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Article

Distribución y correlación espacial de especies arbóreas por gradiente altitudinal en la Selva Lacandona, Chiapas

Distribution and spatial correlation of tree species along an altitudinal gradient in the *Selva Lacandona*, *Chiapas*

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Resumen

Se analizó el patrón de distribución y correlación espacial de las especies arbóreas a lo largo de un gradiente altitudinal en el Área Natural Protegida (ANP) Metzabok, Selva Lacandona, Chiapas. En cada estrato altitudinal (EA) se instaló una unidad de muestreo de 20 × 50 m, que fue dividida en 10 subunidades de muestreo (SUM) de 10 × 10 m, donde se registraron los fustales. En las SUM se delimitó un cuadro de 5 × 5 m para el registro de latizales, y en su interior se establecieron dos cuadros de 2 × 2 m para el reconocimiento de brinzales. La distribución espacial de fustales, latizales y brinzales se analizó con el índice de *Morisita-Horn*; mientras que, la distribución y correlación espacial de los fustales por categorías de altura (inferior, intermedia y superior) y EA se evaluó mediante la función univariada $K(t)$ y bivariada $K_{12}(t)$ de *Ripley*. El patrón espacial promedio de la clase fustal para las tres categorías de altura a lo largo del gradiente altitudinal fue agregado ($I_\delta = 1.04$), similar que en latizales y brinzales ($I_\delta = 1.16$). La función $K_{12}(t)$ indica que los EA 2, 3 y 5 de la categoría inferior-intermedia mostraron, tanto repulsión como atracción espacial, mientras las denominadas inferior-superior e intermedia-superior tuvieron un comportamiento de independencia y repulsión espacial, respectivamente. Estos hallazgos aportan bases para la implementación de estrategias silvícolas enfocadas a la conservación de las especies arbóreas presentes en el ANP Metzabok.

Palabras clave: Área Natural Protegida Metzabok, dinámica de comunidades, ecología espacial, función *K(t)* de *Ripley*, índice *Morisita-Horn*, patrones de distribución.

Abstract

In this paper the distribution and spatial correlation patterns of tree species along an altitudinal gradient in the *Metzabok* Protected Natural Area (PNA) in the *Selva Lacandona, Chiapas* State was analyzed. A 20 × 50 m sampling unit (SU) was installed in each altitudinal strata (AS), and divided into 10 sampling subunits (SSU) of 10 x 10 m targeting pole-sized trees. Within each SSU, one 5 × 5 m plot was installed to register the saplings, and within this, another two 2 × 2 m plots were established for the sampling of seedlings. The spatial distribution of pole-sized trees, saplings and seedlings was analyzed with the Morisita-Horn index; whereas the distribution and spatial correlation of pole-sized trees by height categories (lower, middle and higher) and AS was evaluated using Ripley's univariate $K(t)$ and bivariate $K_{12}(t)$ functions. The mean spatial pattern of the pole-sized class for the three height categories along the altitudinal gradient was clumped ($I_\delta = 1.04$), as were the patterns of the saplings and the seedlings ($I_\delta = 1.16$). Ripley´s $K_{12}(t)$ function indicates that AS 2, 3 and 5 of the lower-middle height classes showed both spatial repulsion and attraction, while lower-higher and middle-higher had a behavior of independence and of spatial repulsion, respectively. These findings provide the basis for the implementation of forestry strategies focused on the conservation of the tree species distributed in the *Metzabok* PNA.

Key words: Protected Natural Area of *Metzabok*, community dynamics, spatial ecology, Ripley´s $K(t)$ function, Morisita-Horn index, distribution patterns.

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Introduction

Spatial ecology offers a variety of tools to assess the degree of aggregation that make it possible to infer the scale of variation of the ecological parameters (Ver Hoef *et al.*, 2018). In general, these tools are methods that break down the variability of a parameter, defining the analysis scales in terms of different radii of action in which the distance to the nearest neighbors is established (Dale and Fortin, 2014). All the methods determine and describe the spatial patters that allow assessing hypotheses regarding various ecological processes associated to the forest dynamics of an ecosystem (Rozas and Camarero, 2005; Martensen *et al.*, 2017).

According to Condit *et al*. (2002), the analysis of the spatial pattern describes the horizontal distribution of the individuals in a community in quantitative terms and is essential for understanding how a group of species uses the resources in its surroundings. Hubbell (2001) cites three general distribution patterns: i) random, in which individuals are distributed haphazardly due to the environmental homogeneity, following a non-selective pattern; ii) uniform, occurring at certain distances as a result of negative interactions between individuals, and iii) aggregate, in which the individuals of a species are isolated from other species by the limitation of its dispersion or the specialization of their habitat.

There are various methods for identifying the spatial patterns in the form of indexes (Aguirre-Calderón, 2002; Rozas and Camarero, 2005; Ledo *et al.*, 2012; Dale and Fortin, 2014); two of the most robust are the Morisita-Horn index (Morisita, 1959), which estimates the variation of the type and intensity of the pattern along a scalar spatial gradient, and Ripley's *K* function, which analyzes the distance to the nearest neighbor and informs about the spatial pattern observed as a function of distance *d* (Ripley, 1977; Dixon, 2013).

