Testing aggregation hypotheses among Neotropical trees and shrubs: results from a 50-ha plot over 20 years of sampling

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Abstract: Spatial patterns of tropical trees and shrubs are important to understanding their interaction and the resultant structure of tropical rainforests. To assess this issue, we took advantage of previously collected data, on Neotropical tree and shrub stem identified to species and mapped for spatial coordinates in a 50ha plot, with a frequency of every five years and over a 20 year period. These stems data were first placed into four groups, regardless of species, depending on their location in the vertical strata of the rainforest (shrubs, understory trees, mid-sized trees, tall trees) and then used to generate aggregation patterns for each sampling year. We found shrubs and understory trees clumped at small spatial scales of a few meters for several of the years sampled. Alternatively, mid-sized trees and tall trees did not clump, nor did they show uniform (regular) patterns, during any sampling period. In general (1) groups found higher in the canopy did not show aggregation on the ground and (2) the spatial patterns of all four groups showed similarity among different sampling years, thereby supporting a "shifting mosaic" view of plant communities over large areas. Spatial analysis, such as this one, are critical to understanding and predicting tree spaces, tree-tree replacements and the Neotropical forest patterns, such as biodiversity and those needed for sustainability efforts, they produce. Rev. Biol. Trop. 60 (3): 1015-1023. Epub 2012 September 01.

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Plants are sessile organisms and exhibit spatial patterns. Such patterns are either random, uniform (regular), or have different degrees of clumping (Ludwig & Reynolds 1988), and have been observed in all plant communities (Van Gardingen *et al.* 1997, Wiegand *et al*. 2006). They are at once the effect of plant mechanisms (e.g., dispersal, predation, pathogenic disease, herbivory) and tolerances (e.g., germination, competition) but can also affect the way those mechanisms and tolerances operate. For example, bird-dispersed trees that invade fields after abandonment from agriculture create perching sites that cause higher degrees of clumping for other bird-dispersed trees (Myster & Pickett 1992). After dispersal, seed processes such as predation, pathogenic disease, and germination also have distinct spatial patterns and distinct spatial scales at which they operate (Verdu & Garcia-Fayos 1998, Myster 2003, Svenning & Wright 2005). Indeed the idea of a plant's "neighborhood" (*sensu* Turkington & Harper 1979) presupposes a defined spatial area where each individual plant can influence local events, or be influenced by them, for example in competition with other plants.

Such concerns about both plant spatial patterns themselves, and how those patterns influence plant community structure, functions and dynamics, have long been issues in temperate and tropical forests (Janzen 1970, Gray & Spies 1997, Condit *et al.* 2000). The spatial pattern of species diversity and the mechanisms creating that pattern, for instance, have been of interest (He *et al.* 1997, Itoh *et al*. 1997, Plotkin *et al.* 2000b, Myster 2012). Alternatively the spatial patterns of individual tree species, where most individual species clump at some spatial scale (Hubbell 1979, He *et al.* 1997, Condit *et al.* 2000, Plotkin *et al.* 2000a, Picard *et al.* 2009), and how those patterns relate to a species' abundance (He *et al.* 1997, Condit *et al.* 2000) and stem size (He *et al.* 1997, Itoh *et al.* 1997) has also generated studies. Interpretations of pattern have depended on the scale where expressed, ranging from small-scale biotic mechanisms (e.g., dispersal, predation, herbivory: Everham *et al.* 1996, Myster & Santacruz 2005, Plotkin *et al.* 2000a) to larger-scale abiotic gradients (e.g., light, topography, edaphic factors: Svenning 1999). Important plant patterns, such as biodiversity, and long-tem management and conservation objectives, such as sustainability, are both consequences of how plant spaces create plant-plant replacements. Consequently, analysis of tropical tree spatial patterns is critical to the future of these forests.

In this study we suggest that an analysis of horizontal spatial patterns, of groups of tree and shrub species that represent the vertical spatial structure of forests, may be a fruitful way to investigate this issue. We will expand on past spatial analysis of Neotropical trees to include: (1) stems down to 1cm dbh, (2) an entire 50ha plot, and (3) five consecutive samplings spanning 20 years of forest growth and dynamics. In addition we will use O-ring analysis " (Wiegand & Moloney 2004), which is a refinement of Ripley's K-function (Plotkin *et al.* 2000b) and an improvement of simpler aggregation methods (Hubbell 1979, Condit *et al.* 2000) used in past studies of rainforest tree spatial patterns.

