y)}, \tag{8}$$

which is the ratio of two random quantities. The expected value of this ratio can be computed from $\mathbb{E}[s(x)]$ and $\mathbb{E}[s(x, y)]$ using the

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