Recruitment patterns and potential mechanisms of community assembly in an Andean cloud forest

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Abstract

Question: What are the conditions necessary for the establishment and development of seedlings and an early stage sapling community in an old-growth cloud forest? Cloud forests are one of the most threatened ecosystems in the world; however, recruitment patterns in these forests remain largely unknown.

Location: Cloud Forest, Northern Peruvian Andes.

Methods: We constructed a sapling community model through the unconstrained technique of non-metric multidimensional scaling. We related the distribution of saplings of each species to the distance from conspecific adult (potential parent) trees through a point pattern analysis. We also used zero-inflated Poisson models to investigate the relationship between sapling distributions and environmental conditions and forest structure.

Results: We found that recruitment in woody plant species tends to be widely spread throughout the forest. The distribution of some sapling species was either positively or negatively related to the position of adult conspecific trees. Several species tended to occur within particular microhabitat conditions, with some differentiation between canopy and understorey species.

Conclusions: Cloud forest species recruitment may require the cover provided by the forest canopy. Under closed canopy conditions, both dispersal assembly and niche assembly mechanisms appear to simultaneously influence sapling distribution. The different strategies of various species may result in a trade-off between the importance of microhabitat conditions and distance mechanisms, with one prevailing over the other, depending on species and forest structure conditions.

Introduction

Tropical montane cloud forests are unusual and fragile ecosystems. They are also one of the most threatened (Brown & Kappelle 2001), since their existence depends on specific environmental conditions (Hamilton 1995; Pounds et al. 1999). Human pressure has played a major role in the disappearance and fragmentation of cloud forests (Hamilton 1995; Bubb et al. 2004; Bruijnzeel et al. 2011), although climate change may also have an impact on these forest systems by changing the pattern and frequency of dry season mist (Pounds et al. 1999; Still

et al. 1999). This in turn affects cloud formation and consequently the micro-environmental characteristics required for forest maintenance and development (Ledo et al. 2009). Cloud forests have been identified as a forest type with high levels of species endemism, displaying one of the highest levels of biodiversity in the world (Gentry 1992; Churchill et al. 1995; Hamilton 1995). The global area occupied by cloud forests is relatively unknown, and estimations by different researchers vary. Bruijnzeel et al. (2011) estimate that 56% of the original forest still remains; however, other researchers are not so optimistic, stating that 90% or more of cloud forest cover has been

lost (Gentry 1992; Hamilton 1995; Bubb et al. 2004). Moreover, it has been reported that the natural recovery of cloud forests is not possible and the loss is irreversible (Hamilton et al. 1995). However, little research has been conducted with regard to recruitment patterns in cloud forests (Williams-Linera 2002), despite the fact that recruitment patterns are undoubtedly a major element in the maintenance of forest diversity. This information would give us an insight into cloud forest conservation.

Recruitment is the cornerstone process of forest maintenance and plays a fundamental role in maintaining forest dynamics. Recruitment includes the processes of pollination, flowering, seed development, seed dispersion and seedling survival and establishment. At any given site, several factors can influence seedling establishment and recruitment success or failure. These processes can be (1) abiotic: a plant can be constrained by the number and quality of sites available for establishment (Nathan & Muller-Landau 2000) or (2) biotic: a plant can be constrained by competition, predation and herbivory (Clark et al. 2007). In addition, pollination, dispersal and seed arrival constitute important stochastic components. Given the complexity of all of these processes, the mechanisms of species reproduction and why a given species establishes in a particular place remain unclear. In tropical forest ecology, these questions have been addressed mainly in the framework of understanding species co-existence and diversity maintenance (Wright 2002). A number of ecological theories attempting to answer these questions have been put forward in recent decades (Chesson 2000). There are three main groups of theories: those based on niche differentiation and strong species specialization (Janzen 1970; Grubb 1977); dispersal assembly theories, based on the distribution of new individuals in relation to the parent trees (Janzen 1970; Connell 1971); and null model theories (Hubbell 2001). In each case, the mechanisms underlying the different theories of species co-existence are based on the spatial distribution of seedlings and early stage saplings (Janzen 1970; Tilman 1982; Chesson 2000; Wright 2002).

Among the abiotic processes that could influence seedling distribution in species-rich forests, dispersal plays a fundamental role in determining potential locations for species recruitment. Specifically, dispersal limitation has been reported to strongly affect recruitment assembly (Wright 2002) because species distribution might be limited by the maximum dispersal distance from mother trees. A second process that also partially explains the spatial pattern of woody species in cloud forests is niche association, or habitat differentiation (Mejía-Domínguez et al. 2012; Ledo et al. 2013). Response to gap openings (Denslow 1987; Denslow & Guzman 2000; Zavala et al. 2007; Zhu et al. 2014) is a part of this process. The spatial result of this process is that a particular species will be abundant or appear exclusively where some particular niche conditions are present, but the species will be scarce or non-existent where conditions are not favourable. As a result of these two abiotic processes (dispersal limitation and niche associations) two competing cluster patterns of seedlings can be expected: dispersal limitation will result in cluster patterns independent of habitat conditions, and niche association will result in species clusters corresponding to niche distributions. The most important biotic process influencing sapling distribution is herbivory, specifically when prey–predator preferences exist (Burkey 1994; Mangan et al. 2010). This process is well documented for most forest types (e.g. tropical forests; Chesson 2000) and it may also be expected in cloud forests, with a potential impact on sapling establishment depending on herbivore preferences (Janzen 1970). This gives rise to the concept of distance dependence. Along with these biotic and abiotic processes, pollination, dispersal and seed arrival are not deterministic but are stochastic in nature. This might imply the existence of unpredictable spatial patterns.

Cloud forests have some unique characteristics that may influence tree species recruitment patterns. Cloud forests have lower light conditions than other forests because of the frequent cloud cover (Bruijnzeel et al. 2011), and light availability may be the main factor affecting cloud forest recruitment (Bader et al. 2007). However, soil nutrients and condition may also be important limiting factors because cloud forest soils have low redox rates, extremely reduced chemical environment (Santiago 2000), toxicity of redox components and low pH (Gambrell & Patrick 1978). Canopy species alter understorey and light conditions (Montgomery 2004; Ledo et al. 2013) and thus may create a variety of niches suitable for recruitment. Gap tree response studies have seldom been conducted in cloud forest although this process may also be important in determining seedling recruitment. Santiago (2000) noted that although most seedlings in cloud forests are shade-tolerant, they do not tolerate shade in later developmental stages and consequently gap opening appears to be a key process in cloud forest regeneration. Carvalho et al. (2000) observed that most canopy species are shade-tolerant during the first developmental stages. This indicates that young individuals of canopy species remain in the understorey until a gap occurs, and then resume growth until they reach the canopy, as long as they survive the disturbance that caused the gap opening. Moreover, Arriaga (2000) found relationships between gap size and species regeneration and showed that smaller gaps had higher diversity than larger ones, which were dominated by pioneer and vine species. Similarly, Carvalho et al. (2000) found that recruitment is 'gap size-specific' for many cloud forest tree species, and Arévalo & Fernandez-Palacios (1998) stated that the occurrence of a gap also explains the

presence of shade-intolerant tree species in the cloud forest canopy. However, neither Carvalho et al. (2000) nor Denslow (1980) found evidence that gaps favour species recruitment of other species in species-rich tropical forests. Hence, the effect of canopy opening on cloud forest recruitment in particular, and tropical forests in general, is still unknown (Hubbell et al. 1999). Gap dynamics may also influence species distributions in cloud forests. Further, montane cloud forests occur mainly at high altitudes (Foster 2001; Ledo 2012) and typically have high UV-A and UV-B radiation levels (Piazena 1996).

