



Original article

Different spatial organisation strategies of woody plant species in a montane cloud forest

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ABSTRACT

The coexistence of a high number of species in the forest is a central issue in tropical ecology. In this paper, we aim to characterise the spatial pattern of woody species in an Andean montane cloud forest to determine whether differences exist among the species in terms of spatial organization and if so, whether these differences are related to the life-form, primary dispersal mode, shade tolerance or the diameter distribution of the species. For this purpose, we analysed the spatial pattern of each species as well as the spatial relationships between young and adult individuals. Almost all the analysed species showed a cluster pattern, followed by a random pattern at larger distances. The cluster size is more evident for the young trees whereas adult trees tended to be more randomly distributed. The shade-tolerant species showed greater distances of aggregation than gap or medium-shade-tolerant species. Species primarily dispersed by wind and small birds showed larger distances of aggregation than species dispersed by mammals or big birds. All the under-story woody plants showed a notable cluster pattern, whereas canopy trees showed a variety of spatial patterns, with clustering at small scales being the most frequent. In the case of emergent trees, association was found between young and adult individuals on a large scale. Positive associations between young and adult individuals predominate at small scales for medium and shade tolerant species and at larger scales for bird-dispersed species whereas negative spatial associations at smaller scales were found for shade tolerant species and wind dispersed species. Our study confirms that conspecific organization varies among the woody plants in the analysed forest, and that the spatial pattern of woody plants is partially linked to shade tolerance, primary dispersal mode and life form of the species.

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1. Introduction

The spatial pattern and arrangement of individuals of any species is fundamental in ecological theory (Dale, 1999; Condit et al., 2000) and provides us with an understanding of the interactions among the elements of the ecosystem and dynamics that take place (Legendre, 1993; Picard et al., 2009). Therefore, the study of ecosystems should include an analysis of plant distribution (Law et al., 2001) to provide an insight into the ecological processes underlying population dynamics (He et al., 1996). Data regarding the distribution of trees are essential when analysing the way in which trees use the resources available to them (Condit et al., 2000), and resource usage patterns are thought to differ from one species to another (Picard et al., 2009). Furthermore, by analysing the spatial distribution of individuals of each species in a forest,

their different niches can be characterised (Kneitel and Chase, 2004) and the contribution of different factors to the formation of this pattern can be identified. These factors include dispersal strategies, establishment requirements, development, competition and mortality processes as well as physical processes such as soil formation or rock scouring. Hence, by analysing the distribution patterns of the different species, it is possible to shed light on the role of each species and the interactions which exist among them (Saldaña-Acosta et al., 2008).

Spatial analysis methods based on the second-order characteristics of the distribution of individuals have recently been developed in a wide range of fields. Point pattern techniques, for example, have been widely used in ecology to analyse the spatial structure of ecosystems. The $K(d)$ function (Ripley, 1977) and related functions have been employed to describe the second-order properties of the spatial pattern as a function of the inter-point distance in a wide range of ecological applications (Dixon, 2002; Wiegand et al., 2007; Picard et al., 2009). In addition, several functions have been developed to analyse bivariate spatial point processes (Lotwisch and

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Silverman, 1982; Wiegand and Moloney, 2004), allowing us to analyse the spatial relationships between two types of points at different scales. The challenge associated with spatial analysis techniques is to relate the spatial pattern to the ecological and physical processes which underlie it (Perry et al., 2006).

The cloud forest ecosystem is one of the least understood (Luna-Vega et al., 2001). Literature on the dynamics and ecology of montane cloud forest species is scarce, and inventory data are limited. Although this ecosystem is considered extremely fragile due to its dependence on the existence of specific ambient conditions (Gomez-Peralta et al., 2008), it harbours high levels of species endemism (Gentry, 1992a) and displays one of the highest levels of biodiversity in the world (Gentry, 1992b; Churchill et al., 1995). Today, tropical montane cloud forest is one of the most threatened ecosystems in the world (Stadtmüller, 1987; Hamilton, 1995; Gomez-Peralta et al., 2008). Human pressure has probably played a major role in the disappearance and fragmentation of cloud forests (Sarmiento, 1993; Aubad et al., 2008), although climate change is also having an impact on them (Pounds et al., 1999; Still et al., 1999; Foster, 2001).

The main objective of this paper is to examine the different conspecific spatial arrangement strategies of the different woody plant species in a montane cloud forest. For this purpose, the spatial pattern of the woody plant species was analysed, as was the spatial association between the young and adult individuals of each species. The relationship between the species pattern and diameter distribution, shade tolerance, primary dispersal method and life-form was also investigated.

It is hoped that the information obtained will help to advance our understanding of spatial organisation in woody plant species and therefore, aid the development of strategies aimed at maintaining the diversity and stability of the ecosystem.

2. Material and methods

2.1. Study site and data collection

The location of the study was amontane cloud forest known as “Monte de Neblina de Cuyas” (UTM 642700–644300W and

9493300–9490499N, 17S Zone, Datum WGS84). The forest is situated on “Cerro Chacas”, in the western Andean cordillera in the Ayabaca province of the Piura region of northern Peru and the zone has been designated an Important Bird Area IBA005 (Freile and Santander, 2005). The study site covers a total area of 171 hectares and is situated between 2359 and 3012 m above sea level (Fig. 1). The total cloud forest area currently covers ~400 ha, although it is gradually shrinking, probably as a result of land use change (to cultivated farmland or livestock grazing), which may lead to the disappearance of habitats for a number of key species (Ledo et al., 2009). The likelihood of mining activity in the near future poses a serious threat which is likely to result in the complete disappearance of the forest.

