

3 RESULTADOS

3.1 BETA DIVERSITY AND OLIGARCHIC DOMINANCE IN THE TROPICAL FORESTS OF SOUTHERN COSTA RICA

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3.1.1 Resumen

DIVERSIDAD BETA Y DOMINANCIA OLIGÁRQUICA EN LOS BOSQUES TROPICALES DEL SUR DE COSTA RICA

Estudios recientes han demostrado la existencia un patrón consistente de fuerte dominancia de un pequeño subconjunto de especies arbóreas en los bosques neotropicales. Estas especies han sido llamadas 'hiperdominantes' cuando son muy abundantes y frecuentes a grandes escalas geográficas y 'oligarcas' a escalas de paisaje regional. Aunque tanto los factores ambientales como los procesos estocásticos influyen en el ensamblaje de la comunidad y la diversidad beta, es menos clara la contribución de las especies oligárquicas a la variación de la composición de la comunidad. Con ese fin, establecimos 20 parcelas de 1 ha (5 sitios con 4 tipos de bosque por sitio) en bosques tropicales húmedos de tierras bajas del suroeste de Costa Rica. Los cuatro tipos de bosque fueron: bosque primario de cima, ladera y ripario, y bosque secundario. Los objetivos fueron: (1) Analizar cómo la composición de la comunidad responde a las diferencias en la topografía, la etapa de sucesión y la distancia entre parcelas para los diferentes grupos de especies (todas, oligarcas, especies comunes y raras / muy raras). (2) Identificar las principales especies oligárquicas que mejor caracterizaron los cambios en la composición de la comunidad entre los tipos de bosques. De un total de 485 especies de árboles, lianas y palmas registradas en este estudio, solo 27 especies (es decir, 5.94%) fueron consideradas como especies oligarcas al contribuir al 37.41% de todos los individuos registrados y con una frecuencia > 50%. La composición de la comunidad de plantas difirió significativamente entre los tipos de bosques, contribuyendo así a la diversidad beta a escala de paisaje. Las especies oligarcas fueron el componente de la comunidad mejor explicado por variables geográficas y topográficas, permitiendo una caracterización confiable de la diversidad beta a lo largo del paisaje

3.1.2 Abstract

Recent studies have reported a consistent pattern of strong dominance of a small subset of tree species in neotropical forests. These species have been called “hyperdominant” at large geographical scales and “oligarchs” at regional-landscape scales when being abundant and frequent. Forest community assembly is shaped by environmental factors and stochastic processes, but so far the contribution of oligarchic species to the variation of community composition (i.e., beta diversity) remains poorly known. To that end, we established 20.1-ha plots, that is, five sites with four forest types (ridge, slope and ravine primary forest, and secondary forest) per site, in humid lowland tropical forests of southwestern Costa Rica to (a) investigate how community composition responds to differences in topography, successional stage, and distance among plots for different groups of species (all, oligarch, common and rare/very rare species) and (b) identify oligarch species characterizing changes in community composition among forest types. From a total of 485 species of trees, lianas and palms recorded in this study only 27 species (i.e., 6%) were nominated as oligarch species. Oligarch species accounted for 37% of all recorded individuals and were present in at least half of the plots. Plant community composition significantly differed among forest types, thus contributing to beta diversity at the landscape scale. Oligarch species was the component best explained by geographical and topographic variables, allowing a confident characterization of the beta diversity among tropical lowland forest stands.

Key words

Beta diversity, community composition, Neotropical forests, oligarch species, topographic habitats

3.1.3 Introduction

Hyperdominance has recently emerged as a key concept in the study of tree diversity and functioning in tropical ecosystems (Fauset *et al.*, 2015; ter Steege *et al.*, 2013). ter Steege *et al.*, 2013 defined hyperdominant species as those accounting for half of all individuals inferred at the scale of the tree communities of the Amazon basin. The concept of hyperdominance has its roots in a seminal paper of Pitman *et al.*, (2001), which reported a consistent pattern of dominance by a relatively small but abundant set of tree and palm species, called “oligarchs”, in the upland tropical forests of eastern Ecuador and southern Peru. Since then, evidence has accumulated