The aim of this study was to identify the conditions necessary for establishment and development of the seedling and early-stage sapling community (hereafter saplings) in a montane cloud forest. Our approach was observational. Although linking observed spatial patterns with specific ecological processes poses difficulties (Law et al. 2001; McIntire & Fajardo 2009; Brown et al. 2011), observational studies can be used to help identify the most likely underlying processes, or at least to identify a number of plausible mechanisms from an entire suite of possibilities. Hence, we will attempt to develop a comprehensive framework (McIntire & Fajardo 2009), presenting the current knowledge of cloud forest recruitment mechanisms and proposing hypotheses for the potential underlying mechanisms leading to observed patterns of species distributions. We first obtained a snapshot of the sapling community and analysed the overall composition and assembly of the saplings through univariate and multivariate statistical analyses. Second, we analysed the importance of both density dependence and niche assembly mechanisms for each species. To accomplish this, we studied the distance dependence between saplings and conspecific adult (potential parent) trees of each species through a point pattern analysis. We then used zero-inflated Poisson models to analyse how saplings of each species responded to environmental, topographical and forest structure conditions. We hypothesized that the importance of density dependence and niche association processes on sapling distribution may differ among sapling species. Whereas some species may be more sensitive to distance from parent trees, other species may need particular niche conditions to establish. These preferences may also be related to functional traits, such as shade tolerance. We inferred the existence of these mechanisms from the observed patterns, and therefore, we are uncertain that the underlying mechanisms exist, but hypothesize and submit evidence of the observed spatial patterns. We expect that some observed species distribution patterns will conform to density dependence, and others will exhibit niche association processes. If the resulting species distribution pattern fulfils both conditions, then we assume that both mechanisms act on that species and that we cannot separate them. In addition, we postulate that both dispersal

assembly processes (Janzen 1970; Connell 1971) and niche assembly processes (Grubb 1977; Tilman 1982) are not mutually exclusive in explaining species distribution and can act together, even affecting different species to different extents. We expect that our results will help explain the underlying mechanisms driving recruitment spatial patterns in tropical cloud forests and also the processes maintaining forest diversity. This knowledge is crucial for developing adequate strategies for cloud forest conservation.

Methods

Study site

The study site was a montane cloud forest in northern Peru (UTM 642700–644300W and 9493300–9490499N, 17S Zone, Datum WGS84) in the western Andean cordillera. The site consisted of 171 ha within a total forested area of about 400 ha at an altitude from 2359 to 3012 m a.s.l. It was a remnant patch of the original cloud forest that once occupied the Andean belt. There has been no economic activity or anthropogenic disturbance within the forest; hence, the study site is an uneven-aged, primary forest stand. The forest has a very dense canopy, a high degree of diversity and numerous endemic and threatened species (Ledo et al. 2012a). Environmental and physiographic conditions are fairly homogeneous throughout the forest. It has podzol-like soils, and the mean annual temperature ranges between 10 and 14 °C. There are high levels of precipitation, particularly in the rainy season (Dec–May), although rain can occur at any time of the year. In ENSO (El Niño Southern Oscillation) years, the level of precipitation increases. During the rainy season, the presence of fog is more intense, covering the majority or often the entire forest throughout the day. Fog is also present during the dry season, enveloping the forest for at least half of the day. Because of this persistent fog, relative humidity ranges between 80% and 100% throughout the year.

Inventory

The inventory was performed between March and August 2008. Three 1-ha plots were established in the inner part of the forest, in which all woody plants higher than 1.3 m (regardless of diameter) were mapped; we recorded the diameter and height of each plant, as well as the species name. The three study plots were located in an old-growth forest and each plot had similar species composition, topography and environmental conditions (Table 1, App. S2; Ledo et al. 2013). The plots were located within 1.5 km of each other (Ledo et al. 2012b). To map the location of the trees, sampling points were established within the plot. The UTM coordinates and elevation of the first point was mea-

Table 1. Stand characterization in plots. N, number of trees; N, $d_0 < 5$ cm, number of trees with diameter <5 cm (with percentage over total trees); N, $d_0 \geq 80$ cm, number of trees with diameter ≥80 cm (with percentage over total trees); BA, basal area (m²·ha⁻¹); H_0, Hart's dominant height – average height of the 100 largest trees per ha – (m); N fallen trees, number of dead fallen trees in the plot; N species, number of different woody species (lianas not included) recorded; Simpson, $d_0 \geq 20$ cm is Simpson dominance index (Simpson 1949; modified by Magurran 1988) calculated for mature trees; Elevation: mean elevation (m a.s.l.); Slope: mean slope (degrees); GSF: mean Global Site Factor, including variance in brackets; H_W: mean humidity with respect to control, including variance in brackets; T_W: mean temperature with respect to control, including variance in brackets; and soil is the estimated value of soil surface rockiness (see Methods section), including variance in brackets.

Variable	Plot I	Plot II	Plot III
N	3340	5654	4421
N, $d_0 < 5$ cm	2660 (80%)	4623 (82%)	3718 (84%)
N, $d_0 \geq 80$ cm	13 (0.4%)	19 (0.3%)	43 (1%)
BA (m²·ha⁻¹)	31.03	51.56	77.94
H_0 (m)	15.84	19.68	18.763
N fallen trees	37	158	27
N species	38	37	41
Simpson, $d_0 \geq 20$ cm	0.897	0.922	0.866
Elevation (m a.s.l.)	2530	2675	2563
Slope (degrees)	58.4	43.4	52.9
GSF	0.188 (0.007)	0.122 (0.003)	0.116 (0.002)
H_W	−0.402 (0.816)	1.4107 (0.053)	0.927 (0.010)
T_W	0.836 (6.220)	0.206 (5.653)	0.067 (0.436)
Soil	5.51 (1.04)	5.74 (0.75)	5.83 (0.49)