The inventory was carried out between March and August 2008. All woody plants above 1.3 m were mapped in three 1-ha experimental plots and each species was recorded. In order to make a better assessment of large, irregular shaped trees, two perpendicular diameter measurements were taken at 1.30 m (DBH) on all of the mapped plants. The plots were located in an ‘old-growth’ stand with relatively homogenous physiography and environmental conditions across all three; slope ~58%, podzol-like soil, relative humidity ~80–100, mean annual temperature ~10–14 °C and canopy openness value of 0.06. The three experimental plots had a J-shape diameter distribution typical of uneven-aged stands. As can be seen from Table 1, the number of trees differed somewhat among plots although the size:class ratio was similar in each.

In order to correctly identify each species, samples of the woody plants were collected during the fieldwork and compared to catalogued specimens in the main herbaria of the region: Trujillo Herbarium Truxillense (HUT) (where most of the botanical collection associated with this study is deposited), Herbario Antenor Orrego (HAO), Herbarium de la Universidad de Piura (UPADI), Herbario Universidad Nacional de Cajamarca (CPUN), and Herbario Universidad Nacional Pedro Ruiz Gallo (PRG). The help of experts on specific taxa was also enlisted where necessary although due to the botanical complexity of the tropical montane cloud forest and the lack of documentation, it was not possible to identify all the plants at species level. Hence, the unidentified species are termed ‘Morphospecies (Ms)’ in both the inventory and the data analysis.

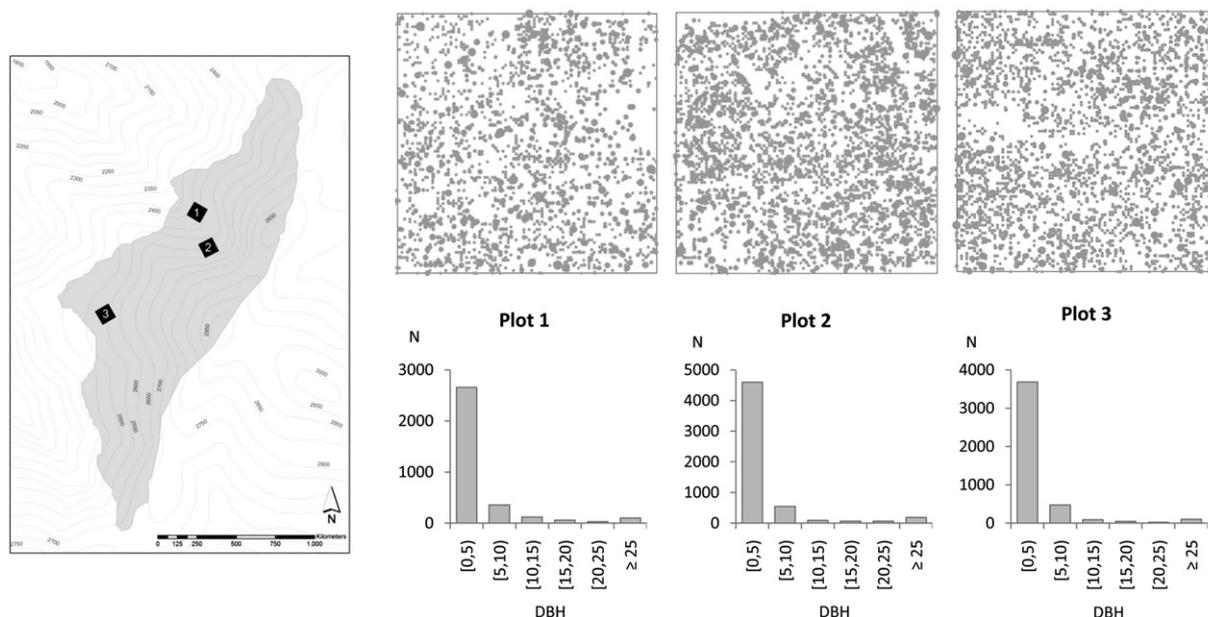


Fig. 1. Left: Map of the studied forest and plot distribution. Upper right: Map of the overall woody plant distribution, where each tree is represented by a circle with a radius proportional to the diameter of the tree. Lower right: Diameter distribution of the woody plants.

Table 1

Stand characterisation in plots. N , tree number; $N, d_0 < 5$ cm, number of trees with a diameter less than 5 cm (as a percentage of total trees); $N, d_0 \geq 20$ cm, number of trees with a diameter greater than or equal to 20 cm (as a percentage of total trees); DBH, quadratic mean diameter at breast height (cm); G , basal area (m^2/ha); QMH, quadratic mean height (m); H_0 , Hart's dominant height (m); N fallen trees, the number of fallen trees in the plot, and N species, the number of different woody species recorded (excluding lianas).

	Plot 1	Plot 2	Plot 3
N	3340	5654	4421
$N, d_0 < 5$ cm	2660 (80%)	4623 (82%)	3718 (84%)
$N, d_0 \geq 20$ cm	133 (5%)	270 (6%)	134 (4%)
DBH	10.88	10.78	14.98
G	31.03	51.56	77.94
QMH	4.78	5.12	5.04
H_0	15.84	19.68	18.763
N fallen trees	37	158	27
N species	38	37	41

Cloud forests often display a 'punctuated' distribution, forming 'islands' of vegetation (Howard, 1970). It is probable that the forest in which this study was conducted has been isolated for many decades. As a result, there is a notable presence of unusual flora as well as endemic and threatened species included in the 2010 IUNC Red List of Threatened Species (<http://www.iucnredlist.org/>).