We test these four specific hypotheses suggested by previous forest tree studies:

Hypothesis 1: Shrubs (<4m maximum height) and understory trees (4-10m) will clump at the small scale of a few meters (Myster & Pickett 1992, Condit *et. al.*2000, Picard *et al.* 2009).

Hypothesis 2: Mid-sized (10-20m) and tall (>20m) trees will not show significant clumping at any spatial scale and year of sampling due to the spacing out effects of prolonged competition, but will show uniform (regular) tree spatial patterns at some spatial scales as they do in Boreal forests (Pham *et al.* 2004, Neeff *et al*. 2005, Picard *et al.* 2009).

Hypothesis 3: There is a relationship between vertical spatial structure and horizontal spatial structure, where woody groups found farther up in the canopy are also arranged farther apart on the ground, reducing clumping and promoting random and uniform (regular) distribution patterns (Pham *et al.* 2004, Picard *et al.* 2009).

Hypothesis 4: Trees and shrubs will aggregate at similar spatial scales –within their group– for different sampling years, thus supporting a "shifting mosaic" perspective of plant communities as individual trees die and new recruitment occurs over time (Watt 1947, Hubbell 1979).

MATERIALS AND METHODS

In this study we used data collected in a 50ha plot (500mx1 000m) managed by the Smithsonian Tropical Research Institute. The plot is located in Barro Colorado Island (BCI: 9°9' N, 79°51' W) formed during the creation of the Panama canal, where rainfall averages 2 500mm per year, with a four month dry season between January and April, and with temperature ranges of 38°C-18°C (Condit *et al.* 2000). The plot was established in 1981 (Hubbell & Foster 1983) and first sampled between 1981 and 1983, when all free-standing woody stems≥1cm diameter at breast height (dbh) were measured to the nearest millimeter, located on the ground at least to the closest meter (x, y coordinates), and identified to species (Condit *et al.* 1996a, Condit *et al.* 1996b, Condit 1998). The plot has been resampled in 1985, 1990, 1995, 2000, 2005 and 2010. One may visit http://www.theplantlist.org/tpl/record/

kew-313975 for nomenclature and https://ctfs.arnarb.harvard.edu/webatlas/datasets/bci/ for more information about the plot.

In a previous study (Hubbell & Foster 1990), all species that had at least 1 000 stems in the first sampling were divided into four groups (Table 1) based on their role in defining the strata and vertical structure of the rainforest: (1) shrubs (<4m maximum height), (2) understory trees (4-10m), (3) mid-sized trees (10-20m) and (4) tall trees (>20m). Together, the stems in these four groups were over 80% of the total stems in that first sampling (Hubbell & Foster 1990). We first applied these groups to data collected in 1985, 1990, 1995 and 2000, but could not use data sampled in 2005 and 2010 because it is not yet generally available. In future papers, we will be using the results from this analysis as a baseline where we will compare and contrast the species group spatial patterns with the spatial patterns from each individual species mentioned in Table 1. Finally, seed masses are given in Table 1 (Sautu *et al.* 2006, http://www.data.kew.org/sid/weight/htm) as a correlate to the species groupings and hence, further justification for those groupings.

Then we used O-ring spatial statistics, which includes an edge correction improvement on the popular Ripley's K function (Ripley 1981, Plotkin *et al.* 2000b, Myster 2003, Loosmore & Ford 2006, Picard *et al.* 2009, Myster & Malahy 2010), to generate spatial patterns for all stems in each of the four groups for every sampling year using Programita software (Wiegand & Moloney 2004). The O-ring statistic is a point-pattern statistic that considers the mean number of neighbors in a ring of radius r around an individual, thus isolating specific distance classes. This analysis allows an exploration of clumping at different spatial scales with a 95% confidence interval calculated from the highest and lowest values taken from 95 simulations of the null model, which defines significant clumping at those scales where the computed point is above the confidence interval and a significant uniform pattern at those scales when the computed point is below the confidence interval. These confidence intervals were computed for every year and species group, but were so similar within each group that only the interval average is given in the figures.

