



Micro-scale habitat associations of woody plants in a neotropical cloud forest

Alicia Ledo, David F.R.P. Burslem, Sonia Condés & Fernando Montes

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Nomenclature

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Ledo, A. (corresponding author, alicialedo@gmail.com) & **Condés, S.** (sonia.condes@upm.es): Universidad Politécnica de Madrid, Escuela Técnica Superior de Ingenieros de Montes, Ciudad Universitaria, s/n. 28040, Madrid, Spain

Burslem, D.F.R.P. (d.burslem@abdn.ac.uk): School of Biological Sciences, University of Aberdeen, Cruickshank Building, St Machar Drive, Aberdeen AB24 3UU, UK

Montes, F. (fmontes@inia.es): CIFOR-INIA, Carretera de La Coruña Km 7.5, 28040, Madrid, Spain

Introduction

The spatial structure of plant populations conveys important information that may help to understand the maintenance of the high diversity of species-rich plant communities (Law et al. 2001). Numerous studies have observed that tropical tree species have clumped distributions (Condit et al. 2000; Plotkin et al. 2002; Wiegand et al. 2007). The main causes of aggregation are dispersal limitation (Hubbell et al. 1999) and associations with heterogeneous environmental conditions (Clark et al. 1993; Harms et al. 2001). It is now widely accepted that both factors play an important role in species distribution, although the relative importance of each factor may differ among study systems. For example, in a lowland forest in Peru measured environmental variables explained 40% of variation in species distribution (Phillips et al. 2003), while environmental variables alone explained only 10–12% of variation in tree distribution for lowland forests in Panama

(Chust et al. 2006). Spatial variation that remains unexplained in these studies may arise because of unmeasured environmental correlates, and autocorrelation due to dispersal limitation (Pacala & Tilman 1994; Hubbell et al. 1999). Consequently, future mechanistic theories and models must take into account not only habitat partitioning but also dispersal limitation (Chave 2004). Other mechanisms, such as gap recruitment, may also play a role in species clustering (Hubbell et al. 1999; Plotkin et al. 2000). However, the role of stand structure and light availability are not often included in analyses of habitat associations, although a number of studies have determined that elevation, slope (Harms et al. 2001; Comita et al. 2007; Suzuki et al. 2009) and soil nutrients (John et al. 2007; Bohlman et al. 2008) define habitats for tropical forest trees.

Analysis of niche partitioning presents an additional difficulty because the niche concept differs among authors (Morin 2011). Some authors include only physical

Abstract

Questions: Species–habitat associations may contribute to the maintenance of species richness in tropical forests, but previous research has been conducted almost exclusively in lowland forests and has emphasized the importance of topography and edaphic conditions. Is the distribution of woody plant species in a Peruvian cloud forest determined by microhabitat conditions? What is the role of environmental characteristics and forest structure in habitat partitioning in a tropical cloud forest?

Location: Cloud Forest, north Peruvian Andes.

Methods: We examined species–habitat associations in three 1-ha plots using the torus-translation method. We used three different criteria to define habitats for habitat partitioning analyses, based on microtopography, forest structure and both sets of factors. The number of species associated either positively or negatively with each habitat was assessed.

Results: Habitats defined on the basis of environmental conditions and forest structure discriminated a greater number of positive and negative associations at the scale of our analyses in a tropical cloud forest.

Conclusions: Both topographic conditions and forest structure contribute to small-scale microhabitat partitioning of woody plant species in a Peruvian tropical cloud forest. Nevertheless, canopy species were most correlated with the distribution of environmental variables, while understorey species displayed associations with forest structure.

environmental variables within their definition of a plant's niche (MacArthur 1972), while others include both environmental and biotic variables (Chase & Leibold 2003; Grubb 1976). Limiting resources and competitive exclusion have also been introduced into the definition of the niche (Hutchinson 1957). In addition to characterizing the variables implicated in habitat or niche partitioning, it is also important to clarify the spatial and temporal scale of analysis. Habitat–species associations vary with the scale of observation (Gentry 1988; Kneitel & Chase 2004; Paoli et al. 2006), and microhabitat diversity may possess a dynamic component reflecting spatio-temporal variation in resource availability (Chase & Leibold 2003; Leigh et al. 2004).

In this paper we present a study of species habitat associations in a montane cloud forest in the Peruvian Andes. At our study site the majority of free-standing woody plant species display a clumped distribution, and the size of clusters is partially related to primary dispersal mode, life form and shade tolerance (Ledo et al. 2012). Cloud forests are extremely fragile ecosystems, and their existence depends on the convergence of high humidity and suitable temperature conditions (Hamilton 1995). Cloud forests also occur in environments that typically possess steeper gradients in elevation than lowland environments (Bruijnzeel et al. 2011). Hence, we predict that changes in environmental conditions and their importance as drivers of species distributions may be more apparent in montane cloud forest than in lowland tropical forests, where a significant proportion of previous research has been conducted.