2.2. Data analysis

2.2.1. Stand structure analysis at species level

In each plot, the diameter at breast height (DBH) of all the trees included in the analysis and the number of individuals (N) per diameter class were recorded for each species (Appendix 2). Species were classified into 'life-form' categories, defined as the percentage of individuals of each species in each vertical layer. The four different vertical layers of trees identified in the forest were termed 'emergent', 'canopy', 'mid-story' and 'under-story' trees. Emergent trees were considered to be those species with individuals higher than 100% dominant height (H_0) according to the Hart criteria (the average height of the 100 largest trees). Where more than 80% of the mature trees (DBH > 20 cm) of given species had a height of between 50 and 80% the H_0 , these species were classified as canopy trees. Where more than 80% of the mature trees were between 30 and 50% the H_0 , these species were classified as mid-story trees and where more than the 80% of trees were below 30% the H_0 , the species were classified as under-story trees.

2.2.2. Dispersion, life-form and shade tolerance

Information regarding seed dispersal is scarce for most species in tropical countries since their taxonomy is hardly known. The approach used in this study to determine the dispersal mode was that described by Gentry (1982) and a number of other authors such as Seidler and Potkin (2006), which assigns the most probable main dispersal mode based on the gross fruit morphology. Cumulative field observations of the shape and size of the fruit were used to identify the most probable primary dispersal vector for each species (Appendix 1). Additionally, in the majority of cases the assigned dispersal vector was observed and verified through field observations (species dispersed either by wind or by birds or mammals). The growth-mortality form of each species was characterised using the Weibull distribution function adjusted in accordance with the diameters of each species. The Weibull distribution function, which was first used to quantify diameter distribution by Bailey and Dell (1973), is expressed as: $F = 1 - e^{-((x-a)/b)^c}$ and the density function is $f(y) = (c/b)((x-a)/b)^{c-1} e^{-((x-a)/b)^c}$, where parameters a , b and c are those proposed in Dubey's percentile method (1967). In this study, x = DBH of each tree; $a = d_{\min}$ is the minimum diameter

included in the analysis (in this case 0 because there were no restrictions and all trees were included), $b = \chi_{63} - a \approx \chi_{63}$ is the scale factor, and c is the shape factor $c = \ln(\ln(1 - 0.97)/\ln(1 - 0.17))/\ln((\chi_{97} - a)/(\chi_{17} - a))$ where χ_{17} , χ_{63} , χ_{97} are the percentiles (17, 63 and 97 respectively) of the diametric distribution. This function produces different shapes depending on the value of the c parameter. When $c > 1$ the function produces a hump-shaped pattern, if $c < 1$ the function is J-shaped.

To determine the degree of shade-tolerance of the species, any existing documentation was studied and the information was validated using the field measurements from the present study. The main sources of literature were: Revista Peruana de Biología (<http://sisbib.unmsm.edu.pe/bvrevistas/biologia/biologianew.htm>), Revista del museo de historia natural ARNALDOA, (http://www.scielo.org.pe/scielo.php?script=sci_serial&pid=1815-8242&lng_es/nrm_iso), Revista de biología tropical, (http://www.scielo.sa.cr/scielo.php?pid=0034-7744&script=sci_serial), Ecología en Bolivia (http://www.scielo.org.bo/scielo.php?script=sci_serial&lng=es&pid=1605-2528&nrm=iss).

The information was also contrasted using the following procedure: Where a species displayed a marked cluster pattern, showing a hump-shaped pattern using the Weibull function (Weibull shape parameter $c > 1$), it was inferred to be a gap species. If a species did not show a strong cluster pattern and the resulting Weibull exhibited a J-shape function ($c < 1$), it was classified as a shade-tolerant species. Those species which did not show the above described characteristics across the study plots (or where our results do not coincide with the existing literature) were classified as medium-shade tolerant species.

2.2.3. Spatial pattern analysis of each species

The spatial pattern of all the individuals of each species at different life-stages (fine trees [DBH ≤ 2.5 cm], intermediate (2.5–10) cm and adult trees [DBH > 10 cm]) was analysed. For this purpose, the $L(d)$ function (Besag, in discussion of Ripley, 1977) was calculated for each species in each plot:

$$\hat{L}(d) = \sqrt{\frac{\hat{K}(d)}{\pi}} - d,$$

where d is the distance and $K(d)$ is given by $\lambda \hat{K}(d) = \sum_{i=1}^n \sum_{j=1}^n \delta_{ij}(d)/n$ where n is the number of individuals, λ is the density n/A (A being the area of the plot) and $\delta_{ij}(d)$ (d_{ij} being the distance from tree i to tree j) is given by $\delta_{ij}(d) = \begin{cases} 1 & \text{if } d_{ij} \leq d \\ 0 & \text{if } d_{ij} > d \end{cases}$.

Boundary effect correction was carried out according to Ripley (1977), substituting δ_{ij} for ω_{ij} , which is the inverse of the fraction of a circumference centred on tree i and passing through tree j , contained within the plot.

To assess the conspecific spatial relationship between young and adult individuals of each species belonging to either the canopy or emergent strata in each plot, the bivariate $L_{rs}(d)$ function (Dale, 1999) was used:

$$L_{rs}(d) = \sqrt{\frac{K_{rs}(d)}{\pi}} - d$$

where $K_{rs}(d)$ is given by $(\lambda_r + \lambda_s) \cdot \hat{K}_{rs}(d) = 1/(n_r + n_s) (\sum_{i=1}^{n_r} \sum_{j=1}^{n_s} \omega_{ij}(d)/n_r + \sum_{i=1}^{n_s} \sum_{j=1}^{n_r} \omega_{ji}(d)/n_s)$, n_r and n_s are the number of individuals of class r and class s respectively; λ_r and λ_s are the intensity of points of class r and s respectively.