RESULTS

Over the five samplings, shrubs had a mean density of 1 502stems/ha, understory trees had a mean density of 1 087stems/ha, mid-sized trees had a mean density of 460stems/ha and tall trees had a mean density of 769stems/ha. Both shrubs (Fig. 1) and understory trees (Fig. 2) were significantly clumped at small

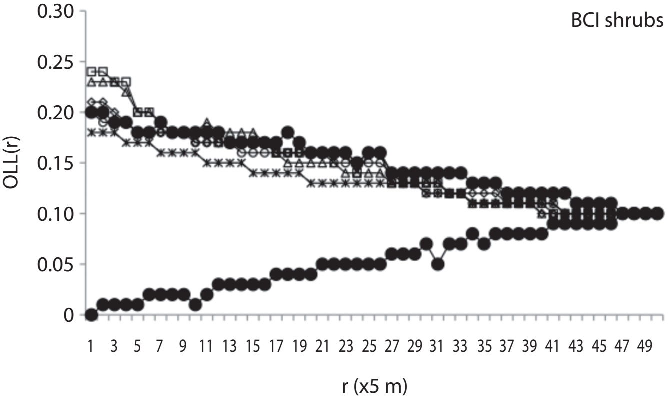

Fig. 1. O-ring statistic pattern for all BCI shrubs over an increasing spatial scale. Year 1 sampling (is indicated by a star), year 2 sampling (open triangle), year 3 sampling (open square), year 4 sampling (open diamond), and year 5 sampling (open circle). The 95% confidence interval is indicated by a black circle. The x-axis is the scale of aggregation in units of 5 meters. The y-axis is the O-ring aggregation index.

TABLE 1

The scientific names of the most common tree species sampled in the 50 ha plot in the first sampling, their seed masses per 1 000 seeds, and their growth form (S=shrubs, U=understory trees, M=midsize trees, T=tall trees)

Species	Seed mass (g), if known	Growth form
Acalypha diversifolia	not known	S
Alseis blackiana	0.1	T
Beilschmiedia pendula	4 744	T
Capparis frondosa	97	S
Cordia lasiocalyx	140.7	M
Coussarea curvigemmia	not known	U
Cupania sylvatica	not known	U
Desmopsis panamensis	not known	U
Drypetes standleyi	not known	T
Eugenia galalonensis	not known	U
Eugenia oerstedeana	not known	M
Faramea occidentalis	300	U
Guarea guidonia	127	M
Guarea sp. nov.	not known	M
Guatteria dumetorum	not known	T
Hasseltia floribunda	20	M
Hirtella triandra	not known	M
Hybanthus prunifolius	13	S
Lacistema aggregatum	35.2	U
Maquira costaricana	not known	M
Mouriri myrtilloides	68-85	S
Ocotea skutchii	not known	T
Oenocarpus mapora	not known	M
Ouratea lucens	not known	S
Picramnia latifolia	57	U
Piper cordulatum	3.12	S
Poulsenia armata	75	T
Pouteria unilocularis	not known	T
Prioria copaifera	53.153	T
Protium panamense	2.668	M
Protium tenuifolium	84-1 300	M
Psychotria horizontalis	6	S
Pterocarpus rohrii	178	T
Quararibea asterolepis	250	T
Randia armata	104	U
Rheedia edulis	289	M
Rinorea sylvatica	not known	S
Simarouba amara	219	T
Sorocea affinis	not known	S
Swartzia simplex v. *grandiflora*	1 149	U
Swartzia simplex v. *ochnacea*	1 087	U
Tabernaemontana arborea	429	T
Tachigalia versicolor	1 140	T
Tetragastris panamensis	302	T
Trichilia tuberculata	151	T
Virola sebifera	701	M

S=shrubs, U=understory trees, M=midsize trees, T=tall trees.