We examined fine-scale species–habitat associations in three 1-ha plots in a Peruvian Andean cloud forest and analysed whether and to what extent these habitat associations act on the species composition of the woody plant community. We tested the prediction that species–habitat associations exist among species in this community, and consequently, that the presence of different microhabitats would affect species distributions. We addressed the question of whether (1) topographic and environmental conditions, (2) forest structure or (3) a combination of the two factors acting together were most important. This approach reflects our interest in understanding the relative importance of forest structure and microenvironmental conditions on small-scale habitat partitioning. Moreover, it sheds light on the mechanisms that lead species distributions and community assembly.

Methods

Study site

This study was conducted in Monte de Neblina de Cuyas, which is a neotropical montane cloud forest situated in northern Peru (Piura region, Ayabaca province), in the western Andean range (4°34–36' S; 79°41–43' W). This is a

relic forest that once formed part of a larger cloud forest belt that occupied an extensive area of the Andean range (Gentry 1995). The main cause of the decline in forest cover was probably conversion for agriculture and pasture, although we cannot verify this. The Monte de Neblina de Cuyas cloud forest currently covers 400 ha. To our knowledge, the only anthropogenic disturbance that has ever occurred is illegal logging, although this is rare and only affects the edges of the forest. Most of the illegal logging and extraction of medicinal plants takes place in secondary forest near local villages. To our knowledge, no hunting activity exists or has existed in the area.

The study site was situated at altitudes ranging from 2359 to 3012 m a.s.l. The main part of the study area is situated on southwest-facing slopes. According to Köppen (1936), the location has a cold temperate climate with a dry winter. The mean annual temperature is 15 °C, varying between 8.5 °C and 18 °C. Mean annual precipitation is around 1200 mm, and is generally very intense during the summer (December–May). In years when the ENSO (El Niño Southern Oscillation) phenomenon occurs, the precipitation increases substantially (Romero et al. 2007). In the winter the frequency of winds increases and gales sometimes occur. The forest has been identified as an Important Bird Area (Freile & Santander 2005), even though it has now been seriously altered (Ledo et al. 2009). There is a high level of endemism in the forest and several taxa included in the IUCN Red List are threatened by the on-going loss of habitat.

Plot establishment and light measurements

The inventory was carried out between March and August 2008. Three 1-ha plots were established in randomly selected locations in the inner part of the forest, at least 200 m from the forest edge, to avoid edge effects (Fig. 1). All freestanding woody plants ≥ 1.3 m in height (diameter at breast height, DBH), without any diameter restriction, were mapped in each 1-ha plot. To map the woody plants, different sampling points were situated in the plot. The UTM coordinates and elevation of the first point (a corner) were measured using a GPS device, and from this information, the actual coordinates and elevation of each plot were obtained. Once all the woody plants had been measured at the first sampling point within a radius of approximately 15 m (using a vertex hypsometer and a compass), the next sampling point was located. The distance and angle between sampling points were double-checked to corroborate their exact positions. This process was repeated until the whole plot was covered. Every plant was numbered and the species, diameter (measured with a calliper) and height (measured with a vertex hypsometer) were recorded.

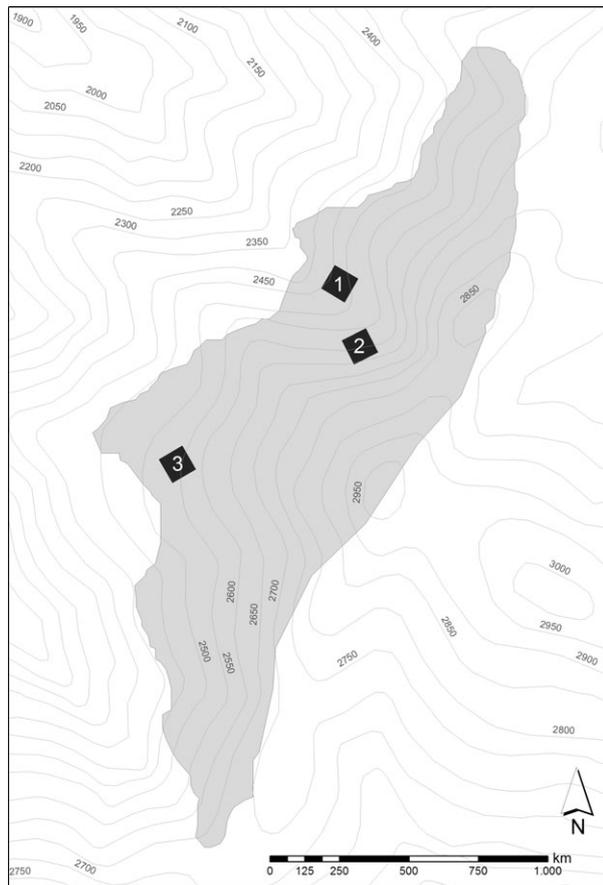


Fig. 1. Map of the study site and plot locations. The coordinates of the central point for plots 1, 2 and 3 were 4°59'07" S-79°70'52" W; 4°59'30" S-79°70'43" W; 4°59'69" S-79°71'03" W respectively.