The maximum distance of analysis was 50 m. Both functions were calculated for the empirical data at distance lags (d) of 0.5 m. Thereafter, an envelopment test was carried out to check for deviations from the null hypothesis, comparing the empirical function with the 95% quantile bounds of the complete spatial

randomness (CSR) null model for the univariate analysis and with the antecedent conditions null model (Wiegand and Moloney, 2004) for the bivariate analysis. The antecedent conditions null model was considered the most appropriate to analyse the relationship between young and adult trees since the latter were obviously present in the stand first and thus condition the pattern of the younger trees. To build the 95% quantile bounds of the null model, a number of simulations, which in turn depend on the significance level and the number of points (Dixon, 2002), are randomly generated. In all our analyses, 99 simulations (K) were used to build the 95% quantile bounds of the null model. $K = 99$ corresponds to a probability error of $\alpha = 0.01$ [$1/(K + 1)$; $K =$ number of simulations], which is an acceptable and recommended value (Illian et al., 2008). The Loosmore and Ford (2006) goodness-of-fit test was then performed to assess significance levels over the distance intervals of interest.

When the empirical $L(d)$ function appears above the upper 95% quantile bounds of the null model, it means that the elements included in the analysis are clustered at these distances. When the empirical $L(d)$ function appears below the 95% quantile bounds, this indicates that the elements are regularly distributed at these distances. When the empirical $L_{rs}(d)$ function appears above the 95% quantile bounds of the null model, it indicates attraction between the two classes of points included in the analysis. When it appears below the 95% quantile bounds, it indicates repulsion between the two classes at these distances.

The patterns identified for each species in the different plots can be considered replicates of the same spatial process in each species. The $L(d)$ calculated for the three plots was standardised into the $L^{st}(d)$ and the $\bar{L}_{rs}^{st}(d)$ by translating the 95% quantile bounds of the CSR null model to $(-1, 1)$ for each distance d (Pardos et al., 2008): $\hat{L}_i^{st}(d) = a(d) + b(d)\hat{L}_i(d)$ where $b(d) = 2/(L_i^{sup} - L_i^{inf})$, $a(d) = 1 - b(d)L_i^{sup}(d)$; L_i^{sup} and L_i^{inf} , being the upper and lower 95% quantile bounds of the CSR null model respectively. For each species, the $L^{st}(d)$ function was calculated as the average of the standardised $L^{st}(d)$ for the three replicates. Analogously, the bivariate $\bar{L}_{rs}^{st}(d)$ was calculated from the $L_{rs}(d)$ functions for the three plots.

The spatial pattern was analysed separately for each species. The relationship between the pattern and the dispersal mode, shade tolerance and life form was examined and the species were grouped according to each factor. All the computations were performed using a software package developed using VisualBasic©Microsoft Corporation (available through the authors).

3. Results

3.1. Analysis of stand structure at species level

The composition from one plot to another was quite similar, the number of individuals only differing substantially in a small number of species. The stand variables for each species can be seen in Appendix 2.

A total of 53 species belonging to 30 families of woody plants were found in the plots (Table 2). The number of individuals varied among species and life-forms. Under-story species were found to be the most abundant, amounting to >65% of the trees in the plots. The most abundant species in the three plots were *Solanum* Ms1 and *Piper elongatum*, both gap species. The bigger trees belonged to the *Meliosma* and *Lauraceae* genera.

The life-form categories of each species are shown in Table 2.

3.2. Dispersion, life-form and shade tolerance

The most probable dispersal method for each species is shown in Table 2. A visual summary of the number of species in the

different categories (dispersal modes, life forms and shade tolerance) can be seen in Fig. 2.

Birds constitute the primary seed dispersal mechanism in the studied cloud forest and most of the species dispersed by small birds belong to the under-story and mid-story groups. The seeds of canopy and emergent tree species tend to be dispersed by larger birds, mammals or gravity (Fig. 2).

Regarding the shape of Weibull's distribution function, a J-shape was obtained for all of the dominant species whereas a hump shaped pattern was obtained for berry-fruit bearing species dispersed by small birds. However, species with a bellflower rather than a berry fruit (also dispersed by small birds) displayed a J-shaped Weibull distribution function (Appendix 2). All of the dominant species were categorised as shade-tolerant, whereas in the mid-story and under-story strata, different degrees of shade tolerance were found (Table 2).

3.3. Spatial pattern of each species

The spatial pattern reflected by the $L(d)$ function was fairly consistent between plots for each species. Differences in the pattern at any scale of observation are correlated with the number of elements included in the analysis. The most commonly identified pattern for each species (when all the trees are included in the analysis) is a cluster pattern at small distances followed by a random pattern and, in some cases, a regular pattern. The distance at which the random pattern occurs differed among species. In the case of individuals with a DBH ≤ 2.5 cm, greater aggregation was found for all species with the exception of eight in the inferior strata and *Persea* Ms and *Drimys* Ms in the emergent strata, although this may be due to the fact that there were fewer individuals of these species with a DBH ≤ 2.5 cm. Trees with a DBH > 10 cm were more randomly distributed than younger individuals in all the analysed species. Interestingly, when the only trees considered in the analysis are those with a DBH ≤ 2.5 cm, the number of species displaying a cluster pattern is greatest at distances of between 5 and 10 m whereas in the case of trees with a DBH > 10 cm, the number of species displaying a cluster pattern at this distance decreases (Fig. 3).