It has been said that, in the tropical rain forests, species are distributed according to abundance hierarchies; usually, the lowest number of species corresponds to rare taxa, while there are few abundant taxa and many with an intermediate abundance (Martínez-Ramos and Álvarez-Buylla, 1995; Franklin and Rey, 2007; Yili *et al.*, 2013).

Certain authors (John *et al*., 2007; Blach-Overgaard *et al*., 2010) suggest that the main limiting factors for the display of a given spatial pattern by a certain species are either abiotic (altitude, latitude, temperature, luminosity, precipitation, evapotranspiration, soil type, topography and slope) or biotic (competition within and between species and depredation).

According to Fossa (2004) and Hernández *et al.* (2018), the assessment of spatial patterns along altitude gradients is an essential tool for predicting the behavior of the species and the dynamics of the vegetal flow between strata, particularly in the face of climate change scenarios and for conservation purposes (Cruz, 2013). Meta-analyses at a global level have suggested that tree species are being displaced toward higher altitudes as a result of the climate change, and precisely the higher areas of the tropics are where these changes have been reported with the greatest consistency, due to the reduction of the interval of distribution of these taxa (Parmesan, 2006; Brown *et al.*, 2016).

According to Montañez *et al*. (2010), the higher the altitude, the greater the probability of finding a clumped pattern of tree individuals; therefore, it is inferred that the distribution pattern necessarily must be different in the lower tropical lands (Hubbell, 2001). Consequently, those species that prove unsuccessful to adapt to these environmental changes will disappear as a result of physiological stress (Parmesan, 2006; Brown *et al*., 2015), while the current interspecies relationships of those that do adapt successfully will be disturbed (Root *et al*., 2003).

In Mexico, Martínez-Ramos and Álvarez-Buylla (1995) point out that trees in humid rain forests generally have a clumped distribution because they exhibit a low dispersion and a high mortality during the early stages. In contrast, Zarco *et al.* (2010) cite a mainly random distribution for tree species in the tropical forest of *Tabasco*, although at certain sites they observed a clumped pattern in the lower stratum. This is similar to the results obtained by Martínez-Ramos (2006), who recorded a clumped pattern at the *Montes Azules* Biosphere Reserve in *Chiapas*, which he relates to land with an irregular topography and with the availability of sunlight for the undergrowth. Despite this research, studies on the spatial distribution along the altitude gradients are scarce across the country (Hernández *et al.*, 2018), even more so in the tropical rain forests.

This highlights the importance of identifying the spatial distribution patterns of tree species in the tropical rain forests, given the high functional and structural complexity of these environments (Condit *et al*., 2002; Lohbek *et al*., 2015), as well as the threats that they face (Arroyo-Rodríguez *et al*., 2017).

Particularly in *Chiapas*, the *Selva Lacandona* is one of the most fragile systems; its forest cover has decreased by 70 % in the last decades due to the expansion of agriculture and livestock breeding expansion and to illegal timber extraction (Martínez-Ramos, 2006); the same factors affect several of their protected natural areas, as in the case of the *Metzabok* Flora and Fauna Protection Area (Conanp, 2006).

The purpose of the present research is to analyze and describe the distribution and spatial correlation pattern along an altitude gradient of the tree species in the *Metzabok* Protected Natural Area, in the *Selva Lacandona* of *Chiapas*. The spatial distribution pattern is expected to differ between development stages (seedling, sapling, and pole-sized tree) and height categories (lower, intermediate, higher), and along the altitude gradient, regardless of the index utilized.

Materials and Methods

Study area

The present research was carried out at the *Metzabok* Protected Natural Area (PNA), located in the northeast of the *Selva Lacandona* (17°08’ 36’’N and 91°34’42’’ W), in the *Lacandona* sub-community of *Puerto Bello Metzabok, Ocosingo, Chiapas*. This PNA has a surface area of 3 368 ha, at an altitude of 545 to 950 m (Conanp, 2006). The climate is Af(m)w”(i)g, warm humid with rains throughout the year, a mean annual temperature of 24 °C and a mean annual precipitation of 3 160 mm (García, 2004). The soil types are redzins, luvisols, gleysols, vertisols, cambisols and litosols (Sánchez-Gutiérrez *et al.*, 2017). According to the classification by Miranda and Hernández-X (2014), the predominant vegetation is high evergreen tropical rain forest.

Altitude stratification and sampling

Five altitude strata were determined (AS1= < 600 masl, AS2= 600-700 masl, AS3= 700-800 masl, AS4= 800-900 masl, and AS5= > 900 masl) based on the generation of level curves at intervals of 100 m using the Global Mapper software, version 15. In each stratum, a 20 × 50 m (1 000 m^2) sampling unit (SU) was installed, as shown in Figure 1; these sampling units were divided into ten 10 × 10 m (100 m^2) sampling sub-units (SSU). In each SSU, all individuals of the stem class (reproductive trees) with normal diameter (DN) ≥ 2.5 cm were measured with diametric tape (Richter Messwerkzeuge, 283D/10M model) and located by their Cartesian coordinates (x, y) (Linzaga -Román *et al*., 2011; Dale and Fortin, 2014); the lower left corner of the plane was taken with respect to the slope of each SU as the origin (0, 0), as suggested by Ruiz-Aquino *et al*. (2015). Within Each SSU, a 5 × 5 m square was installed at random in order to register its saplings (young trees with a ND of < 2.5 cm and a height of > 1.5 m), and in each of these squares, two 2 × 2 m squares were established for the inspection of individuals classified as seedlings (with a height of < 1.5 m) (Zarco *et al.*, 2010).