reinforcing the existence of a general pattern of oligarchic dominance in tropical forest, especially in the neotropics (Svenning, Kinner, Stallard, Engelbrecht & Wright, 2004; Vormisto, Svenning, Hall & Balslev, 2004; Macía & Svenning, 2005; Williams, Viers & Schwart, 2010; Williams, Trejo & Schwart, 2017; Macía, 2011; Arellano, Cala & Macía, 2014; Arellano *et al.*, 2016; see Pitman, Silman & Terborgh, 2013; for a detailed review), whereas “oligarch” refers to abundant and frequent species at regional-landscape level, “hyperdominant” defines species very abundant and frequent at large geographical scales (e.g., the Amazon basin). Practical implications of the so-called oligarchic dominance would drastically simplify model parameterization of trophic interactions and critical ecosystem services, such as water, carbon, and nutrient cycling (ter Steege *et al.*, 2013). In fact, Fauset *et al.*, (2015) found that dominance of forest function was even more concentrated in a few species than dominance of tree abundance, with half of the carbon stock and half of woody productivity controlled by only $\approx 1\%$ of hyperdominant tree species across the Amazon basin.

However, studies to date have mainly focused on the effects of oligarch dominance on alpha diversity, less is known of how oligarchic dominance impacts beta diversity. Beta diversity can be defined as the variation in community composition among a set of sites within a given spatial or temporal extent (Anderson *et al.*, 2011; Whittaker, 1960). Beta diversity of oligarch communities in tropical forests can be explained by three main hypotheses as follows: (a) Species composition is uniform over large areas, as individuals of all species are able to grow equally well at all sites but differences in abundance are shaped by biological interactions independent of environmental conditions. The best competitors become dominant, whereas less good competitors remain rare at all sites (Legendre, Borcard & Peres-Neto, 2005; Tuomisto & Ruokolainen, 2006; but see Pitman *et al.*, 2013). As a result, beta diversity will be generally small as the same oligarchic species dominate at landscape level. (b) Species composition fluctuates in a random, autocorrelated way. This hypothesis derives from the neutral diversity model (Hubbell, 2001), where individuals of all species are able to grow equally well and all species are competitively equal, but with limited propagule dispersion that spatially structures community composition (Legendre *et al.*, 2005; Tuomisto & Ruokolainen, 2006). So, different sets of dominant species will appear at local scales and beta diversity will intrinsically increase with geographical distance. Finally, (3) oligarchies are mainly structured by the same niche mechanisms that generate spatial heterogeneity in tree species composition and abundance (Pitman *et al.*, 2013). Oligarch species usually show broader environmental tolerances than less

common ones (Arellano *et al.*, 2014; Brown, 1984; Phillips *et al.*, 2003; Slatyer, Hirst & Sexton, 2013), but they are not necessarily indifferent to environmental heterogeneity, showing higher abundances in the most favorable habitats (ter Steege *et al.*, 2013). As a result, beta diversity will increase with environmental heterogeneity, but this increase is mainly driven by differences in oligarchic abundance and not by turnover in species identity.

However, dispersal limitation and niche mechanisms are not mutually exclusive; both structure forest communities and are responsible for patterns of beta diversity across the landscape (de Cáceres *et al.*, 2012; Legendre *et al.*, 2009; Qiao *et al.*, 2015). On the one hand, propagule limited dispersion and successful recruitment close to conspecifics produce clustered distributions of populations and contribute to community similarity and characterization of oligarch patterns at local scales (de Cáceres *et al.*, 2012; Chain-Guadarrama, Finegan, Vilchez & Casanoves, 2012). On the other hand, niche differentiation and environmental gradients determine competitive abilities and dominance hierarchies, structuring oligarch communities in space (Arellano *et al.*, 2014, 2016; de Cáceres *et al.*, 2012; Pitman *et al.*, 2013; Prada & Stevenson, 2016; Sesnie, Finegan, Gessler & Ramos, 2009). Whereas most of the studies have shown that both mechanisms contribute to changes in community composition (Baldeck *et al.*, 2013; de Cáceres *et al.*, 2012; Chain-Guadarrama *et al.*, 2012; Condit *et al.*, 2002; Legendre *et al.*, 2009; Prada & Stevenson, 2016; Vormisto *et al.*, 2004), more work is needed to understand how variation in geographical scale affects the partitioning of beta diversity.