Shade-tolerant species displayed aggregation at the greatest distances; up to 45–50 m in the cases of *Eugenia* Ms and *Parathesis* Ms, the most abundant shade-tolerant species in the under-story. This cluster pattern is especially notable in the case of individuals with a DBH ≤ 2.5 cm. When the trees are not separated into diameter classes and/or where trees with a DBH > 10 cm are considered, the maximum distance at which aggregation occurs is 40 m in the case of *Meliosma* Ms and *Morus insignis*, which are among the most abundant genera in the canopy layer. Gap species presented the shortest distances at which an aggregated distribution pattern occurs; only *Senecio* Ms was clustered at distances of over 40 m whereas clustering was only present at distances under 20 m for many of these species.

Species primarily dispersed by either wind or small birds presented the greatest distances at which clustering occurs when all the individuals are included in the analysis. The seven species which displayed clustering at 50 m (although not necessarily at smaller distances) belonged to one or other of these two classes. Clustering occurs at shorter distances in species whose seeds are primarily dispersed by mammals or large birds. In this group, *Ruagea glabra* presented the maximum distance at which aggregation occurs, which was 40 m. Interestingly, where the trees considered are those with a DBH either ≤ 2.5 cm or > 10 cm, the wind dispersed species presented the shortest distances at which clustering occurs (none of the species displayed an aggregated pattern beyond 30 m in the case of trees with a DBH ≤ 2.5 cm, and only one species showed clustering in trees with a DBH > 10 cm).

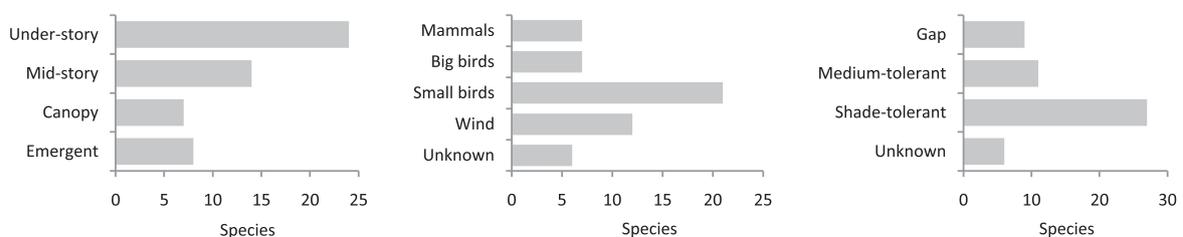
Table 2

Classification of the species found in the plots according to dispersal mode, shade tolerance, and life-form (section 2.2.2).

Family	Specie	Dispersal mode	Shade tolerance	Life-form
Acanthaceae	<i>Aphelandra acanthifolia</i> Hook	Small birds	Medium-tolerant	Mid-story
Actinidiaceae	<i>Saurauia</i> Ms	Mammals:Bats	Gap	Under-story
Araliaceae	<i>Oreopanax raimondii</i> Harms.	Wind	Shade-tolerant	Emergent
Bignoniaceae	<i>Delostoma integrifolium</i> D. Don	Small birds	Shade-tolerant	Canopy
Boraginaceae	<i>Tournefortia</i> Ms2	Wind	Medium-tolerant	Under-story
Compositae	<i>Critoniopsis sevilana</i> (Cuatrec.) H.Rob.	Wind	Shade-tolerant	Canopy
Compositae	<i>Fulcaldea laurifolia</i> (Humboldt and Bonpland) Poirot ex Lessing	Wind	Shade-tolerant?	Mid-story
Compositae	<i>Senecio</i> Ms	Wind	Gap	Mid-story
Elaeocarpaceae	<i>Vallea stipularis</i> Mutis ex L.F.	Small birds	Shade-tolerant	Mid-story
Guttiferae	<i>Cusia flaviflora</i> Engl.	Small mammals	Shade-tolerant	Canopy
Icacinaeae	<i>Cironella incarum</i> (J.F.Macbr.) R.A.Howard	Small birds	Shade-tolerant	Canopy
Icacinaeae	<i>Citronella</i> Ms	Small birds	Shade-tolerant	Under-story
Lauraceae	<i>Nectandra</i> Ms	Big birds + small mammals	Shade-tolerant	Mid-story