sured with a GPS. Once all the trees within a radius of ca. 15 m from the first sampling point were mapped, using a vertex hypsometer and a compass, the next sampling point was located. The distance and angle between sampling points were double-checked to ensure accuracy (Ledo 2012; Ledo, 2015). This process was repeated until the entire plot was covered. 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 (Ledo et al. 2012a,b). The help of experts on specific taxa was also enlisted where necessary. 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 to species level. The unidentified species are referred to as 'Morphospecies' (Ms) henceforth. A list of the species recorded in the plots can be found in App. S1. A summary of the stand and forest structure variables in the plots can be found in Table 1. It can be seen that the presence of a higher number of very large trees (DBH > 80 cm) was particularly notable in Plot III, and, as a consequence, this plot presented a larger mean DBH and basal area (G) than Plots I and II. In contrast, Plot II contained a substantially larger number of trees in smaller diameter classes. In Plot I, there was a small gap that was almost completely covered with pioneer herbs, in which

the recruitment of woody plant saplings was non-existent. There were also dissimilarities in the study plots – although not very notable – in terms of the percentage of individuals belonging to different species, which was somewhat higher among pioneer trees (Ledo et al. 2012a,b). These differences in composition may have resulted from historical events and disturbances. For example, varying gap sizes due to tree-fall may lead to the establishment of different pioneer species. More detailed information about the plots has been reported in Ledo et al. (2012b, 2013) and Ledo (2015). All the inventoried data are available by contacting the first author.

To assess recruitment and micro-environmental conditions, 46, 42 and 42 subplots of 4 m² were randomly established within each plot (total, 130 subplots). In these subplots, the species and number of saplings were recorded. We considered as saplings all individuals with height <1.3 m. This definition included both seedling and early stage saplings. As no information about the species exists, we cannot make a clear distinction between them. The recruitment inventory was performed towards the end of the rainy season, when water is uniformly distributed throughout the soil and the environmental conditions are more homogeneous. Six HOBO Pro-v2 HT dataloggers were installed in the centre of the subplots to record relative humidity and absolute temperature. One of the devices was a reference measurement device, which was kept at a fixed point in the forest, while the others were re-located every 2 d at a height of 1.3 m above the forest floor. The humidity and temperature values assigned to each subplot were the result of subtracting the value recorded in the subplot from the reference measurements. This was necessary to ensure comparability of data collected across both the rainy and dry seasons. A Nikon Coolpix 4500 camera with a FC-E8 fish-eye lens (Nikon Corporation, Tokyo, Japan) was used to take hemispherical photographs for assessing the light environment. The camera was positioned 20 cm above the ground in the centre of the subplots. The optical axis of the lens was levelled vertically and oriented towards the north by using a compass with an incorporated bubble level. The camera was placed above ground level because the effects of understorey foliage attenuate light near the forest floor (Montgomery 2004). The photographs were analysed using Hemiview® 2.1 Canopy Analysis Software (Delta-T Devices Ltd., Hitchin, UK) to obtain values for Global Site Factor (GSF). GSF is the total radiation at that point (calculated as the sum of direct and indirect) relative to that in the open. Therefore, lower values of GSF indicate lower light radiation at that point. In order to determine the elevation, slope, curvature and aspect, a 2-m × 2-m pixel digital elevation model was built for each plot using the XYZ location of the trees in ArcMap® v9.2.

The observed soil surface rockiness was also recorded for each subplot; this was defined as a continuous variable ranging from (1) big fixed rocks to (4) clay. Similarly, the observed organic matter cover, which is the percentage of soil covered by organic matter such as leaves, was codified using a continuous variable from (1) parent material to (8) total cover with a substantial layer of organic matter, with the intermediate levels being a gradation from parent material to organic matter on the basis of the ratio between organic matter and stones. The mean values obtained for these variables in the plots are provided in Table 1 and App. S2.

Sapling community in the forest

We studied the spatial correlation of sapling density by fitting the empirical variograms of sapling distribution (Cressie 1993). We performed a geostatistical analysis using the geoR package (Ribeiro & Diggle 2001). Then, we constructed a sapling community model, which included the saplings of different species found, along with the environmental and stand variables measured in the plots. For this purpose, we used the unconstrained technique of non-metric multidimensional scaling (NMDS; Legendre & Legendre 1998) to analyse the overall pattern of dispersion in sapling species composition. We interpreted the ordination with respect to the major explanatory variables by fitting thin plate splines, using general additive models, and interpolating the fitted values on the unconstrained ordination diagram. The variables included in this analysis were: (1) topographical variables: elevation, slope, aspect, curvature of the terrain (curvature), soil composition ($soil_{compos}$) and soil cover ($soil_{cover}$); (2) environmental variables: GSF and mean, maximum and minimum of temperature and humidity of the control-corrected values; and (3) stand structure and composition variables: number of trees (N), average and maximum tree height, basal area (BA) and number of tree species. Forest structure variables were calculated in a 10-m circle centred at the middle of the subplots. We selected this distance because this is the maximum distance to which saplings were significantly and spatially related to mature trees (Fig. 2). Hence, this may be the distance at which the influence of standing trees on sapling distribution is higher. This distance has also been found to be the maximum distance at which neighbourhood effects are noticeable (Canham et al. 2004). Dead standing trees were included in tree density (number of trees, basal area and height) but not tree species richness (number of species). We used the Bray-Curtis distance in calculation of the dissimilarity matrix, because it is one of the most appropriate distance metrics for community ecology data (Legendre & Fortin 1989). We tested the accuracy of the model by calculating the stress, which is a goodness-of-fit statistic that involves the calculation of the squared correlation between fitted values and ordination distances (Borcard et al. 2011). The environmental variables were also fitted onto the first two axes of the NMDS ordination. We calculated the correlation coefficients and P-values of the linear fitting of those variables by running 999 permutations. All analyses were conducted in R (R Foundation for Statistical Computing, Vienna, AT) with the *nmds* and *envfit* functions from the 'vegan' package.

Study of density and distance mechanisms acting on sapling assembly

We studied the spatial (distance) dependence of saplings in relation to the spatial distribution of adult conspecific trees in each plot using the $K_{rx}(d)$ function developed by Montes & Cañellas (2007). This function allowed us to identify positive, negative or independent spatial associations between a point pattern (the standing trees) and a variable measured at sampling points (sapling density) and the scale at which it occurred. To test this, we calculated the empirical $\hat{K}_{rx}(d)$ function compared with the 0.95 quantile bounds built through 999 simulated patterns of the toroidal shift null model (Goreaud & Pélissier 2003), which shifts sapling density points whilst keeping the spatial pattern of the parents unchanged. If positive spatial association between sapling density and parent trees exists, the empirical $\hat{K}_{rx}(d)$ function is above the 0.95 quantile bounds. In contrast, the function will be below the 0.95 quantile bounds if spatial repulsion exists. If both saplings and trees are independently distributed, the empirical function would be within the quantile bounds. The maximum analysis distance was 50 m (half the distance along one side of the plot), and boundary effect correction was carried out according to Ripley (1977), which is calculated as the inverse of the fraction of a circumference centred on point i and passing through point j. The empirical functions were calculated for the data at distance lags (d) of 0.5 m. A significance level of 0.01 was considered for all the analyses. The pseudo P-value was calculated using the Loosmore & Ford (2006) test for spatial analysis.