The number of woody plants found in the plots was 4500 individuals ha^{-1} . The mean DBH was 12.2 cm. About 80% of the measured woody plants had a DBH of less than 5 cm, whereas 5% had a DBH more than 20 cm; comprising 180 individuals ha^{-1} . There were 39 different woody plant species per ha; however, only 22 species were represented by more than 50 individuals per plot. We classified those species into two main categories, according to life form: canopy species (comprising canopy and emergent species) and low stature species (comprising understorey and pioneer gap species). Detailed information on the woody plant species measured in the plots and their spatial organization can be found in Ledo et al. (2012).

Forty-two randomly selected locations were sampled for light in each plot by taking hemispherical photographs with a FC-E8 fish-eye lens attached to a Nikon Coolpix 4500 camera body. The camera was levelled horizontally 20 cm above the ground and oriented to true north using a compass with a spirit level. We processed the images using the software Hemiview (Hale & Edwards 2002). Values were obtained for visible sky, direct site factor,

indirect site factor and global site factor (GSF). We derived elevation in the plots from the first point measured with the GPS device, using the X , Y and Z coordinates of all the measured woody plants and auxiliary points; ca. 5000 points per ha. We then built a digital elevation model (DEM) for each plot in ArcMap® v. 9.2 and derived slope, curvature and aspect on a 2×2 m grid.

Habitat differentiation and species–habitat associations

We used three different sets of variables to define eight microhabitats, based on environmental (topographic) or forest structure characteristics, or a combination of the two. The first set of variables was altitude (\geq or $<$ 2500 m a.s.l., which was roughly the median altitude across the plots), slope (\geq or $<$ 35%, values for slope $>$ 35% are considered steep slope; Pachauri & Pant 1992) and the curvature (concavity–convexity of the terrain, derived from the DEM). In a previous analysis of the correlations between each species and a longer list of environmental variables (elevation, slope, aspect, curvature, soil cover, temperature and humidity), these three variables were most strongly associated with species distributions (A Ledo, unpubl. data). These variables have also been used to define habitats in previous studies of lowland tropical tree communities (Harms et al. 2001; Gunatilleke et al. 2006). The second analysis defined habitats according to forest structure variables: (1) woody plant number per 5-m quadrat (\geq or $<$ 10, which was roughly the median number of woody plants in 5-m quadrats across the plots), (2) canopy height (\geq or $<$ 17 m, which was Hart's dominant height across the plots) and (3) global site factor (\geq or $<$ 0.17, which was roughly the median GSF value across the plots). The third analysis combined elevation (\geq or $<$ 2500 m a.s.l.), canopy height (\geq or $<$ 17 m) and number of woody plant species (\geq or $<$ 10 in 10-m quadrats, which was roughly the number of species in 10-m quadrats across the plots). Species richness was considered a forest structure variable in this case because tropical tree species present very different morphological structures, hence, a larger number of species implies a greater variety of tree morphology and therefore different forest structure. The resulting habitats are defined in Table 1.

We analysed species habitat associations using the torus-translation test proposed by Harms et al. (2001) and slightly modified by Comita et al. (2007). Only those species represented by more than 50 individuals within the plot were included in the analysis. This method is more conservative than goodness-of-fit tests based on the χ^2 statistic or the randomized habitat method (Plotkin et al. 2000; Harms et al. 2001) because it accounts for spatial autocorrelation in stem locations in tests of habitat association (Harms et al. 2001). It achieves this by generating a

Table 1. Variables used to define habitats under the three different criteria.