Lauraceae	<i>Ocotea</i> Ms1	Big birds + small mammals	Shade-tolerant	Canopy
Lauraceae	<i>Ocotea</i> Ms2	Big birds + small mammals	Shade-tolerant	Mid-story
Lauraceae	<i>Persea</i> Ms	Big birds	Shade-tolerant	Emergent
Melastomataceae	<i>Miconia media</i> (D. Don) Naudin	Small birds	Gap	Under-story
Melastomataceae	<i>Miconia denticulata</i> Naudin	Small birds	Gap	Under-story
Melastomataceae	<i>Miconia firma</i> Macbr.	Small birds	Gap	Under-story
Meliaceae	<i>Guarea</i> Ms	Small mammals + gravity	Shade-tolerant	Canopy
Meliaceae	<i>Ruagea glabra</i> Triana and Planchon	Small mammals + gravity	Shade-tolerant	Canopy-emergent
Monimiaceae	<i>Siparuna muricata</i> (Ruiz and Pavon) A.DC.	Bat?- small birds	Shade-tolerant	Mid-story-canopy
Moraceae	<i>Morus insignis</i> Bureau.	Wind	Shade-tolerant	Canopy
Myrsinaceae	<i>Myrsine latifolia</i> (Ruiz and Pavon) Sprengel	Small birds	Gap to Medium	Mid-story
Myrsinaceae	<i>Parathesis</i> Ms	Small birds	Shade-tolerant	Under-story
Myrtaceae	<i>Eugenia</i> Ms	Small birds	Shade -tolerant	Under-story
Myrtaceae	<i>Myrcianthes fimbriata</i> (Kunth) McVaugh	Small birds	Medium-tolerant	Mid-story
Myrtaceae	<i>Myrcianthes discolor</i> (Kunth) McVaugh	Small birds	Medium-tolerant	Mid-story
Myrtaceae	<i>Myrcianthes</i> Ms	Small birds	Medium-tolerant	Mid-story
Papaveraceae	<i>Bocconia integrifolia</i> Humb. and Bonpl.	Wind	Medium-tolerant	Under-story
Piperaceae	<i>Piper elongatum</i> (Poir. ex Vahl.) C.DC.	Mammals: Bats	Gap	Under-story
Polygalaceae	<i>Monnina pilosa</i> H. B. and K. var. <i>glabrescens</i> Ferreyra	Wind-invertebrates	Gap	Under-story
Polygalaceae	<i>Monnina ligustrifolia</i> Kunth	Wind-invertebrates	Medium-tolerant	Under-story
Ranunculaceae	<i>Clematis</i> Ms	Wind	Medium-tolerant	Under-story
Rubiaceae	<i>Palicourea</i> Ms	Small birds	Shade-tolerant	Mid-story
Rubiaceae	<i>Randia boliviana</i> Rusby	Small mammals+gravity	Shade-tolerant	Under-story
Sabiaceae	<i>Meliosma</i> Ms1	Big birds + small mammals	Shade-tolerant	Emergent
Sabiaceae	<i>Meliosma</i> Ms2	Big birds + small mammals	Shade-tolerant	Emergent
Saxifragaceae	<i>Escallonia</i> Ms	Birds	Shade-tolerant	Emergent
Solanaceae	<i>Cestrum auriculatum</i> L'Hér	Small birds	Shade-tolerant	Mid-story
Solanaceae	<i>Ichroma squamosum</i> S.Leiva and V.Quipuscoa	Small birds	Medium-tolerant	Mid -story
Solanaceae	<i>Lycianthes inaequilatera</i> (Rusby) Bitter	Small birds	Medium-tolerant	Under-story
Solanaceae	<i>Solanum</i> Ms1	Small birds	Gap	Under-story
Solanaceae	<i>Solanum</i> Ms2	Small birds	Medium-tolerant	Mid-story
Solanaceae	<i>Solanum oblongifolium</i> Dunal	Small birds	Shade-tolerant	Under-story
Urticaceae	<i>Boehmeria caudata</i> Sw.	Invertebrates?	Shade-tolerant	Under-story
Winteraceae	<i>Drimys</i> Ms	Wind	Shade-tolerant	Emergent-canopy
–	Morphospecie 1	–	–	Under-story
–	Morphospecie 2	–	–	Under-story
–	Morphospecie 3	Wind	–	Under-story
–	Morphospecie 4	–	–	Under-story
–	Morphospecie 5	–	–	Under-story
–	Morphospecie 6	–	–	Under-story