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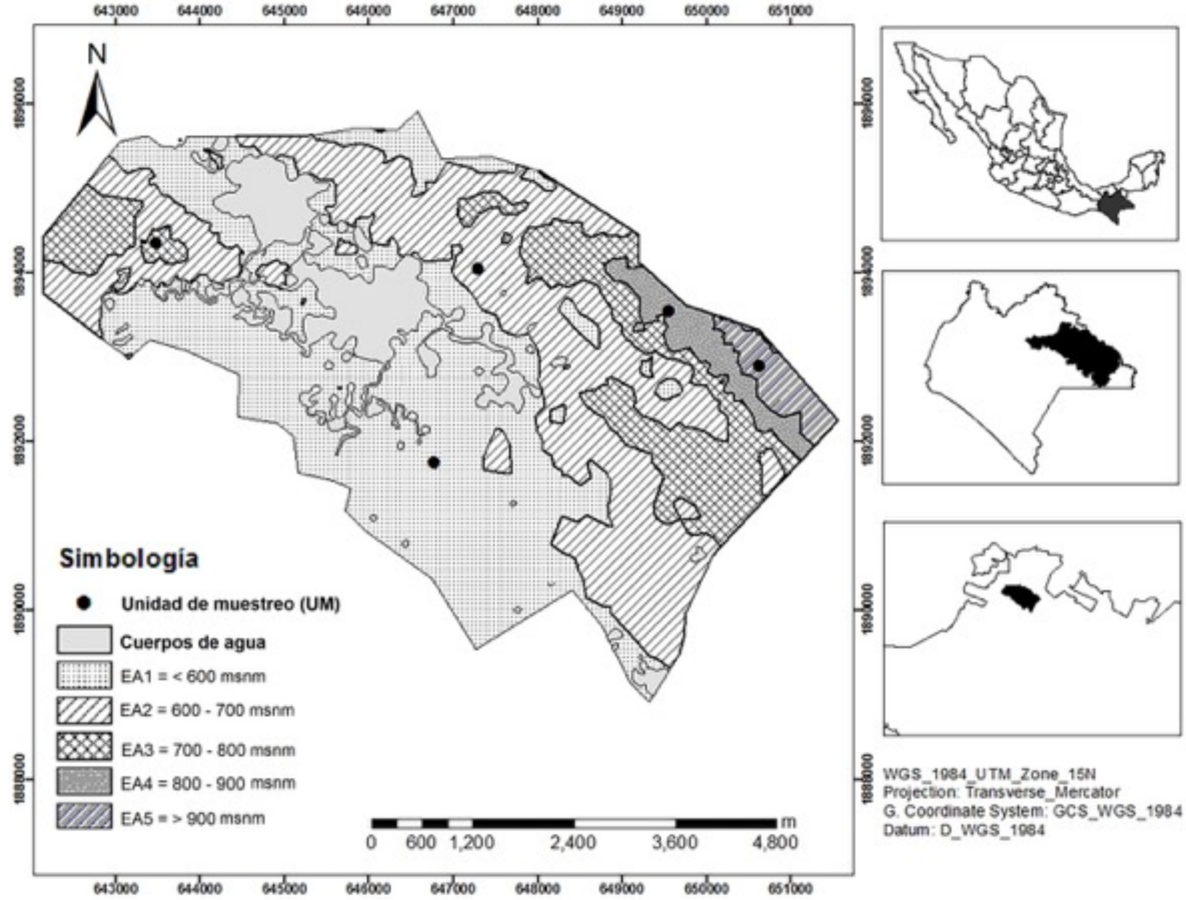


Simbología = Simbology; *Unidad de muestreo* = Sampling unit; *Cuerpos de agua* = Bodies of water; *EA* = AS

Figure 1. Location of the sampling units (SU) in each altitude stratum (AS) of the *Metzabok* Protected Natural Area, in the *Selva Lacandona* of *Chiapas*.

The taxonomic identity of the individuals was determined with the support of the staff of the "ECOSCH-H" Herbarium of the *Colegio de la Frontera Sur* (*Ecosur*) (College of the Southern Border) in *San Cristóbal de las Casas*, *Chiapas*. The nomenclature was validated on the website Tropicos.org of the Missouri Botanical Garden (2008).