The spatial relationship between parent and saplings for a given species in the three different plots could be considered as replicas of the same spatial process (Ledo et al. 2012b), so it is possible to detect general patterns (subtracting the effect of local conditions). Hence, the mean $\bar{K}_{rx}(d)$ function was calculated by standardizing $\hat{K}_{rx}(d)$ via translation of the 0.95 quantile bounds of the toroidal shift null model to the interval $(-1, 1)$ for each distance d, and calculating the mean $\bar{K}_{rx}^{st}(d)$ for the three plots according to Pardos et al. (2008). The spatial analyses were performed using software developed by the authors in Microsoft® VisualBasic®, available by contacting the authors.

Relationship between saplings and microhabitat factors

The definition of habitat differs among authors (Morin 2011). In this study, the term microhabitat refers to the environmental conditions (such as humidity and temperature) together with topographical (such as elevation and slope) and forest structure conditions (such as number of trees per ha). See Chase & Leibold (2003) and Ledo et al. (2013) for more details about different habitat/niche definitions. In order to study the effect of microhabitat factors on the number of established recruits, we fitted a regression model for each species. The response in these models was the number of counts per subplot, which we assumed was Poisson-distributed. Since the response exhibited many more zero counts than those expected from the assumed distribution, fitting an ordinary generalized model would have led to a severe bias in the predictions. In order to deal with this distribution, we opted for a zero-inflated Poisson approach (Zuur et al. 2009). Zero-inflated models predict the probability that an event occurs through a binomial process (i.e. sapling occurrence in a subplot) and, conditional to event occurrence, the model predicts the event's abundance through a count process (i.e. Poisson-distributed number of saplings in a subplot, provided that any saplings were present at all). The parameters involved in the binomial and Poisson processes are estimated simultaneously. These parameters are π (probability of having a zero count in a given subplot) and λ (expected number of saplings in a given subplot). Both π and λ can be expanded as a function of covariates, making it possible to infer the effect of microhabitat factors on sapling occurrence and abundance. Topographic, environmental and forest structure variables were sequentially included in both parts of the models. Covariates considered as correlated were alternately tested to prevent collinearity problems. Variable selection was based on the significance of the tested variables and the improvement in terms of the Akaike information criterion (AIC) of each fit. A visual check of the Pearson residuals was carried out in order to detect possible model bias. We used the *glm* and *zeroinfl* functions from the 'stats' and 'pscl' packages, respectively. We checked for correlation among observations at plot and subplot levels by fitting empirical semivariograms for each species (Cressie 1993) and obtained non-correlated structures in every case.

Results

Saplings in the forest

A total of 53 woody species were found in the plots (App. S1), whereas only 26 species were identified as recruits (Table 2). Conclusive identification of saplings at the species level was not feasible in 7% of the cases, although the morphological characteristics observed suggest that most of them belong to the same species. Sapling density was 41 045 saplings·ha^{-1} (variance = 59 745) in the forest, and they tended to be widely spread throughout the forest, sapling density being relatively constant under the forest canopy (App. S2). The offspring of under-canopy species were relatively abundant, while the offspring of canopy species were scarce (Table 2).

The results of the calculated empirical variogram did not reveal spatial correlation among plots (App. S3), indicating that recruitment density correlation is extremely local and occurs at distances of <10 m, which is the minimum distance among subplots. From a statistical perspective, this allowed us to assume that no spatial correlation among subplots existed in the former analysis.

The NMDS ordination separated species into loosely differentiated groups (Fig. 1), with a non-metric fit of $R^2 = 0.96$ and reducing the stress to 0.192. The environmental factors that were significantly correlated when fitted to the two NMDS vectors were GSF (topographical), minimum humidity and maximum temperature (environmental), and number of trees (forest structure). It can be seen in Fig. 1 that the typical species in a mature cloud forest, such as *Meliosma* Ms, *Parathesis* Ms, *Persea* Ms or *Morus insignis*, are indirectly associated with the variable 'number of trees', whereas some pioneer species, such as *Solanum* Ms and *Tournefortia* Ms, are indirectly associated with the GSF. Under-canopy species, such as *Miconia* spp., *Miconia firma* and *Lycianthes inequilatera*, were indirectly related to 'minimum humidity'.

Density and distance mechanisms acting on saplings

The analysis produced uniform results among plots for each species, which agrees with our hypothesis of the same mechanism acting on saplings and confirms that it is correct to consider plots as replicates. Most species showed negative spatial association between saplings and conspecific adult trees at distances up to 10 m, supporting the Janzen-Connell hypothesis; however, *Critoniopsis sevillana*, *Myrcianthes* Ms, *Ocotea* Ms, *Ruagea glabra* and *Senecio* Ms did show positive association with the parent trees at short distances (Fig. 2). *Ruagea glabra* is known to be a resprouting species, so the observed pattern may be due to new clonal stems.

Sapling microhabitat association

The abundance of saplings of different species was explained by different environmental or forest structure factors (λ parameter in Table 3). The density of ten out of the 13 most abundant species, and 11 out of the 20 analysed, was related to some explanatory variable. A wide

Table 2. List of the sapling species found in the plots, indicating number of saplings (*N*), and percentage (%) of each species for the results from all three plots. Number of standing trees of each species found in the plots (M). Growth form and shade tolerance of the found species from Ledo et al. (2012b).

Species	*N*	%	M	Growth Form	Shade Tolerance
Aphelandra acanthifolia	10	0.56	55	Mid-storey	Medium-tolerant
Cestrum auriculatum	18	1.00	200	Mid-storey	Shade-tolerant
Cironella incarum	3	0.17	67	Canopy	Shade-tolerant
Critoniopsis sevillana	27	1.50	282	Canopy	Shade-tolerant
Delostoma integrifolium	14	0.78	213	Canopy	Shade-tolerant
Drymis Ms	27	1.50	210	Emergent	Shade-tolerant
Eugenia Ms	61	3.39	973	Understorey	Shade-tolerant
Iochroma squamosum	54	3.00	188	Mid-storey	Medium-tolerant
Lycianthes inaequilatera	250	13.88	431	Understorey	Medium-tolerant
Meliosma spp.	19	1.05	335	Emergent	Shade-tolerant
Miconia spp.	46	2.55	457	Understorey	Gap
Miconia firma	108	6.00	658	Understorey	Gap
Morus insignis	10	0.56	187	Canopy	Shade-tolerant
Myrcianthes	50	2.78	169	Mid-storey	Medium-tolerant
Myrsine latifolia	2	0.11	45	Mid-storey	Gap to medium
Ocotea Ms	31	1.72	59	Emergent	Shade-tolerant
Oreopanax raimondii	1	0.06	150	Emergent	Shade-tolerant
Parathesis Ms	365	20.27	1022	Understorey	Shade-tolerant
Persea Ms	7	0.39	251	Emergent	Shade-tolerant
Piper elongatum	52	2.89	2216	Understorey	Gap
Ruagea glabra	9	0.50	430	Emergent	Shade-tolerant
Senecio Ms	16	0.89	48	Mid-storey	Gap
Siparuna muricata	15	0.83	110	Mid-storey	Shade-tolerant
Solanum Ms1	348	19.32	3920	Understorey	Gap
Solanum Ms2	5	0.28	326	Understorey	Medium-tolerant
Tournefortia Ms	129	7.16	115	Understorey	Medium-tolerant
Unknown	124	6.89	–	–	–