Topographical variables				Forest structure variables				Topographic and forest structure variables			
Habitat	Elevation	Slope	Curvature	Habitat	Canopy height	Number woody plants	GSF	Habitat	Elevation	Canopy height	Number species
Upper elevation, high slope, spurs (UeHsS)	≥ 2550	≥ 35	+	Higher canopy, dense area, bright place (HcDaBp)	≥ 17	≥ 10	≥ 0.17	Upper elevation, higher canopy, rich composition (UeHcRc)	≥ 2550	≥ 17	≥ 10
Upper elevation, high slope, gullies (UeHsG)	≥ 2550	≥ 35	-	Higher canopy, dense area, shady place (HcDaSp)	≥ 17	≥ 10	< 0.17	Upper elevation, higher canopy, poor composition (UeHcPc)	≥ 2550	≥ 17	< 10
Upper elevation, low slope, spurs (UeLsS)	≥ 2550	< 35	+	Higher canopy, openness area, bright place (HcOaBp)	≥ 17	< 10	≥ 0.17	Upper elevation, lower canopy, rich composition (UeLcRc)	≥ 2550	< 17	≥ 10
Upper elevation, low slope, gullies (UeLsG)	≥ 2550	< 35	-	Higher canopy, openness area, shady place (HcOaSp)	≥ 17	< 10	< 0.17	Upper elevation, lower canopy, poor composition (UeLcPc)	≥ 2550	< 17	< 10
Lower elevation, high slope, spurs (LeHsS)	< 2550	≥ 35	+	Lower canopy, dense area, bright place (LcDaBp)	< 17	≥ 10	≥ 0.17	Lower elevation, higher canopy, rich composition (LeHcRc)	< 2550	≥ 17	≥ 10
Lower elevation, high slope, gullies (LeHsG)	< 2550	≥ 35	-	Lower canopy, dense area, shady place (LcDaSp)	< 17	≥ 10	< 0.17	Lower elevation, higher canopy, poor composition (LeHcPc)	< 2550	≥ 17	< 10
Lower elevation, low slope, spurs (LeLsS)	< 2550	< 35	+	Lower canopy, openness area, bright place (LcOaBp)	< 17	< 10	≥ 0.17	Lower elevation, lower canopy, rich composition (LeLcRc)	< 2550	< 17	≥ 10
Lower elevation, low slope, gullies (LeLsG)	< 2550	< 35	-	Lower canopy, openness area, shady place (LcOaSp)	< 17	< 10	< 0.17	Lower elevation, lower canopy, poor composition (LeLcPc)	< 2550	< 17	< 10

null distribution of stem densities in defined habitats by iteratively translating the habitat map, shifting it by a chosen quadrat size increment, across the stationary stem distribution map in the four cardinal directions and assessing stem density per habitat at each translation. To avoid boundary effects, the plot is modelled as a torus and the habitat map is translated from one edge to the corresponding location on the opposite edge. To test the statistical significance of a species–habitat association, the actual stem density per habitat is compared to the distribution of stem densities obtained from the translated habitats maps. The P -value for the association is then calculated by comparing how many times the density of stems of each species in the actual map associated with some habitat is higher (for positive associations) or lower (for negative associations) than the density of stems in the distribution derived from all torus-shifted maps. Further details on the method are given in Harms et al. (2001). In this paper we defined habitats on the basis of a 2×2 m grid of quadrats in each 1-ha plot, which gave one real and 2499 torus-translated habitat maps. For these analyses, we used the R code developed by K. Harms and the modification proposed by L. Comita, which includes the stem density of each species in the defined quadrats instead of the total density (number of stems of all species) in the quadrats (R Foundation for Statistical Computing, Vienna, AT). We carried out these analyses for each plot separately and considered that P -values lower than 0.05 reflected spatial association (either for negative or positive values) between the analysed species and the habitat.

Since the three plots were situated within the same forest, separated by less than 1 km, and showed similar topographic, environmental and forest structure characteristics (Appendix S1, Fig. 1), species–habitat associations were expected to be equivalent across the three plots, and we view a combined analysis pooling data across all three plots as providing the most robust estimates of the importance of species–habitat associations. To conduct this analysis, we summed the number of woody plants per habitat across all plots for the translated habitats map and the actual map from the previous analysis. In this case, the number of 2×2 -m quadrats from translated maps available for calculating the P -value of the species–habitat associations was 7497 for habitats represented in all three plots and 4998 for habitats represented in only two plots. The actual number of species for comparison was the sum of the number of woody plants per habitat in the actual plots considered. We again considered that P -values lower than 0.05 (either for negative or positive values) provided evidence of a significant species–habitat association, although we also identify associations with P -values in the range 0.05–0.1 because these may reflect spatial non-randomness that is

biologically important even though we lack sufficient statistical power to detect it.

One shortcoming of the habitat torus translation method is that some casual associations may arise due to the autocorrelation of species distributions and not to genuine species–habitat associations (Harms et al. 2001). We attempted to mitigate this problem by using three separate plots instead of a one large plot. However, 5% of associations are expected to be false positives (type 1 errors), which equates to 8.8 associations based on the number of habitats and the number of species we analysed. On the other hand, most of the P -values we obtained were lower than the 0.05 threshold. Hence we believe our approach was robust and provides results that are comparable to other studies that have adopted the same analytical technique (Harms et al. 2001; Gunatilleke et al. 2006; Comita et al. 2007).

All the analyses were performed in R.

Results

The coverage of each habitat defined by the three sets of variables on each plot is shown in Fig. 2.