Spatial distribution analysis

Three height categories (lower, intermediate, higher) —obtained from the inflection curves in the paper by Sánchez-Gutiérrez *et al.* (2017)— were used for estimating the spatial distribution of the pole-sized trees. The spatial distribution pattern of the seedling and sapling development stages, as well as the height categories of the pole-sized trees, were determined using the Morisita-Horn index (Morisita, 1959); when their value is equal to 1, the distribution is random; when it is > 1, it is clumped, and when it is < 1, it is uniform (Morisita, 1959; Zarco *et al*., 2010; Rivera-Fernández *et al*., 2012). The Morisita-Horn index is defined in equation (1):

$$I_\delta = q \sum_{i=1}^{q} ni \, \frac{(ni - 1)}{N\,(N-1)} \qquad (1)$$

Where:

I_δ = Spatial distribution index

q = Number of squares

ni = Number of individuals in the i^{th} square

N = Total number of individuals in all the q squares

In order to obtain a more statistically robust and graphically representative index (Rozas and Camarero, 2005; Ledo *et al*., 2012; Dale and Fortin, 2014), Ripley's $K(t)$ function was also calculated (Ripley, 1977) for the spatial distribution of the height categories of the pole-sized trees, based on equation (2):

$$K\,(t) = n^{-2}\,|A| \sum \sum_{i \neq j} W_{ij}^{-1}\, I_t\big(u_{ij}\big) \qquad (2)$$

Where:

n = Number of individuals of the sampling unit (SU-A)

$|A|$ = Surface area of the SU-A (m^2)

u_{ij} = Distance between the i^{th} and j^{th} individual in the SU-A

t = Distance between two trees (m)

$I_t(u)$ = 1 if $u \leq t$ and 0 $u > t$

W_{ij} = Proportion of the circumference of a circle with a center in SU-A (the summation of two the pairs of individuals $\leq t$)

The variance was established by using the transformation of the square root of Ripley's $K(t)$, and the significance of the $L(t)$ was determined based on *Monte Carlo* simulations (Besag, 1977). The maximum and minimum limits of $L(t)$ were defined with a confidence interval of 99 %:

$$L(t) = \sqrt{\frac{K(t)}{\pi} - t} \qquad (3)$$

Where:

$K(t)$ = Ripley's univariate function

π = 3.1416

t = Distance (m)

If the value of $L(t) = 0$, the spatial pattern with a t radium is random; $L(t) > 0$ indicates clumping and $L(t) < 0$ indicates a uniform pattern.

Spatial correlation

The spatial correlation between height categories (lower-intermediate, lower-higher, and intermediate-higher) of the pole-sized tree species was analyzed using the L_{12} (t) bivariate function, derived from the K_{12} (t) function (Ripley, 1977):

$$L_{12}(t) = \sqrt{\frac{K_{12}(t)}{\pi}} - t \qquad (4)$$

Where:

$K_{12}(t)$ = Ripley's bivariate function

π = 3.1416

t = Distance (m)

A $L_{12}(t)$ value = 0 indicates that the two groups are spatially independent; $L_{12}(t) > 0$ refers to a positive association (attraction), and $L_{12}(t) < 0$ expressed a negative association (repulsion). The significance ($p \leq 0.01$) of $L_{12}(t)$ was determined with Monte Carlo simulations (Besag, 1977; Dale and Fortin, 2014), and the maximum and minimum limits were defined with a 99 % confidence interval. Ripley's univariate and bivariate patterns were generated with the Toolbox software (Fisher, 2000).

Results and Discussion

Spatial distribution patterns of tree specie

According to the Morisita-Horn index, the spatial distribution pattern of the tree species for pole-sized tree species in all five AS and for all three height categories (lower, intermediate and higher) had a clumped average behavior ($I_\delta = 1.04$) (Table 1), contrary to the proposed hypothesis. This finding is similar to that reported for the *Selva Lacandona* of *Chiapas* in the study by Martínez-Ramos (2006), according to whom more than 60 % of the tree taxa were distributed in a clumped form.

Table 1. Values of the Morisita-Horn index for pole-sized trees (height categories: lower, intermediate, higher), saplings and seedlings in five altitude strata (AS) of the *Metzabok* Protected Natural Area in the *Selva Lacandona*, *Chiapas*.

Altitude stratum (AS)	Pole-sized trees			Saplings	Seedlings
	Lower	Intermediate	Higher		
AS1 (< 600)	1	1	1.1	1.3	1.1
AS2 (600 – 700)	1	1.3	1.3	1.1	1.1
AS3 (700 – 800)	1	1	0.8	1.1	1.2
AS4 (800 – 900)	1.1	1	1	1.1	1.6
AS5 (> 900)	1.3	1	0.8	1.0	1.0

It is worth noting that the general pattern recorded in the present study shows the differences when analyzed by AS. The lower height category exhibited a random and a clumped pattern at a lower and higher altitude, respectively (AS4 and 5) (Table 1). The cause of the clumped pattern is considered to be the clearings formed by natural disturbances: the fall or death of trees, pests and diseases (Brown *et al.*, 2015); these are colonized by pioneer species, whose regeneration depends on sunlight and seeds with a lower range of dispersion (Hubbell, 2001).

However, the presence of both spatial patterns (random and clumped) in the present studio can also be the result of human activities that have modified the habitat and directly affected the survival, reproduction and establishment of the species, as proven by Pavón-Hernández and Rico-Gray (2004) for a transformed landscape in the state of *Veracruz*, Mexico.