range of different explanatory covariates appeared as important for the different sapling species (Table 3). In some cases, a linear relationship was found, indicating a direct response of sapling density to factors. For example, the density of *Parathesis* Ms saplings increased with an increase in the number of trees. In other cases, the response of density to a particular explanatory variable was non-linear, indicating the existence of an optimal value of that variable which maximized the response. This was the case for *Ocotea* Ms and a number of other tree species (Table 3). *Ocotea* Ms and *Parathesis* Ms saplings, both of which are shade-tolerant and typical cloud forest species, were more abundant in areas with a large number of trees than in areas with fewer trees (Tables 2 and 3). In addition, *Eugenia* Ms, an abundant under-canopy shade-tolerant species showed a preference for specific soil conditions. However, the density of *Miconia firma*, *Tourfertia* Ms and *Solanum* Ms2 (all pioneer species) responded to humidity and temperature rather than to forest structure conditions.

The probability of a species being absent (π parameter in Table 3) was not explained by any factor for approximately half of the species when considering only the most abundant, and also all the analysed species (seven out of 13 and 12 out of 20, respectively). This fact indicates that

the probability of occurrence of these species is constant throughout the plots. Nevertheless, higher GSF values were the main factors explaining the absence of some species. The most common and abundant under-canopy species, *Eugenia* Ms and *Parathesis* Ms, occurred mainly in areas with lower GSF (Tables 2 and 3). Surprisingly, the absence of *Piper elongatum*, a gap species, was also related to high GSF values.

Discussion

The regeneration process is crucial for maintaining complex tropical ecosystems, although the processes involved in determining the spatial presence of saplings in tropical forests are still relatively unknown. This is particularly true in the case of the cloud forest ecosystem, which has received little attention in comparison to other types of tropical forest. In this study of an Andean old-growth forest, we found that recruitment in woody plant species tends to be widely spread throughout the forest and that sapling density is relatively constant under the forest canopy (App. S2). However, some groups of species can be discerned. The results from the NMDS suggest recruitment habitat specialization in the species (Fig. 1), because
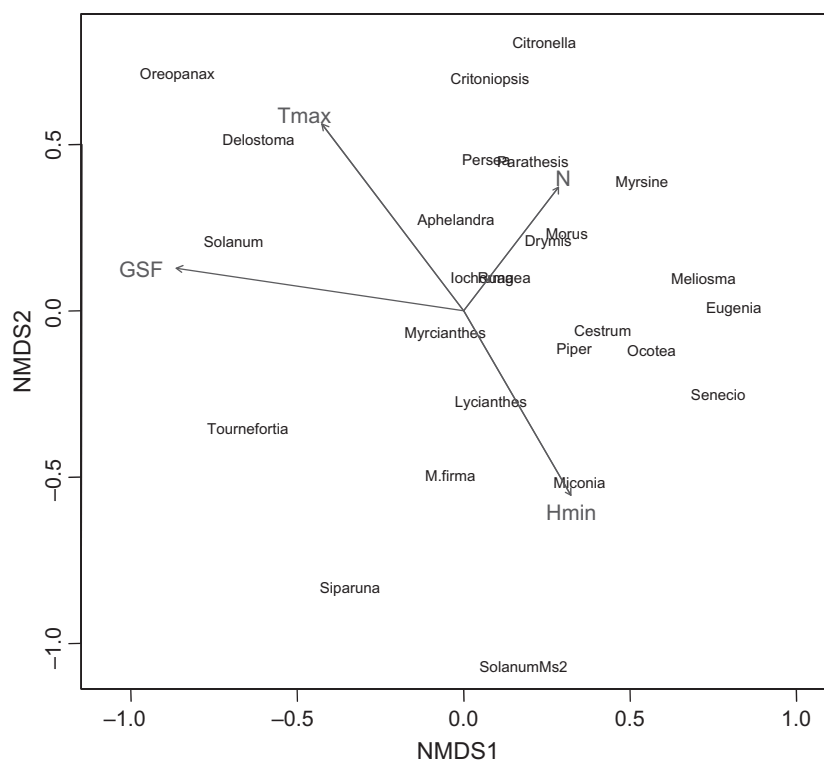
Fig. 1. Results from the NMDS analysis ordination of saplings found in the 130 subplots measured in the cloud forest, including the ordination axes of variables with a significant correlation coefficient ($P < 0.1$): Maximum temperature (T_{max}), Global Site Factor (GSF), minimum humidity of control-corrected values (H_{min}) and number of standing trees (N).

different species showed different niche preferences (Table 3). The regeneration niche may be somewhat different for canopy and understorey species (Fig. 1, Tables 2 and 3) and related to species functional traits, as shown in other studies (Comita et al. 2010; Kobe & Vriesendorp 2011). The distribution of many species was negatively related to the position of adult conspecific trees, in accordance with the Janzen-Connell hypothesis (Fig. 2). However, some species showed positive density dependence, reflecting different recruitment strategies among species (Fig. 2). These findings show that the processes governing spatial patterns of recruitment in cloud forests, both density dependence and niche specialization, may be acting together.

Distance-dependent spatial mechanisms acting on sapling distribution

In many of the analysed species, sapling distribution depended on the spatial distribution of conspecific adult trees, although the scale and sign (i.e. positive or negative) of this distance interaction varied among species (Fig. 2). Successful sapling establishment of some species was found to be limited to close proximity (0–5 m) to

conspecific adult trees (Fig. 2), which may reflect negative distance dependence mechanisms. However, few species exhibited the opposite pattern – a positive association between saplings and conspecific adult trees at short distances (Fig. 2). We should be cautious about these results because for some of the analysed species, <30 individuals were found, and therefore, the possibility of obtaining type II statistical errors increases. Regardless, we found the Janzen-Connell effect at shorter distances in this cloud forest, as has been found in other tropical studies (Clark & Clark 1984; Peters 2003). Trees in the studied forest are notably shorter than trees in wet tropical forests, and canopy width size is notably smaller, which might ultimately reduce their effects on recruitment distance. In addition, most of the analysed species were understorey species (Table 2), with smaller canopies than the emergent trees. If it is assumed that the agents of these distance-dependent mechanisms are herbivores or pathogens, our findings would support the notion that species-specific herbivores or pathogens reduce the density of conspecific saplings [as originally reported by Janzen (1970) and Connell (1971)], acting only on some groups of species. However, if the herbivores or pathogens are not species-specific, our results may alternatively

Table 3. Results of the zero-inflated Poisson models (ZIPs) calculated for each species. Positive values in λ (explaining density) indicate positive relationships with those variables. π is the probability of not observing any seedlings in the plot, with higher values of π indicating a higher probability of seedling absence. Results in bold grey in λ and π correspond to species with a limited number of individuals (<20); hence, the results of the models may be spurious. Species with less than ten individuals were not considered in the analysis (Table 2). No significant variables is indicated by "–".