Associations between species and microhabitats defined by topographic variables

When plots were analysed separately, 19 out of 22 species showed a significant ($P < 0.05$) positive association to at least one habitat, and 15 out of 22 species showed a negative association to a habitat (Appendix S1). Pooling the information from the three plots, we found six positive species–habitat associations and two negative associations, representing a total of eight species (36%) that showed spatial association or repulsion for at least one topographic habitat. Three of these were canopy species and the other three were low-stature species (Table 2, Appendix S1). Canopy species are less rich (eight species) than low-stature species (14 species) in this community, from which we saw that the proportion of species that are habitat-associated is higher for canopy species than understorey species (37 vs. 21%). The habitat with the highest number of positive associations is low-elevation steep spurs, where two below-canopy medium- or shade-intolerant species (*Aphelandra acanthifolia* and *Cestrum auriculatum*) and one canopy species (*Critoniopsis seviliana*) were significantly associated, followed by low-elevation steep gullies where one canopy species (*Persea* Ms) and one understorey species (*Solanum* Ms2) were significantly associated (Table 2, Appendix S1).

When the threshold for detecting a significant association in the combined analysis was lowered ($P < 0.1$), we found 11 positive species–habitat associations and five

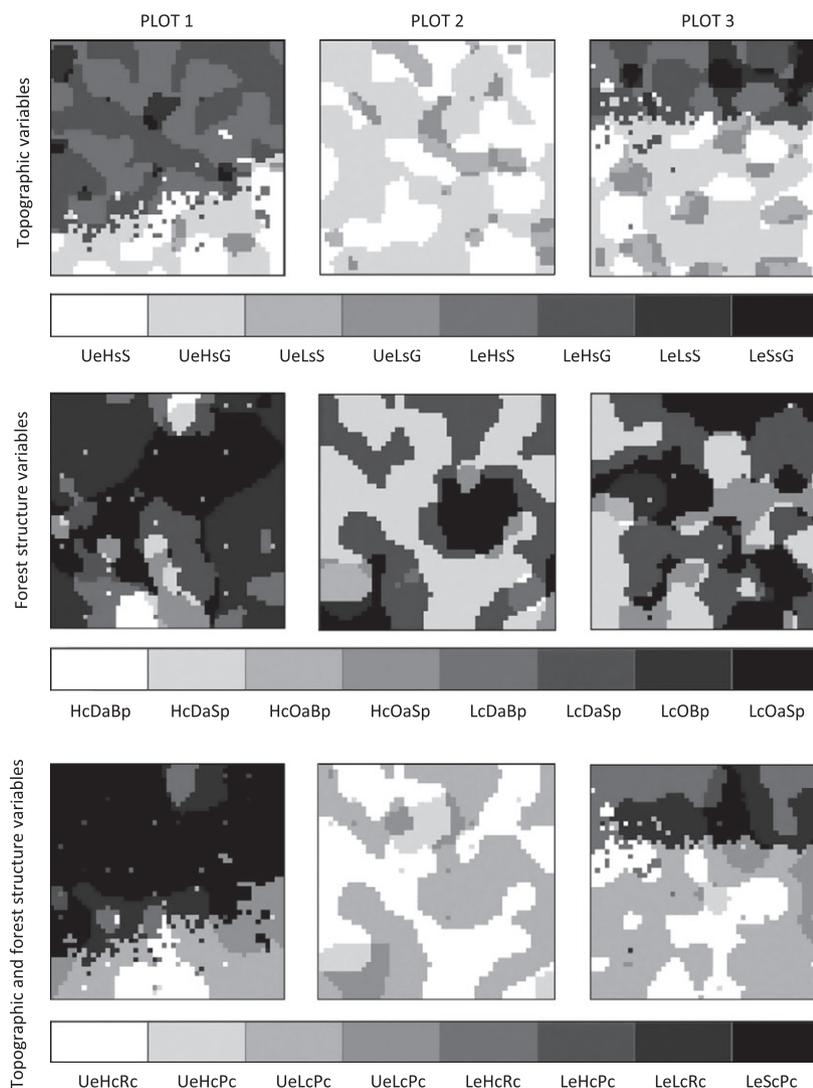


Fig. 2. Habitat distribution in the plots based on (a) topographic variables, (b) forest structure variables and (c) topographic and forest structure variables for habitat definition.

negative associations, representing a total count of 14 (54%) species (Table 2, Appendix S1).