A cluster pattern was found at short distances for canopy species, except in the cases of *Ruagea glabra* and *Drimys* Ms where the cluster pattern continued up to 40 m. However, all the emergent and canopy species showed an aggregated pattern at certain distances,

with the exception of *Morus insignis*. A number of under-story and mid-story species displayed a cluster pattern at almost all the analysed distances. *Solanum* Ms1, an under-story gap species, was the most abundant species and also presented the highest density

**Fig. 2.** Histograms showing the number of species in each class according to life form, dispersal mode and shade tolerance.

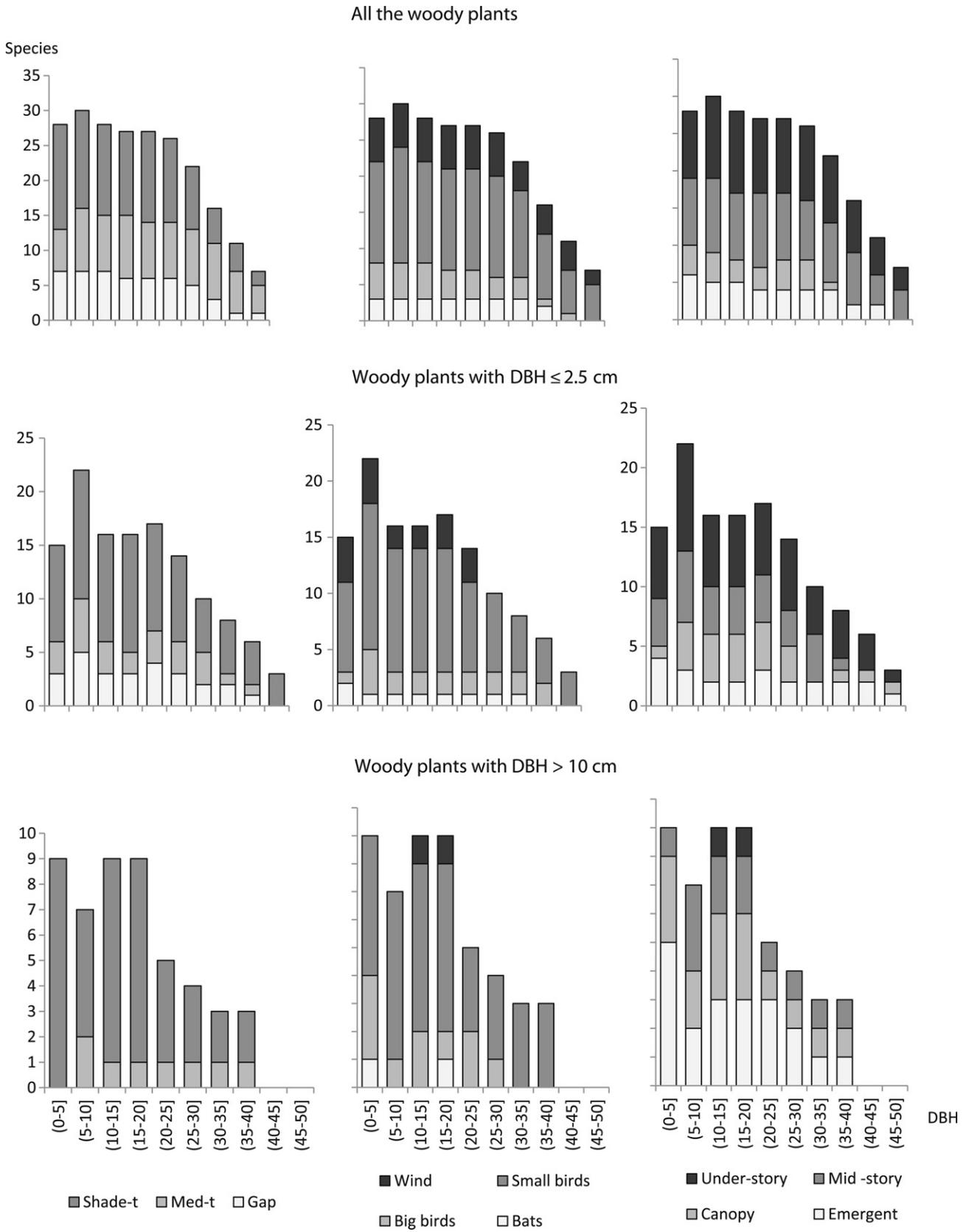


Fig. 3. Histograms showing the number of species which displayed significant ($p < 0.05$) spatial attraction at these distances.

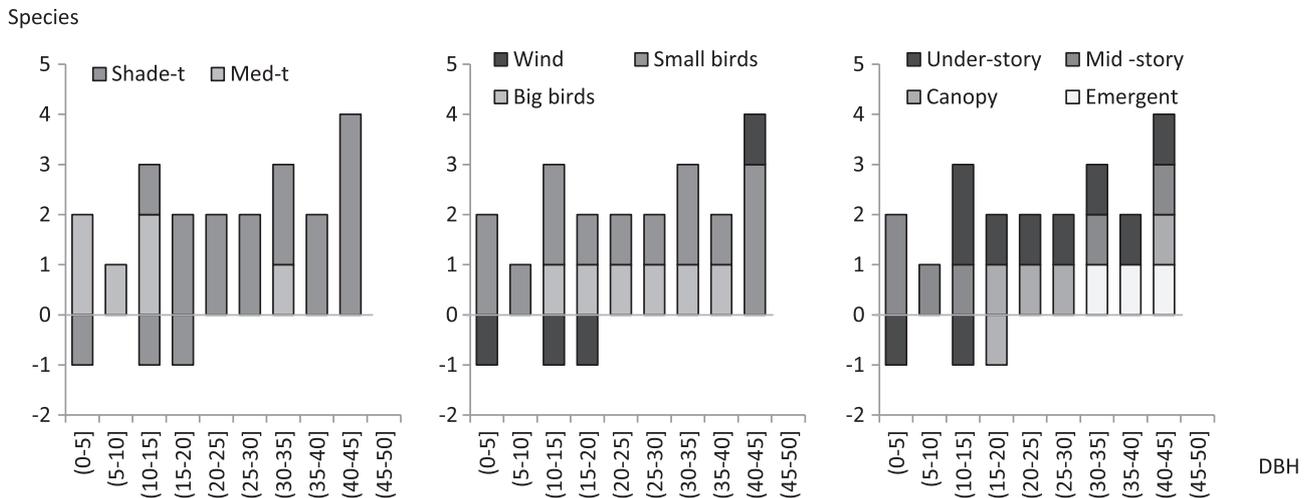


Fig. 4. Histograms showing the number of species which displayed significant ($p < 0.05$) spatial attraction (positive values) or spatial repulsion (negative values) between young and adult trees at these distances.

clusters, as indicated by the much higher $L(d)$ function value in comparison to the other species.

The bivariate analysis illustrated the intraspecific relationships between young and adult trees for the different species. Spatial associations between younger and older individuals were found in all the species analysed, although the distance at which the spatial association appeared differed among species. Almost all the species displayed spatial attraction at shorter distances (up to 10 m), except for *Ruagea glabra* which presented spatial attraction between 5 and 30 m. The only species which showed any repulsion were *Critoniopsis seviliana* (15–20 and 40 m) and *Oreopanax raimondii* (0–5 and 15 m), both shade-tolerant and wind dispersed species (Fig. 4).

Shade-tolerant species showed spatial attraction at medium distances (from 10 m in some species up to 50 m in others) while species of medium shade-tolerance showed attraction at shorter distances, up to 15 m.

The wind dispersed species showed repulsion at short distances (less than 20 m) and attraction at larger distances (beyond 40 m). Only species dispersed by small birds showed spatial attraction at shorter distances, less than 15 m from the parent trees. Furthermore, in the case of species dispersed by small birds, the scale of clustering was greater than for the other groups of species.

The specie with broadest range of spatial attraction between younger and adult trees was *Ichroma squamosum*, which showed attraction at 2 m; 8–16 and 20–30 m.