	λ	π
Aphelandra acanthifolia	–	–
Cestrum auriculatum	–	–
Critoniopsis sevillana	$-H_{min} - H_{min}^2$	–
Delostoma integrifolium	–	–
Drymis Ms	–	–
Eugenia Ms	$soil_{cober} - soil_{cober}^2 + H_{min}$	GSF
Iochroma squamosum	$-GSF$	$-Elevation$
Lycianthes inaequilatera	$H_{min} + N_{adult} - N_{adult}^2$	GSF
***Meliosma* spp.**	–	$\mathbf{N_{tree} - N_{tree}^2 + T_{min}}$
Miconia spp.	–	–
Miconia firma	$H_{min} - H_{min}^2 + G_{tot}$	–
Morus insignis	–	–
Myrcianthes	–	GSF
Ocotea Ms	$N_{tree} + N_{tree}^2 + T_{min}$	–
Parathesis Ms	$N_{tree} + G_{tot} - G_{tot}^2$	GSF
Piper elongatum	G_{tot}	GSF
***Senecio* Ms**	–	–
Siparuna muricata	$\mathbf{N_{tree}}$	$\mathbf{N_{tree} + N_{tree}^2}$
Solanum Ms1	$-T_{min} + slope + soil_{cober} - soil_{cober}^2 - G_{tot}$	–
Tournefortia Ms	$T_{min} - T_{min}^2 + N_{saplings} - N_{saplings}^2$	–

suggest the existence of defence mechanisms in those plants that exhibited spatial attraction between saplings and adult trees. It should be pointed out that we could only hypothesize on the nature of the distance-dependent mechanisms underlying the observed patterns, as we did not carry out any experimental manipulations or additional field measurements to confirm the hypotheses.

Environmental and forest structure factors that affect sapling distribution

Environmental and/or forest structure-related explanatory variables explained sapling occurrence and abundance patterns for six and ten (respectively) out of the 13 most common species. However, there was a divergence in the main explanatory variables affecting sapling density and occurrence of the different species (Table 3). In some cases the species did not respond linearly to a variable, but had an optimal value at which the species occurred (Table 3). In addition to this, in the NMDS, some species groupings were related to environmental variables of temperature, humidity, GSF and number of trees (Fig. 1). These findings suggest different microhabitat preferences among species in the studied cloud forest.

Sapling density was related to different variables for different species. For the abundant under-canopy species *Parathesis* Ms, the main factors explaining sapling density were the number of trees and basal area. Specifically, *Parathesis* had an optimal stand basal area at higher

densities. This is quite reasonable because this species is typically found under the closed canopy of the mature forest. Another abundant under-canopy species was *Solanum* Ms1, a pioneer species. This species avoided areas in which the minimum temperature was lower, and the density of this species appeared to be related to soil cover (indicating an optimal soil organic matter cover) and areas with lower BA (more likely to be micro-gaps, in accordance with its pioneer character). Other species from the under-canopy layer appeared related to different factors, both climatic and forest structure factors. For example *Criptoniopsis sevillana* density was related to humidity conditions, and *Tournefortia* Ms to temperature conditions. In our study, the sapling density of the understorey species was more related to a particular condition rather than the canopy species, which appear more widespread in the forest (Table 3). In summary, our results indicated that the variables accounting for sapling density differed among species and that species-specific functional traits possibly determine these differences.

The main variable affecting sapling occurrence was the amount of light, measured through GSF. The GSF appeared as an important factor for both under-canopy species typical within the mature forest, such as *Eugenia* Ms, and more pioneer species, such as *Myrcianthes* spp. (Table 3). As can be seen in Fig. 1 and Table 1, the canopy openness in the forest was low, with average values of ca. 15%. Recruitment was not observed in the sapling plots situated in the gap present in Plot I. This indicates that the
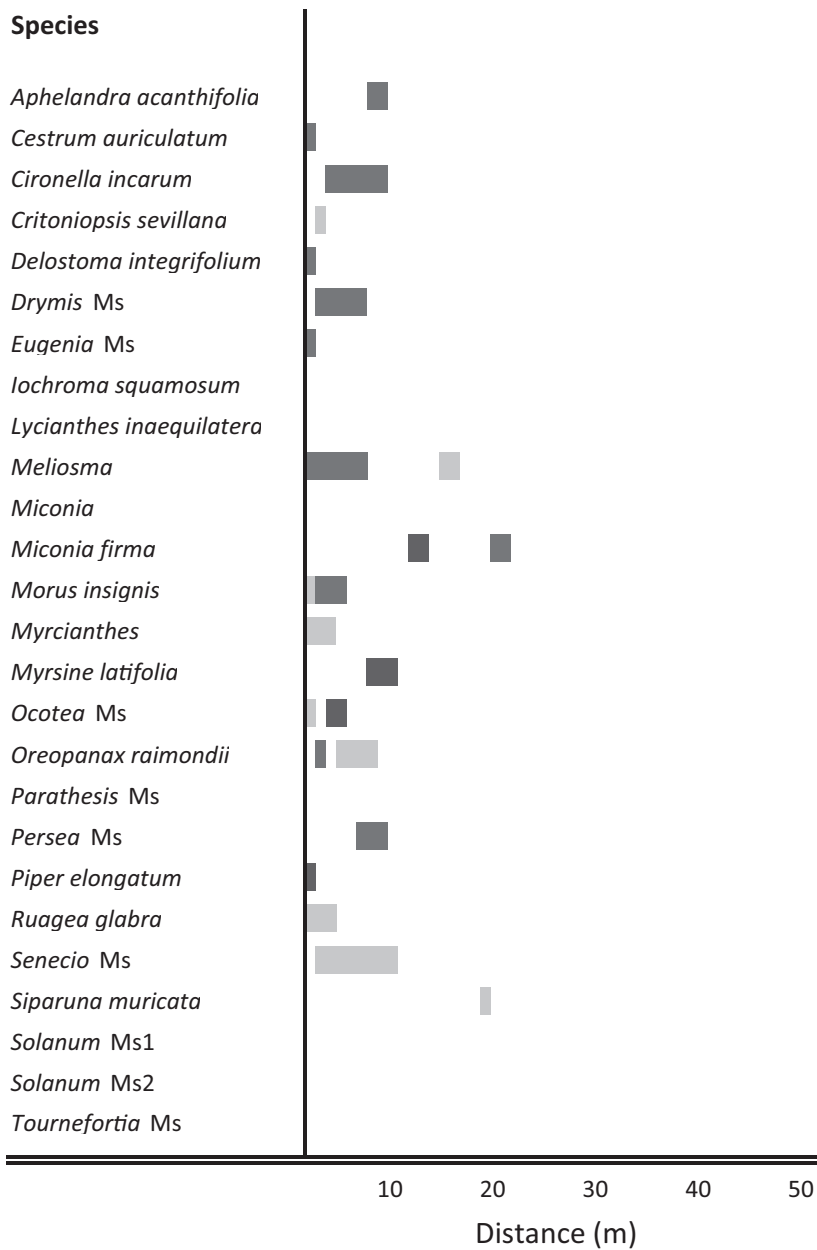
Fig. 2. Distance at which species present positive spatial association (light grey line) and negative spatial association (dark grey line) between seedlings and standing trees and between seedlings and mature trees for current stand and conspecific trees. It should be noted that some of the species had a limited number of saplings (Table 1).