Associations between species and microhabitats defined using forest structure variables

When plots were analysed separately, 18 out of 22 species showed at least one positive association to a habitat, and 17 out of 22 species showed one negative habitat association. In the combined analysis, two species (*Miconia media* and *Piper elongatum*) had significant positive habitat associations and three species (*Piper elongatum*, *Siparuna muricata* and *Solanum Ms1*) had significant negative associations, representing a total of four species (18%) showing a spatial association with a habitat (Table 2, Appendix S1). All four of these species were

low stature species. The habitat with the highest number of associations (*Siparuna muricata* and *Solanum Ms1*, both pioneer species) had low values of canopy height, stem density and a low global site factor, and in both cases the associations were negative. Those pioneer species were therefore disproportionately less abundant in sites with low canopy but less light, which may correspond with young stands in steep shaded gullies.

When the threshold for detecting a significant association in the combined analysis was lowered ($P < 0.1$), we found two positive species–habitat associations and five negative associations, representing a total of five species (22.7%) that showed spatial preference to particular habitat conditions (Table 2, Appendix S1). The number of significant associations was lower than when habitats were defined using topographic variables. Moreover, the

Table 2. Results of the species-association analysis in each habitat, considering the three plots together and the percentage of species associated, when considering the values of the three plots together (P -value <0.05).

	Positive associations															Negative associations																								
	UeHsS	UeHsG	UeLsS	UeLsG	LeHsS	LeHsG	LeLsS	LeLsG	UeHsS	UeHsG	UeLsS	UeLsG	LeHsS	LeHsG	LeLsS	LeLsG	HcDaSp	HcDaBp	HcDaSp	HcDaBp	HcOaSp	HcOaBp	HcOaSp	HcOaBp	LcDaSp	LcDaBp	LcDaSp	LcDaBp	HcOaSp	HcOaBp	LcOaSp	LcOaBp								
Topographic variables																																								
Total P1	4	1	2	2	1	1	0	1	3	0	0	0	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Total P2	0	4	0	2	0	0	0	0	2	1	2	0	0	0	0	0	0	0	1	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0		
Total P3	1	1	1	1	5	5	1	1	4	1	1	1	0	5	0	4	1	0	1	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
All Three Plots	0(0)	0(0)	0(0)	1(1)	3(4)	2(4)	1(1)	1(1)	0(0)	0(0)	1(1)	0(0)	1(2)	0(0)	0(0)	0(2)	0(0)	0(0)	1(1)	0(0)	0(0)	0(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(2)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)			
%	0(0)	0(0)	0(0)	4.5(4.5)	13.6(18.2)	9.1(18.2)	0(4.5)	4.5(4.5)	0(0)	0(0)	4.5(4.5)	0(0)	4.5(9.1)	0(0)	0(0)	0(9.1)	0(0)	0(0)	4.5(9.1)	0(0)	0(0)	4.5(4.5)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(9.1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)		
Forest structure variables																																								
Total P1	4	7	0	1	3	6	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Total P2	3	2	0	1	3	4	1	0	0	0	1	0	1	0	0	0	0	0	1	1	3	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total P3	0	6	3	0	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total Plots	0(0)	1(1)	0(0)	0(0)	0(0)	1(1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	
%	0(0)	4.5(4.5)	0(0)	0(0)	0(0)	4.5(4.5)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	
Topographic and forest structure variables																																								
Total P1	3	0	4	1	4	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Total P2	3	0	5	1	0	0	0	0	1	9	1	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total P3	0	0	2	0	6	2	0	0	1	1	2	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total Plots	0(0)	0(0)	0(1)	1(1)	5(6)	2(3)	0(0)	0(0)	1(1)	0(0)	1(1)	1(2)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)
%	0(0)	0(0)	0(4.5)	4.5(4.5)	22.7(27.3)	9.1(13.6)	0(0)	0(0)	4.5(4.5)	0(0)	4.5(4.5)	4.5(9.1)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)

Values in parentheses indicate equivalent counts and percentages of associations that were significant at $P < 0.1$.

associations to forest structure variables were less consistent among plots (Table 2, Appendix S1).

Associations between species and microhabitats defined using topographic and forest structure variables

When plots were analysed separately 22 species (100%) showed a positive association to at least one habitat, and 17 out of these 22 species showed a negative association (Appendix S1) to habitats, defined on the basis of both topographic and forest structure variables. In the analysis combining data from all three plots, ten species showed positive habitat associations and five species had negative associations ($P < 0.05$). A total of 11 species (50%) showed (either positive or negative) spatial associations with a habitat (Table 2, Appendix S1). These associations were found for canopy (*Drimys* Ms, *Persea* Ms) as well as low-stature (*Cestrum auriculatum*, *Iochroma squamosum*, *Miconia denticulata*, *Miconia media*, *Piper elongatum*, *Solanum* Ms1 and *Solanum* Ms2) species. Five species were positively associated with tall forest at lower elevations with a high species richness (habitat LcHcRC, Table 2), which represents closed canopy mature forest with a high species count. The habitat with the highest number of negative associations represents shorter forest at low elevations with a low species richness (habitat LeLcPc, Table 2), which corresponds to canopy gaps. Under this criterion, many species displayed at least one association (positive or negative) with a determined habitat (Table 2, Appendix S1). Nevertheless, all the most abundant species in the forest (the pioneer *Solanum* Ms1, the understorey species *Piper elongatum* and the canopy species *Drimys* Ms and *Persea* Ms) displayed spatial associations.