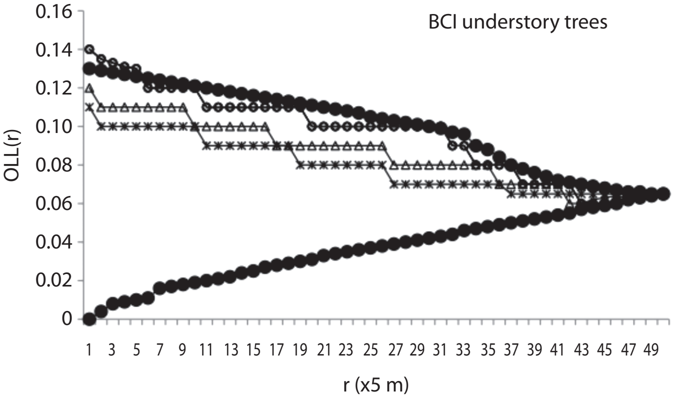

Fig. 2. O-ring statistic pattern for all BCI understory trees. Labeling is as in figure 1.

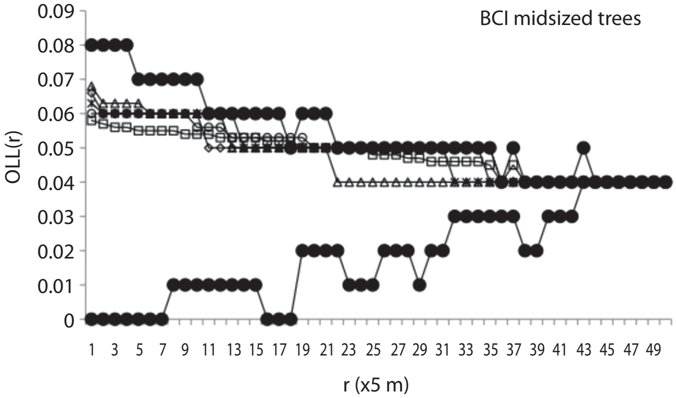

Fig. 3. O-ring statistic pattern for all BCI mid-sized trees. Labeling is as in figure 1.

spatial scales of a few meters for several of the years sampled, supporting hypothesis 1 for those years.

Hypothesis 2 was accepted when mid-sized trees (Fig. 3) and tall trees (Fig. 4) did not clump during any sampling period, but rejected when neither woody group showed significant uniform (regular) patterns at any sampling period either. Taking those results together leads to an acceptance of hypothesis 3. There was also support for hypothesis 4 because of the general similarity of the aggregation patterns within each woody group over the sampling years, as some individual trees of the same group die and others reproduce over the years.

DISCUSSION

Because the spatial placement of plants affects how they reproduce and grow, it may be possible to infer biological process from spatial patterns (Picard *et al.* 2009). The significant clumping seen for those species dispersed by birds has been demonstrated elsewhere where these species have been shown to have a higher degree of clumping than wind and mammal dispersed species (Hubbell 1979, Myster & Pickett 1992, Seidler & Plotkin 2006). Indeed, mode of dispersal and its range have been thought to be key to forest dynamics in general (He *et al.* 1996, Clark *et al.* 2005). This

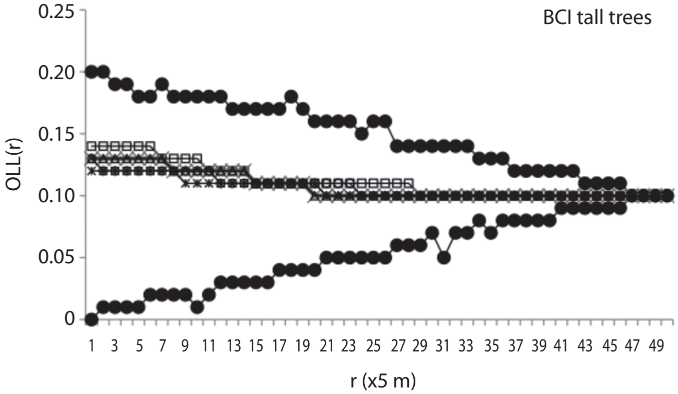

Fig. 4. O-ring statistic pattern for all BCI tall trees. Labeling is as in figure 1.

clumped distribution may also result from specialization for patchy small-scale edaphic habitats (Itoh *et al*. 1997, Condit *et al*. 2000), lingering effects of past disturbance (tree fall gap formation: Condit *et al*. 2000; clearing for agriculture: Myster 2007) or facilitation among species in the same vertical strata group (Wiegand *et al*. 2006).