The intermediate height category exhibited a random behavior $(I_\delta = 1.0)$ along the altitude gradient, with the exception of AS2, which showed a clumped behavior $(I_\delta = 1.3$ (Table 1). The later pattern is due to the inclination of the slope (30 to 70°) revealed by the stratum, as well as to shallow soils that prevent the growth of the root system of the trees, as suggested by John *et al.* (2007) for various tropical taxa in the world.

Other studies (Blach-Overgaard *et al*., 2010) have shown that the cause of the clumped pattern in tropical rain forests is the fact that the rainy season is associated to strong winds, which promote the falling of trees, whereby microclimates are formed that favor repopulation in clusters. According to Martínez-Ramos (2006), the clumped pattern is related to the topographic and edaphic characteristics; however, it has also been suggested that it can be due to deficient dispersion mechanisms of seeds and low seed depredation (Franklin and Rey, 2007; Hosaka *et al*., 2017).

For the higher height category, the distribution of the species (*Sebastiana longicuspis* Standl, *Pseudolmedia spuria* (Sw.) Griseb, *Manilkara zapota* (L.) Royen and *Pouteria reticulata* (Engl.) Eyma) was uniform at a higher altitude and clumped at a lower altitude (Table 1). The clumped pattern in this category is considered to be caused by closeness to the community, as these are areas where the commoners extract timber for domestic use —a situation that generates the formation of clearings which are taken up by a group of species (*Dialium guianense* (Aubl.) Sandwith, *Heliocarpus appendiculatus* Turcz. and *Pseudolmedia oxiphyllaria* Donn. Sm.) that need direct sunlight to grow and develop (Conanp, 2006; Rivera-Fernández *et al*., 2012).

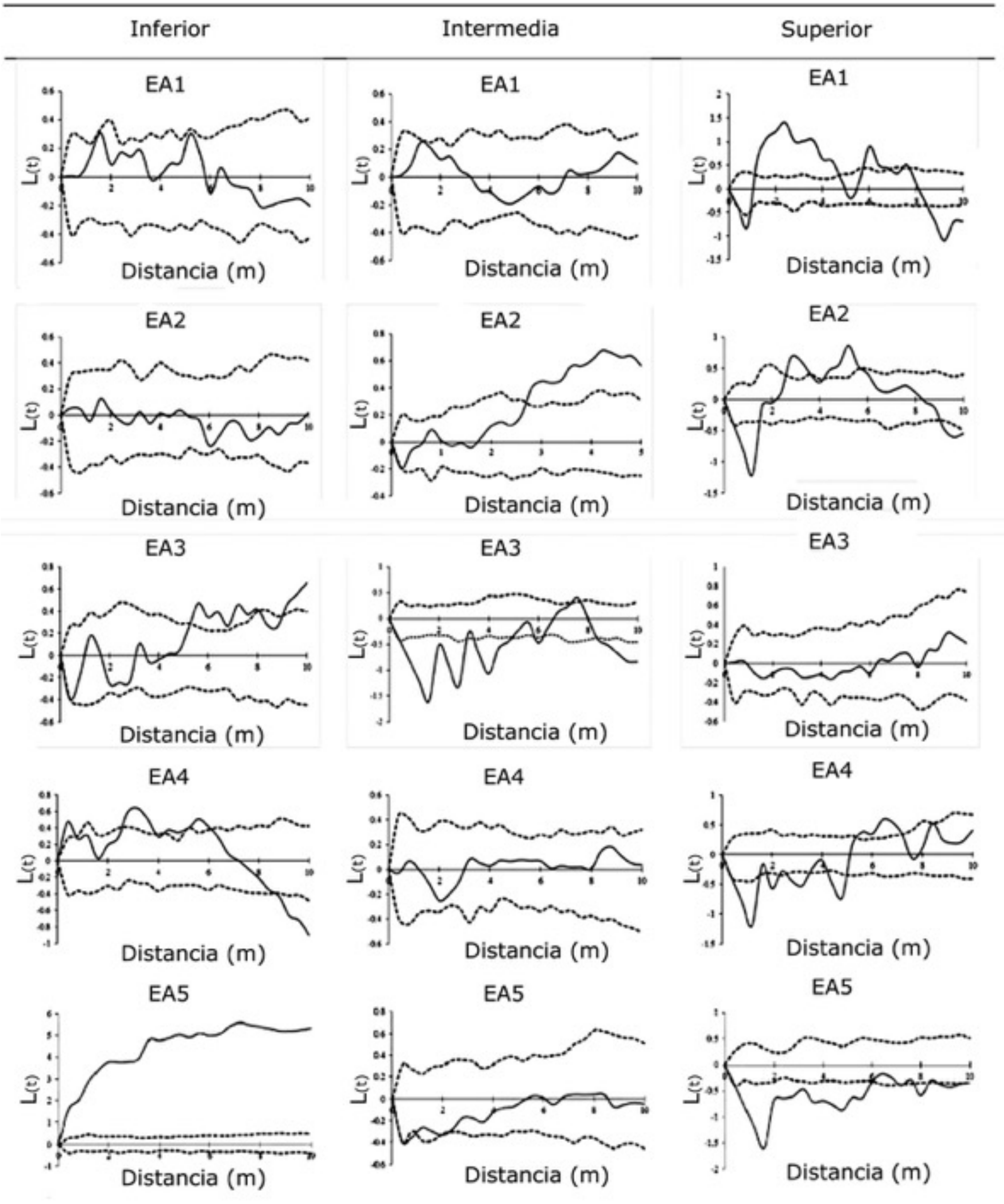
The sapling and seedling development stages profiled a clumped pattern, except for the last AS5 (> 900 masl), in which a random behavior was observed (Table 1). The clearings allow entry of the sunlight, which affects the incorporation and growth of undergrowth plants (Martínez-Ramos, 2006), as in the case of saplings and seedlings. Therefore, any alteration of the characteristics of the canopy has an impact on germination, growth rate, survival and the distribution of the plants (Brienen and Zuidema, 2006; Yili *et al*., 2013), given the specific dominant conditions within the clearing that promote the clustering of the species.