cloud forest species recruit under low light conditions, and possibly have evolved to do so. It is well known that light is a crucial factor in sapling establishment, and its importance has been observed in previous studies conducted in tropical wet forests (Montgomery & Chazdon 2001), as well as in cloud forests (Mejía-Domínguez et al. 2012). However, our results revealed that the level of light required for sapling establishment in the studied cloud forest differs from those reported for tropical rain forests, as also dis-

tances of density dependence differed. While in the latter, the regeneration of different woody species occurred under conditions of 1–30% canopy openness and even up to 50% in gap areas (Chazdon 1988), the most suitable levels of canopy openness in the studied cloud forest were found to be <20% (App. S1). Cloud forest ecosystems are characterized by the presence of clouds and therefore receive less sunlight and have lower evapotranspiration rates than in tropical rain forest. Consequently, woody plant species

typically found in cloud forests are more likely to have developed morphological and physiological adaptations for successful recruitment that enable them to live under low light conditions.

Bader et al. (2007) observed that recruitment decreases towards the forest periphery in an equatorial cloud forest. This agrees with our hypothesis that cloud forest species may have evolved to recruit under closed canopy conditions. Similarly, Williams-Linera (1990) and Ledo et al. (2009) found that vegetation and micro-climatological conditions change at a forest boundary. According to those previous studies and our findings, this decrease in recruitment at the forest margins may be due to changes in the micro-environmental conditions necessary for cloud forest development in conjunction with the existence of dispersal limitations and excessive amount of light. It is therefore clear that the persistence of cloud forests depends on the presence of certain environmental conditions and forest structure characteristics that favour sapling emergence. The absence of these conditions in areas where the forest has retreated may partly explain the apparent irreversibility of cloud forest loss (Hamilton 1995).

Spatial strategies of regeneration in the studied cloud forest

Our results indicate that both habitat preferences and distance-dependent mechanisms may be involved and act together in sapling establishment (Fig. 1, Tables 2 and 3). It follows that both micro-scale biotic and abiotic conditions are important to sapling survival and development. Adult trees are also partly responsible for creating particular microhabitat conditions, for example by changing light values in the understorey (Acevedo & Ataroff 2012). The spatial distribution of adult trees partially depends on the habitat conditions in this cloud forest (Ledo et al. 2013), as in other tropical forests (Harms et al. 2001; Comita et al. 2007). The dependence of saplings on both parent tree spatial patterns and environmental conditions is therefore intertwined. Consequently, the spatial distribution of adult trees influences the spatial distribution of saplings in cloud forests, as elsewhere (Mejía-Domínguez et al. 2012).

The different strategies of the various species, along with the differences in general behaviour according to the forest structure conditions, may result in a trade-off between the importance of habitat and distance mechanisms, with one prevailing over the other, depending on species and forest structure conditions. Moreover, it might be argued that this 'combined' mechanism contributes to maintaining the high level of biodiversity observed in a cloud forest. Since conditions vary throughout the development of the stand, suitable places for recruitment within a given stand will vary, as will the importance of distance mechanisms vs habitat associations. In addition, the species that co-exist in the studied cloud forest have different recruitment strategies. This may lead to greater 'most suitable place' recruitment opportunities, since these 'suitable places' are not fixed but are constantly changing.

References

Acevedo, M.F. & Ataroff, M. 2012. Leaf spectra and weight of species in canopy, subcanopy, and understory layers in a venezuelan andean cloud forest. *Scientifica* 2012: article id 839584.

Arévalo, J.R. & Fernandez-Palacios, J.M. 1998. Treefall gap characteristics and regeneration in the laurel forest of Tenerife. *Journal of Vegetation Science* 9: 297–306.

Arriaga, L. 2000. Gap-building-phase regeneration in a tropical montane cloud forest of north-eastern Mexico. *Journal of Tropical Ecology* 16: 535–562.

Bader, M.Y., Geloof, I.V. & Rietkerk, M. 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecology* 191: 33–45.

Borcard, D., Gillet, F. & Legendre, P. 2011. *Numerical ecology with R.* Springer, Berlin, DE.

Brown, A.D. & Kappelle, M. 2001. Introducción a los bosques nublados del geotrópico: Una síntesis regional. In: Kappele, M. & Brown, A.D. (eds.) *Bosques Nublados del Neotrópico.* pp. 27–40. INBio, Heredia, CR.

Brown, C., Law, R., Illian, J.B. & Burslem, D.F. 2011. Linking ecological processes with spatial and non-spatial patterns in plant communities. *Journal of Ecology* 99: 1402–1414.

Bruijnzeel, L.A., Scatena, F.N. & Hamilton, L.S. 2011. *Tropical montane cloud forest. Science for conservation and management.* Cambridge University Press, Cambridge, UK.

Bubb, P., May, I., Miles, L. & Sayer, J. 2004. *Cloud forest agenda.* UNEP World Conservation Monitoring Centre, Cambridge, UK.

Burkey, T.V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* 97: 533–540.

Canham, C.D., LePage, P.T. & Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Canadian Journal of Forest Research* 34: 778–787.

Carvalho, L.M.T.D., Fontes, M.A.L. & Oliveira-Filho, A.T.D. 2000. Tree species distribution in canopy gaps and mature forest in an area of cloud forest of the Ibitipoca Range, southeastern Brazil. *Plant Ecology* 149: 9–22.

Chase, J.M. & Leibold, M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, IL, US.

Chazdon, R.L. 1988. Sunflecks and their importance to forest understory plants. *Advances in Ecological Research* 18: 1–63.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.