When topographic as well as forest structure variables were combined in the definition of habitats, the number of species with significant associations ($P < 0.05$) was higher (15 species) than when either topographic (nine species) or forest structure (five species) variables were used in isolation. There was also more agreement among plots when habitats were defined using both topographic and forest structure variables (Table 2). Increased consistency of habitat associations among plots is probably indicative of a more robust result. When the threshold for detecting a significant association was lowered ($P < 0.1$), we found 15 positive species–habitat associations and 11 negative associations, representing a total of 16 species (72%) that showed spatial non-randomness with respect to habitat conditions (Table 2, Appendix S1).

Discussion

Species–habitat associations

The habitat association method proposed by Harms et al. (2001) allowed us to corroborate the existence of micro-

habitat associations for woody plant species in a Peruvian cloud forest community. Analogous habitat associations have been observed in a number of tropical lowland forests and are now a widely accepted characteristic of tropical tree communities (Phillips et al. 2003; Chave 2004; Gunatilleke et al. 2006; Lai et al. 2009).

The scale of observation and the variables used to differentiate habitats in our study were different to those employed in previous studies. The fact that biophysical gradients lead to habitat associations at large scales in tropical forests is strongly supported in the literature: one of the clearest examples is the existence of altitudinal vegetation zones (Gentry 1988). Habitat associations also occur at meso-scales of 1–50 ha (Harms et al. 2001; Valencia et al. 2004; Comita et al. 2007) and landscape scales of 400 ha (Paoli et al. 2006), but analyses at small scales have rarely been conducted (but see John et al. 2007). Our analyses using 2×2 m quadrats show that microhabitat differentiation and microhabitat–species association also exist at this very fine scale. Moreover, the scale of species–habitat associations is set more on the mean habitat patch size than on the size of quadrats. Fine-scale analysis is important because it allows us to gain a clearer understanding of micro-niche differentiation, which may be key to biodiversity conservation (Leigh et al. 2004). Both micro- and macro-scale processes need to be considered in theories explaining the maintenance of plant community diversity (Whittaker et al. 2001).

Previous studies have generally defined habitats and species distributions using topographic characteristics, such as elevation or slope (Gunatilleke et al. 2006; Comita et al. 2007), soil nutrients (Pélissier et al. 2001; Phillips et al. 2003; John et al. 2007) or both (Costa et al. 2005; Suzuki et al. 2009). In this paper we examined the importance of both environmental and forest structure variables to the differentiation of microhabitats within the forest. We have carried out a number of analyses to compare the results obtained using different criteria for defining habitats, and have identified clear differences (Table 2). Hence, the way in which habitats are defined is of particular importance. One shortcoming of this method is that the habitats must be selected a priori, and the habitat definition has a notable effect on the results. Without information on the ecological preferences of the species, or the range in which species respond differentially to a variable (e.g. the slope limit for the occurrence of certain species), the selection of variables is inherently arbitrary and may be incomplete if an unmeasured environmental variable is important for certain species. For example, although canopy height is rarely taken into account in analyses of species distributions, we have found that areas with a taller forest canopy might be considered different microhabitats, since the distribution of certain species was related to this variable (Appendix

S1). In our study site, species associated with taller forest included both canopy species, such as *Persea* Ms and *Morus insignis*, and species of low stature, such as *Miconia media*, *Piper elongatum* and *Solanum* Ms. Nevertheless, the effect of arbitrariness in habitat definition in species–habitat associations could be also somewhat reduced if the species were allowed to be associated with combinations of habitats and not only single habitats in the statistical test, as in the method proposed by De Cáceres et al. (2010).

Our use of three replicate plots (instead of one large plot) allowed us to determine whether species–habitat associations were consistent in different parts of the forest. This approach helps to avoid misinterpretations caused by fortuitous species–habitat co-occurrence resulting from dispersal limitation in a given area. We found that while some associations were consistent among plots, many associations only appeared in one or two plots, and the results for the other(s) were different. This divergence was most apparent when forest structure variables were used for defining habitats (Appendix S1). When the three plots were considered together, the number of significant associations decreased. The associations identified at the scale of a single plot, but not in the combined analysis across all three plots, may have arisen either because the distribution of a species coincides with the presence of a habitat that differs in subtle ways between plots in a manner that were not captured by our habitat definitions, or because of spatial variation in the size class and age structure of species' populations, because habitat associations may vary through ontogeny (Comita et al. 2007). However, independent of the cause, our results indicate that habitat partitioning only affects the spatial distribution of some species within a community. It is important to note that these findings are only valid for the habitats we defined and at the scale of analysis used in this paper.