Martínez-Ramos (2006) cites that the clumped pattern is greater in small individuals (with a ND of 1 to 5 cm) than in larger individuals (ND ≥ 10 cm), which have a random distribution. Actually, in the random pattern, individuals are totally independent from the position of any other individual in the population; this behavior occurs only in certain species of temperate forests (Hernández *et al.*, 2018), but it is very common in tree individuals of tropical rain forests (Franklin and Rey, 2007; Yili *et al*., 2013).

The results of this study suggest a certain tendency with altitude gradients and indicate that, at the *Metzabok* PNA, there is a climate variation by gradient that modifies the structure and the makeup of the rain forest; this agrees with other studies on tree structure, composition and diversity performed in the same study area (Martínez-Ramos, 2006; Sánchez-Gutiérrez *et al*., 2017). While in Costa Rica, Cruz (2010) found that, at altitudes between 400 and 900 m, there is no influence of the altitude gradient on the spatial distribution pattern; he also explains that this may be due to the fact that the altitude interval is relatively small, and therefore, the climate conditions do not vary between strata. Consequently, it has been suggested that studies on the vegetation by altitude gradients should be carried out in large geographical expanses (Fossa, 2004).

Spatial distribution of tree species with Ripley's *K(t)* function

According to Ripley's univariate $K(t)$ function, the spatial distribution of the three height categories of pole-sized trees exhibited a significant pattern ($p \leq 0.01$) —clumped, random or uniform— at different distances, which implies that the suggested hypothesis is accepted (Figure 2). This is a similar result to that obtained with the Morisita-Horn index for pole-sized trees (Table 1).



Distancia = Distance; *Inferior* = Lower; *Intermedia* = Intermediate; *Superior* = Higher.

Figure 2. *L*(*t*) univariate distribution values for the three height categories of pole-sized trees in five altitude strata (AS) of the *Metzabok* Protected Natural Area in the *Selva Lacandona* of *Chiapas*.

In general, the lower height category had a clumped pattern, with variation at different distances and altitude strata (Figure 2). AS1 and 4 have a clumped distribution at distances of 1 to 6 m, and a uniform distribution at distances of more than 7 m; AS2 had a random behavior, and the distribution of AS3 was uniform at distances of 1 to 2 m, and a clumped distribution at distances of 3 to 10 m (Figure 2). AS5 had a clumped distribution at all the distances.

The variation in the distribution patterns in the different AS is related to the clearings generated by the intermediate and higher categories, since, having been affected by some disturbance (such as the falling of branches or of the whole tree, tree fellings or death due to pests and diseases), these surfaces are repopulated by species that demand light and which change their initial (clumped) pattern into a random pattern through death processes (Franklin and Rey, 2007; Barreto-Silva *et al*., 2014). Within the study area, the clearings are colonized by *R. guatemalensis* (S. Watson) Bartlett, which coincides with the results obtained by Zarco *et al.* (2010) in rain forests of *Tabasco*, according to whom this species grows and is prevalent in the lower stratum of rain forests where disturbs occur.

The intermediate height category had a mostly random distribution, although at shorter distances the trees adopt a uniform pattern, with the exception of AS2, which as a clumped distribution at distances of 2 to 10 m (Figure 2). The random distribution in this category is due mainly to the timber extraction that took place in the study area during the 1970s (Conanp, 2006), which promoted the mortality of a heterogeneous group of species in space. On the other hand, clumped patterns may be a response to the environmental variability between strata and are ecologically common in large individuals (Dixon, 2013).

In the higher height category, AS1 and 2 exhibited a clumped pattern at distances of less than 8 m (Figure 2), due both to the natural death of certain old trees and to the selective extraction of precious woods such as mahogany (*Swietenia macrophylla* King) and cedar (*Cedrela odorata* L.). In fact, in the years 1975 and 1984, the exploitation of 55 000 m^3 and 20 000 m^3 of common tropical species in the *Selva*

Lacandona was authorized (Vásquez-Sánchez *et al*., 1992), and the timber exploitation by the population of certain areas of the PNA for purposes of building homes is ongoing (Conanp, 2006); these populations leave clusters of the species *M. zapota, P. reticulata, Manilkara chicle* (Pittier) Gilly and *Brosimun alicastrum* Sw standing because their wood is hard and dense, and therefore difficult to handle, which renders them less valuable.