The spatial association between young and adult trees was similar for all the canopy species. They displayed an aggregated pattern at distances greater than 15–20 m, indicating that young trees belonging to canopy species appear mainly (but not exclusively) at distances beyond 20 m from the adult individuals. The emergent species showed attraction between young and adult individuals at distances beyond 30 m. Only *Meliosma Ms2* (which displayed an aggregated pattern at short distances) and *Oreopanax raimondii* (which showed repulsion at short distances) differed from this pattern (Fig. 4).

4. Discussion

A clumped distribution of tree species has been observed in many studies concerned with tropical forests (Condit et al., 2000; Wiegand et al., 2007; Lawes et al., 2008). In the present study, a cluster pattern was found for most of the species when all individuals were included in the analysis. This cluster pattern is most apparent at short

distances, although some species maintain the cluster pattern beyond 30–40 m (Fig. 3). Furthermore, although the pattern of distribution tends towards regularity as tree size increases, the cluster pattern remains even in the case of the larger trees of most species. The results from a number of recent studies support this finding (Condit et al., 2000; Plotkin et al., 2002; Arévalo and Fernandez-Palacios, 2003; Li et al., 2009) although it appears to contradict the common assumption that larger trees in tropical ecosystems are regularly or randomly distributed (Picard et al., 2009).

The under-story and mid-story species displayed highly clustered patterns at short and medium distances, as reported in other studies undertaken in tropical ecosystems (Arévalo and Fernandez-Palacios, 2003; Hardy and Sonké, 2004). These species constitute more than half of all woody plants (Fig. 2) and occupy all the space under the canopy. The differences in light tolerance (i.e. shade-tolerant vs. gap species) lead to the complete occupation of available space in the ecosystem. In the case of gap species, the different cluster sizes observed in the $L(d)$ analysis may be related to the occupancy of different sized gaps. Thus, the pattern of colonisation by species depends on gap size. This finding provides the first evidence as to the probable existence of high levels of species specialisation.

The distribution of canopy and emergent trees reflects the fact that primary seed dispersal is by large birds, so that the spatial pattern and spatial association between young and adult individuals is similar. The under-canopy species are mainly dispersed by small birds and display an aggregated pattern at larger distances. The results of this study appear to indicate that the primary seed dispersal mode plays a role in the final spatial distribution of the forest, which agrees with the finding of studies undertaken in tropical rain forest (Seidler and Potkin, 2006). However, due to the limitations of the approach used to assign the primary dispersal mode for each species, based on the classification of fruit morphology and size from field observations (Levin et al., 2003; Muller-Landau and Hardesty, 2005), these results must be corroborated by direct assessment of dispersal vectors. Moreover, secondary or tertiary dispersion (by gravity or stream water) may be very important in the analysed forest, affecting the seeds in various different ways. Furthermore, asexual regeneration plays a role in determining the spatial distribution of re-sprouting species such as *Ruagea* or *Meliosma*. This phenomenon is rarely studied in tropical rain forests although Arévalo and Fernandez-Palacios (2003) identified characteristic spatial patterns for a number of re-sprouting species in a cloud forest.

The conspecific spatial relationship between younger and older trees is also an important aspect in the ecology of tropical communities, since the main theories concerning biodiversity, such as the Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971) are based on the spatial allocation of new individuals in relation to their parents. In this study, we found various different conspecific spatial associations between young and adult individuals of woody plant species. In the case of mid-story and shade-tolerant species, attraction tended to occur at 15–20 m whereas this distance was around 20–30 m for most canopy and emergent trees. Nevertheless, some young individuals do appear beyond this distance and there were a number of exceptions to this pattern, such as canopy species dispersed primarily by wind, which display spatial repulsion between younger and older individuals (Fig. 4). It would seem that the spatial relationship between younger and older trees differs from one species to another in the analysed forest, suggesting that different species employ different spatial strategies, not only in terms of the general pattern but also the arrangement of the new individuals in relation to their parents.

Conspecific factors in the establishment process (habitat preference and niche), along with the dispersal mode seem to underlie the spatial arrangement of woody species in the forest. These strategies and responses to external factors differ among species, thus leading to an arrangement which allows different tree species in the forest to coexist. The different degrees of gap occupancy by gap species may be related to micro-habitat requirements. Micro-niche differences among pioneer gap species within the stand were also identified by Clark et al. (1993) and the clustering remnant in canopy trees may be related to habitat associations of mature individuals (Comita et al., 2007) or some kind of facilitation process. Furthermore, spatial patterns of mortality differed among species in the analysed forest. A number of species presented similar patterns in younger and adult trees (such as *Critoniopsis seviliana* or *Delostoma integrifolium*) while other species displayed completely different patterns (for example, the *Miconia* or *Meliosma* species). As regards the most probable causes of mortality; although competition induces spatial 'self-organisation' (Picard et al., 2009) it is not the sole cause of mortality in tropical forests (Batista and Maguire, 1998). Aside from competition, mortality may be related to the absence of micro-environmental conditions necessary for development (Clark et al., 1993) and to disturbances caused by pests or diseases (Janzen, 1970; Connell, 1971). The latter causes tend to affect seeds and seedlings more than medium and large trees. It is also possible that certain allelopathic species affect the survival of trees, as previously reported in cloud forests (Feinsinger et al., 1986).

The results from this study suggest that different species can coexist within a given space, forming a 'puzzle' of species with complex intra- and inter-specific relationships that operate at different scales. The adaptation mechanisms and the different conspecific arrangement strategies of woody species may allow them to optimise their use of available resources, such that each species might occupy its most suitable place. It is probable that this partially contributes to the equilibrium and maintenance of the ecosystem. This specialisation may be necessary to maintain the high level of diversity of the ecosystem. Furthermore, it is likely that species dynamism allows the ecosystem to be sustained.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.actao.2011.09.003.

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