There was no significant clumping for trees taller than 10m. The clumping seen for shrubs lower in the canopy may have been lost as growth proceeded because of local neighborhood (He *et al*. 1997) seed and seedling mortality mechanisms such as predation, herbivory, and pathogenic attack, which may be most intense near large conspecifics (Janzen 1970, Okuda & Kachi 1995, Itoh *et al.* 1997). The loss of pattern at larger scales may also be due to the action of distance-dependent mortality agents such as allelopathy, competition, litter fall, depletion of critical nutrients, and shading (Okuda & Kachi 1995). Larger trees are also more widely-dispersed than smaller ones, which may also lead to a lessening of aggregation (Thomson *et al*. 2011).

Results supported, to a degree, a trend found in other tropical studies of clustering for small trees shifting to regularity for medium-sized trees, and finally randomness for the largest trees, that is a shift to regularity with increasing size. No Neotropical trees were uniformly distributed here however (as seen in Picard *et al*. 2009) and so, it seems, competition was not strong enough –in terms of its negative feedback effects– relative to other mechanisms to produce regularity (Wright 1982, Picard *et al*. 2009). Taken together these results show that small scales are critical to non-random spatial patterns (He *et. al.* 1996), suggesting that small-scale phenomena such as dispersal and gap recruitment determine spatial patterns more than adaptation to larger-scale topography, soil differentiation, or water stress (Plokin *et al*. 2000a). Our results then reinforce the view that deviation from randomness is generally caused by either net positive or net negative plant interactions (Wiegand *et al*. 2006).

In conclusion, the analysis did not show a minimum “critical distance” where regeneration increases due to a greater chance of encountering a light gap (Okuda & Kachi 1995). Indeed the spare distribution of most species in tropical forests suggests that density-dependence effects, such as competition, are not overwhelming. We hope that this study can now serve as a baseline dataset for comparison as more sampling occurs in the future. Also, for further research on spatial issues among tropical trees, we plan a follow up study using this same dataset focusing on the spatial patterns of individual species, within each vertical strata group, over the same 20 years sampling period in order to investigate the within-group variation conformity to the pattern of the entire group, and to see if it can be tied to more specific mechanisms and/or life-history strategies of the species.

This large plot and long-term repeated sampling allows for a deeper understanding of the spatial dynamics of Neotropical rainforests (Myster 2012). Our focus on structural differences among common trees and shrubs further illustrates how spatial patterns change with growth form and with plant growth, both horizontal and vertical. In the tropics, important plant patterns, such as biodiversity, and longtem management and conservation objectives, such as sustainability, are both consequences of how plant spaces create plant-plant replacements. As such, detailed analysis of Neotropical tree spatial relationships are critical to the future of these forests.

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RESUMEN

Con datos obtenidos previamente, se identificaron especies de árboles y arbustos neotropicales y se ubicaron con coordenadas espaciales en una parcela de 50ha cada cinco años durante un período de 20 años. Estos datos primero se dividieron en cuatro grupos según los estratos verticales del bosque (arbustos, árboles del sotobosque, árboles medios y árboles altos); después se usaron tres para estudiar patrones de agregación en cada año de muestreo. Los arbustos y árboles del sotobosque se agruparon en pequeñas escalas espaciales de pocos metros en varios de los años del estudio, mientras que los árboles de tamaño medio y grande no se agregaron ni mostraron patrones regulares en ningún período de muestreo. En general: (1) Las especies más altas del dosel perdieron la agregación en el terreno y (2) Los patrones espaciales de todos los grupos de especies mostraron similitud entre los años de muestreo, lo que apoya la idea de un “mosaico cambiante” de las comunidades vegetales en grandes áreas. El análisis espacial, como este, es fundamental para comprender y predecir los espacios arbóreos, el reemplazo de árbol por árbol y los patrones de los bosques neotropicales, tal como la diversidad y aquellos esfuerzos necesarios para garantizar la sostenibilidad, que producen.

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