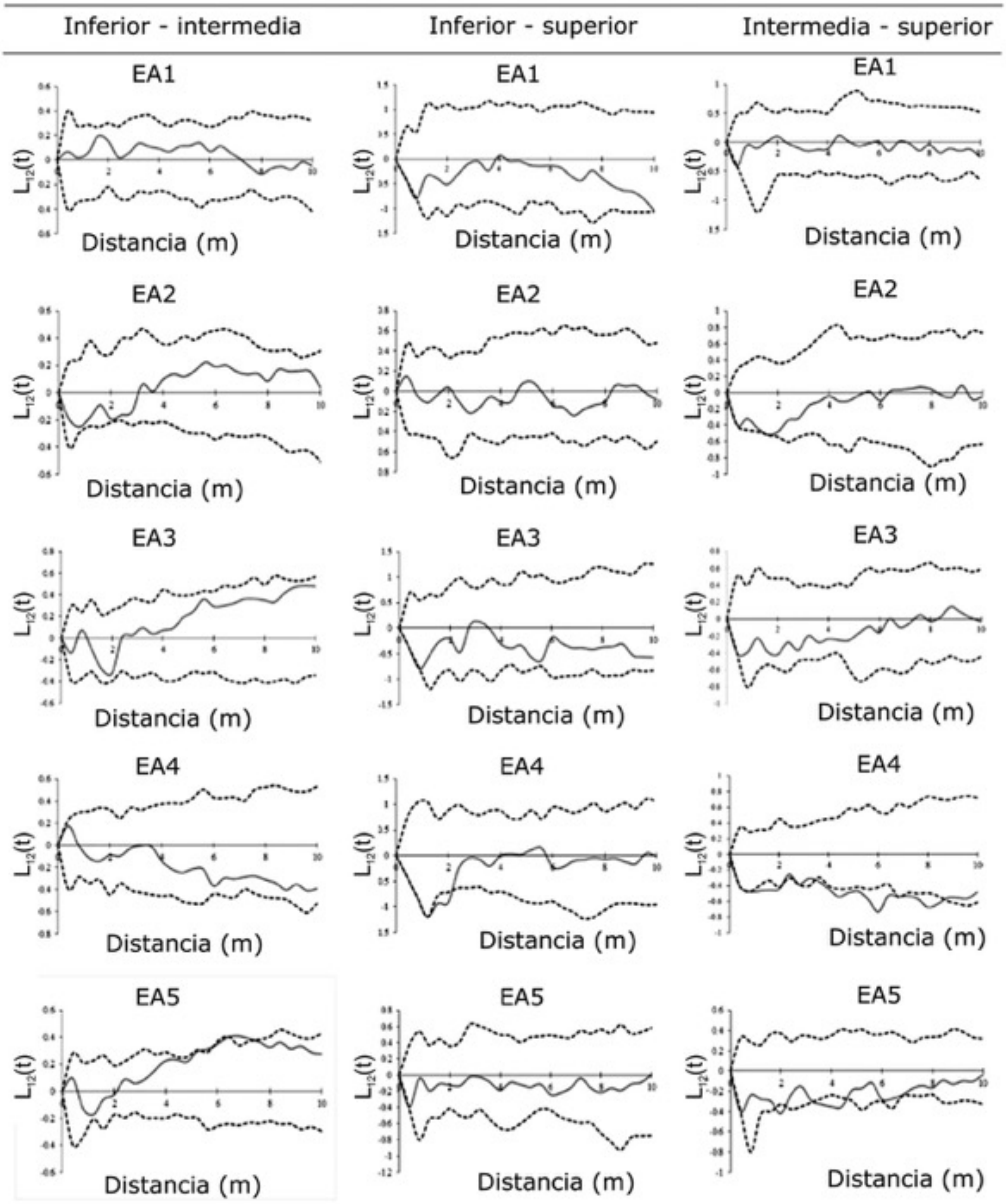
This agrees with the findings of Franklin and Rey (2007) and of Dale and Fortin (2014), according to whom the logical evolution of the spatial pattern with the increasing age of the individuals is caused by the accumulated effect of the disturbances, competition and attack by pathogens. Therefore, a random pattern can change into a clumped or uniform pattern, according to the environmental and anthropic characteristics of the habitat.

Although a uniform behavior is rare in natural assemblies, it may be found in stable environments with minimal disturbances (Antos and Parish, 2002). Indeed, the model proposed by Janzen (1970) states that the consequence of the mortality of trees is a uniform distribution of the surviving adult individuals, as was corroborated by Lan *et al.* (2009) in the tropical rain forests of China, where they observed that these tend to follow a uniform distribution in environments with multiple species.