Churchill, S.P., Balslev, H., Forero, F. & Luteyn, J.L. 1995. Biodiversity and conservation of Neotropical montane forest. *Proceedings of the neotropical montane forest biodiversity and conservation symposium*. The New Botanical Garden, Bronx, NY, US.

Clark, D.A. & Clark, D.B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *The American Naturalist* 1948: 769–788.

Clark, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist* 170: 128–142.

Comita, L.S., Condit, R. & Hubbell, S.P. 2007. Developmental changes in habitat associations of tropical trees. *Journal of Ecology* 95: 482–492.

Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329: 330–332.

Connell, J.H. 1971. On the role of the natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J. & Gradwell, G. (eds.) *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, NL.

Cressie, N.A.C. 1993. *Statistics for spatial data*. Wiley, New York, NY, US.

Denslow, J.S. 1980. Notes on the seedling ecology of a large-seeded species of Bombacaceae. *Biotropica* 12: 220–222.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431–451.

Denslow, J.S. & Guzman, G. 2000. Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science* 11: 201–212.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55: 73–106.

Gambrell, R.P. & Patrick, W.H. 1978. Chemical and microbiological properties of anaerobic soils and sediments. In: Hook, D.D. & Crawford, R.M.M. (eds.) *Plant life in anaerobic environments*. pp. 375–423. Ann Arbor Science, MI, US.

Gentry, A.H. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* 63: 19–28.

Goreaud, F. & Pélissier, R. 2003. Avoiding misinterpretation of biotic interactions with the intertype K12-function: population independence vs. random labelling hypotheses. *Journal of Vegetation Science* 14: 681–692.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52: 107–145.

Hamilton, L.S. 1995. Mountain cloud forest conservation and research: a synopsis. *Mountain Research and Development* 15: 259–266.

Hamilton, L.S., Juvik, J.O. & Scatena, F.N. 1995. The Puerto Rico tropical cloud forest symposium: introduction and workshop synthesis. In: *Tropical montane cloud forests*, pp. 1–18. Springer-Verlag, New York, NY, US.

Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.

Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & De Lao, S.L. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283: 554–557.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–529.

Kobe, R.K. & Vriesendorp, C.F. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters* 14: 503–510.

Law, R., Purves, D.W., Murrell, D.J. & Dieckmann, U. 2001. Causes and effects of small-scale spatial structure in plant populations. *Special Publication – British Ecological Society* 14: 21–44.

Ledo, A., 2012. *On the spatial distribution of woody plant species in a tropical montane cloud forest*. Ph.D. thesis, Universidad Politecnica de Madrid, ES.

Ledo, A. 2015. Protocol for inventory of mapped plots in tropical forest. *Journal of Tropical Forest Science* 27: 240–247.

Ledo, A., Montes, F. & Condés, S. 2009. Species dynamics in a Montane Cloud Forest: identifying factors involved in changes in tree diversity and functional characteristics. *Forest Ecology and Management* 258: 75–84.

Ledo, A., Condés, S. & Alberdi, I. 2012a. Forest biodiversity assessment in Peruvian Andean Montane cloud forest. *Journal of Mountain Science* 9: 372–384.

Ledo, A., Condés, S. & Montes, F. 2012b. Different spatial organization strategies of woody plant species in a montane cloud forest. *Acta Oecologica* 38: 49–57.

Ledo, A., Burslem, D.F.R.P., Condés, S. & Montes, F. 2013. Micro-scale habitat associations of woody plants in a neotropical cloud forest. *Journal of Vegetation Science* 24: 1086–1097.

Legendre, P. & Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107–138.

Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier, Amsterdam, NL.

Loosmore, N.B. & Ford, E.D. 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87: 1925–1931.

Magurran, A.E. 1988. *Ecological diversity and its measurement*, Vol 168. Princeton University Press, Princeton, NJ, US.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M., Valencia, M.C., Sanchez, E.I. & Bever, J.D. 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466: 752–755.

McIntire, E.J. & Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90: 46–56.

Mejía-Domínguez, N.R., Meave, J.A. & Díaz-Ávalos, C. 2012. Spatial structure of the abiotic environment and its association with sapling community structure and dynamics in a cloud forest. *International Journal of Biometeorology* 56: 305–318.

Montes, F. & Cañellas, I. 2007. The spatial relationship between post-crop remaining trees and the establishment of saplings in *Pinus sylvestris* stands in Spain. *Applied Vegetation Science* 10: 151–160.

Montgomery, R.A. 2004. Effects of understory foliage on patterns of light attenuation near the forest floor. *Biotropica* 36: 33–39.

Montgomery, R.A. & Chazdon, R.L. 2001. Forest structure, canopy architecture and light transmittance in old-growth and second-growth stands of lowland rainforest in NE Costa Rica. *Ecology* 82: 2707–2718.

Morin, P.J. 2011. *Community ecology*. John Wiley and Sons, Chichester, UK.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278–285.

Pardos, M., Montes, F. & Cañellas, I. 2008. Spatial dynamics of natural regeneration in two differently managed *Pinus sylvestris* stands before and after silvicultural intervention using replicated spatial point patterns. *Forest Science* 54: 260–272.

Peters, H.A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6: 757–765.

Piazena, H. 1996. The effect of altitude upon the solar UV-B and UV-A irradiance in the tropical Chilean Andes. *Solar Energy* 57: 133–140.

Pounds, A., Fogden, M.P.L. & Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611–615.

Ribeiro, P.J. Jr & Diggle, P.J. 2001. geoR: a package for geostatistical analysis. *R News* 1: 14–18.

Ripley, B.D. 1977. Modelling spatial patterns (with discussion). *Journal of Royal Statistical Society B* 39: 172–212.

Santiago, L. 2000. Use of coarse wood debris by the plant community of a Hawaiian Montane Cloud Forest. *Biotropica* 32: 633–641.

Simpson, E.H. 1949. Measurement of diversity. *Nature* 163: 688.

Still, C.J., Foster, P.N. & Schneider, S.H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608–610.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ, US.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* 78: 356–373.

Williams-Linera, G. 2002. Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11: 1825–1843.

Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

Zavala, M.A., Angulo, O., Bravo, R. & López-Marcos, J.C. 2007. An analytical model of stand dynamics as a function of tree growth, mortality and recruitment: the shade tolerance–stand structure hypothesis revisited. *Journal of Theoretical Biology* 244: 440–450.

Zhu, J., Lu, D. & Zhang, W. 2014. Effects of gaps on regeneration of woody plants: a meta-analysis. *Journal of Forestry Research* 25: 501–510.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer, Berlin, DE.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dispersal mode, shade tolerance, and life form for woody plant species (lianas not included) found in the plots.

Appendix S2. Mean values of the environmental and stand variables measured in the plots. Distributional maps of: elevation, Global Site Factor, which is the total radiation at that point (calculated as the sum of direct and indirect) relative to that in the open, tree density, number of species density and seedling density in Plots 1, 2 and 3.

Appendix S3. Empirical and fitted semivariogram of number of seedlings in the plots.