Variables implicated in microhabitat partitioning and factors involved in species distribution

The inclusion of both environmental and forest structure conditions together discriminated most strongly among species and generated the most consistent results among plots (Table 2). Environmental variables were most strongly correlated with the distribution of canopy species, while forest structure variables displayed associations with the distribution of understorey species. Therefore, the combination of environmental and forest structure variables highlighted associations with a larger number of species across both life forms than either set of variables in isolation.

At intermediate and large scales, elevation is the most important factor determining species occurrence (Gentry 1988; Steege et al. 2006). However, our analyses also

highlight the importance of forest structure and small-scale disturbances. Species that occurred in plot 3 but not in plots 1 and 2 (*Aphelandra acanthifolia* and *Siparuna muricata*) illustrate the role of stand disturbances in species distribution. These species appear to be associated with habitats characterized by lower elevations (Appendix S1). It is therefore potentially surprising that they do not appear in plot 1, which is at a lower elevation. However, the occurrence of these species is related to factors other than altitude. Plot 3 is situated above a track with a gentle slope, and the creation of the track may have facilitated the establishment of disturbance-dependent species that typically occur at forest edges and canopy gaps but not in undisturbed mature forest. This is most noticeable for *Aphelandra*, which is negatively associated with well-developed stands (Appendix S1). The distribution of this species is probably related to specific microclimatic conditions rather than to altitude. These microclimatic conditions arise from dynamic stand processes and are therefore inherently unpredictable. Different microclimatic conditions may also correlate with altitudinal gradients, and indeed they often vary in a parallel manner. A similar interpretation of the importance of environmental conditions on the distribution of species was expressed by Whittaker et al. (2001), who advocated that geographic patterns of species richness should not be termed “latitudinal gradients”.

Evidence of micro-niche partitioning

We found that many species were associated either positively or negatively with specific habitats, and this may be interpreted as an indication of micro-niche separation at the scale of our analysis. Some pioneer species occur in association with microhabitats that indicate specialization to a narrow niche defined by occupancy of micro-gaps. This result conforms to previous research on tropical forest trees (Clark et al. 1993; Chesson 2000), and supports the idea that pioneer species are strongly affected by microclimate conditions. Our results also identified habitat associations for some canopy and emergent species, which suggests that different species and/or functional groups have different patterns of habitat association. Canopy species are more strongly related to micro-topographic variables than understorey species, which appear to depend more on forest structure variables (Appendix S1). These findings support the hypothesis that canopy gaps are particularly important for maintenance of pioneer species (Whitmore 1978; Schnitzer & Carson 2001).

A drawback when attempting to study species–niche association is that there is no universally agreed definition of the ‘niche’ (Morin 2011). Classical micro-niche definitions sometimes include only physical environmental conditions (MacArthur 1972). In other cases, the niche

implies a wide range of variables. Hutchinson (1957) defined the niche as an n -dimensional hypervolume, where each variable n is an environmental or biological variable and the resources that define the requirements of a species to maintain or increase its population. However, the term microhabitat we have been using in this paper is close to the ‘niche’ concept defined by Grubb (1976) and by Chase & Leibold (2003), which includes both environmental and biotic conditions. To avoid confusion, we avoid the term ‘niche’ and replace it here by microhabitat. The microhabitats we defined in this study include both forest structure and environmental variables. This perspective has implications for our understanding of the mechanisms that drive tree species distributions and community structure. Environmental and forest structure conditions may co-vary at small scales, since they are mutually dependent. Soil nutrient availability, another important factor influencing species distributions (John et al. 2007; Bohlman et al. 2008), may also vary in parallel with topography and forest structure.

Many current authors agree that spatio-temporal variation of resource availability is an important mechanism for the maintenance of species richness (Wright 2002). We advocate that both forest structure and environmental characteristics have both static and dynamic components, and these may vary within forests at small scales. In addition, the two sets of variables may co-vary in a variety of ways and/or vary on different temporal and spatial scales. This environmental complexity generates a high diversity of microhabitats and, consequently, a greater range of establishment opportunities for the species that comprise the community. Our results suggest that microhabitat specialization is an important factor contributing to community structure for woody plants of a Peruvian cloud forest.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Results of the species–habitat association analysis when (a) topographic variables (b) forest structure variables and (c) topographic and forest structure variables were used to define habitats. The low-stature and

mid-canopy species are indicated by ‘L’ and the canopy and emergent species with ‘C’. The ‘+’ symbol indicates significant association with plot 1, the ‘•’ symbol with plot 2 and the ‘Θ’ symbol with plot 3. The grey cells indicate a significant association when the three plots are analysed together.