The extremely variable spatial pattern registered in AS3, 4 and 5 (Figure 2) may be due to the difficulty to access these strata, as there are no records of timber exploitation, and it is possible to find *Calophyllum brasiliense* Cambess*., Terminalia amazonia* (J.F. Gmel.) Exell*, Guatteria anomala* R.E. Fr*., M. chicle* and *M. zapota* individuals with a diameter of up to 190 cm and heights above 50 m. Certain authors (Rozas and Camarero, 2005; Linzaga-Román *et al*., 2011) propose that such a variable behavior in the distribution pattern is accounted for by the topographic factors of the site. Thus, it may be suggested that the distribution of species at the *Metzabok* PNA can be associated to the environmental heterogeneity induced by the relief and by the disturbances produced in each site, as suggested by Montáñez *et al.* (2010) and Barreto-Silva *et al.* (2014) for certain tropical rain forests of Colombia.

Spatial correlation patterns

According to the spatial correlation of Ripley's $K_{12}(t)$ function, the bivariates of the AS2, 3 and 5 of the lower-intermediate height category indicated spatial repulsion in distances of less than 2 m and attraction of between 3 and 10 m (Figure 3). The repulsion at a small scale between the two categories would be a consequence of the density-dependent mortality of the seedlings located beneath the crowns of the intermediate and higher height categories; therefore, species of the lower height categories (*Myriocarpa longipes* Liebm. and *Piper psilorhachis* C. DC.) colonize the available spaces, except under the crown of taxa of the higher categories, such as *C. brasiliense*, *T. amazonia* and *G. anomala* (Lan *et al*., 2009).



Distancia = Distance; *EA* = AS; *Inferior-Intermedia* = Lower-intermediate; *Inferior-Superior* = Lower-higher; *Intermedia- Superior* = Intermediate-higher.

Figure 3. Matrix of the ratio of the bivariate $L_{12}(t)$ distribution to the three height categories of the pole-sized tree species in five altitude strata (AS) of the *Metzabok* Protected Natural Area in the *Selva Lacandona* of *Chiapas*.

This behavior can also be caused by depredation processes, as it is more likely that the predators will eliminate those individuals that are closest to the seed tree (Hosaka *et al.*, 2017); this would explain the existence of repulsion between the lower-higher category at near distances, and of attraction in the intermediate-higher, as the distance to the parent tree increases (Rozas and Camarero, 2005; Barreto-Silva *et al*., 2014).

This contrasts with the AS1 and 4, in which the correlation pattern was independent, as it was the same that was observed for all the strata of the lower-higher category. In the intermediate-superior category (*Haematoxylum campechianum* L. and *Hauya elegans* DC. *vs. D. guianense* and *Pouteria durlandii* (Standl.) Baehni, respectively), negative associations (repulsion) occur at different distances; this was more noticeable in the AS4 (Figure 3). This type of behavior is perhaps a response to the high mortality of seeds and lower individuals close to the higher trees. Diseases and depredation are concentrated in the vicinity of the parent trees, which causes density-dependent mortality, as there is a higher probability of survival and seed-producing adults (Janzen, 1970; Franklin and Rey, 2007; Hosaka *et al*., 2017).

Conclusions

The spatial distribution pattern of the tree species is related to the altitude, but it is also influenced by natural and anthropic disturbances. The species of the sapling (*Chamaedorea oblongata* Mart., *Chamaedorea pinnatifrons* (Jacq.) Oerst., *P. oxiphyllaria* and *Chionanthus oblanceolatus* (B. L. Rob.) P.S. Green), and seedling (*R. guatemalensis*, *Eugenia acapulcensis* Steud., *Aphananthe monoica* (Hemsl.) J.-F. Leroy and *P. reticulata*), development stages respectively, are found in a cluster arrangement because most of them grow in disturbed areas with the presence of clearings, though under the canopy of residual pole-sized trees, because their growth and development require more sunlight.

The spatial correlation pattern between height categories is variable. In the lower-intermediate category (with dominant species like *R. guatemalensis* and *P. psilorhachis vs. Garcinia intermedia* (Pittier) Hammel and *Trophis mexicana* (Liebm.)

Bureau) and intermediate-higher (with dominance by *H. campechianum* L. and *H. elegans vs. D. guianense* and *P. durlandii*), there is repulsion at a shorter distance, due to the shade cast by taller individuals, which prevents the entry of sunlight, and an attraction at a longer distance, promoted mainly by a higher probability of survival to attack by predators.

Based on the results, it is possible to propose reforestation strategies and forest restoration strategies that will consider the positive interactions of the ecological assemblies formed by saplings, seedlings, and pole-sized trees in the various height categories and altitude gradients, in order to preserve the structure and spatial composition of the *Selva Lacandona*.

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Conflict of de interests

The authors declare no conflict of interests.

Contribution by author

Facundo Sánchez-Gutiérrez: design of the research, field data collection, information analysis, and drafting of the document; Juan Ignacio Valdez-Hernández: coordination of desk and field work, review of the manuscript; Patricia Hernández-de la Rosa: design and structure of the manuscript, review of the various drafts of the document; Leonardo Beltrán-Rodríguez: information analysis, writing and review of the various drafts of the final document.

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