To that end, we set up our experiment in wet tropical lowland forests in the Golfo Dulce region, southwestern Costa Rica. This region is considered one of the most diverse areas in the country in terms of vascular plants (Cornejo, Mori, Aguilar, Stevens & Douwes, 2012; Weissenhofer, Huber, Zamora, Weber & González, 2001; Zamora, Hammel & Grayum, 2004) and represents the largest remaining tract of lowland rain forest along the Pacific shore of Central America (Gilbert *et al.*, 2016). The complex geological history of the Golfo Dulce region has generated a rich mosaic of landforms (Bagley & Johnson, 2014), where forests have been modified by natural and human actions (Gilbert *et al.*, 2016; Weissenhofer & Huber, 2001), with $\approx 10\%$ of the Golfo Dulce region covered by secondary regrowth (Weissenhofer *et al.*, 2008). Therefore, we investigated differences in plant community composition across forest types differing in topography and successional stage. Topography is not a direct environmental variable, but a proxy that reflects the variation in soil moisture and microclimatic conditions (Legendre *et al.*, 2009; Cáceres *et al.*, 2012), and thus topographic features are often found to correlate with species distribution

patterns (Harms, Condit, Hubbell & Foster, 2001; Whittaker, 1956). Here, we establish the following objectives. (a) To analyze how floristic community composition responds to differences in topography, successional stage and spatial distance among plots for the different groups of species. We hypothesized that variation within different groups (all, oligarch, common and rare/very rare species) is explained by the same factors than overall species richness; thus, oligarch species represent a subset of the community shaping patterns of beta diversity among tropical tree communities. (b) To detect oligarch species suitable to characterize shifts in community composition among forest types. Oligarchs are, by definition, frequent in most of the sites, so we opt to identify which oligarch species contributed significantly to beta diversity among forest types through changes in abundance.

3.1.4 Methods

3.1.4.1 Study area

The study region was located in the Golfo Dulce region, encompassing the Osa Peninsula and the adjacent Piedras Blancas National Park, in Costa Rica, Central America (Supporting information Figure S1). The major regions are tropical wet forests, tropical moist forests, and tropical premontane wet forests (Holdridge, 1967). Altitude on the Osa Peninsula ranges from sea level to 745 m asl on Cerro Rincón. The geomorphology in the area is complex, ranging from alluvial sediment plains to rugged uplands produced by tectonic activity with narrow ridges and long steep slopes (Gilbert *et al.*, 2016; Weissenhofer & Huber, 2001). The region is dominated by basalt, cherts, and limestone lithologies, with inceptisols, ultisols, and mollisols as the most abundant soils at the study sites (Alvarado & Mata, 2016; Gilbert *et al.*, 2016). Annual precipitation ranges from 4,000–5,000 mm in the uplands to 5,500–6,000 mm or more on the peninsula's mountains peaks and in the coastal zone (Gilbert *et al.*, 2016). Precipitation shows seasonal variation, with a rainy season from May to December, and four months of reduced precipitation from January to March. Mean annual temperature ranges between 25 and 27°C (Weissenhofer *et al.*, 2008).

3.1.4.2 Plot establishment and data collection

We selected five sites (La Gamba, Riyito, Agua Buena, Rancho Quemado, and Piro) across the study region where in close proximity we could identify each of the four target forest types (Supporting Information Figure S1). The four forest types were based on physiographic and successional criteria established by previous studies (Clark & Clark, 2000; Weissenhofer *et al.*, 2001): ridge primary forest, slope primary forest, ravine primary forest, and secondary forest. Ridge plots were established in primary forest growing on the relatively flat and well-drained hilltops (300–400 m altitude), exposed to the action of wind and rain. Slope plots were

established in primary forest growing on steep (25–35°) and well-drained slopes. Ravine plots were established in primary forest along streams and adjacent terraces on the bottom of steep slopes. Secondary 25–40 years ago according to owners, commonly on moderate to gentle slopes. Secondary forests were situated in accessible topographic positions and had no correspondence in topography with the other forest types. However, secondary forests were included in this study due to their importance in the Golfo Dulce region, where they cover around 10% of the landscape (Weissenhofer *et al.*, 2008). In each forest type per location, one permanent forest plot was established. Plots were of 1-ha size and were subdivided into 100 subplots of 10 × 10 m following the standards of Alder and Synnott (1992). Plot shape was adapted to the physiography of the terrain, ranging from regular (100 × 100 m) to irregular shapes, especially in the case of the ravine where the subplots were situated along the small streams and adjacent terraces (Supporting Information Figure S2). For further information please visit <http://www.univie.ac.at/bdef/php/approach/>).

We recorded and tagged all individuals comprising trees, palms, and lianas with a diameter at breast height (dbh) ≥10 cm that were mapped in a X-and Y-coordinates system for each plot. Plant samples were collected for taxonomic identification and were deposited at the Herbarium of the University of Costa Rica (USJ). Taxonomic names follow those accepted in the Tropicos database of the Missouri Botanical Garden (www.tropicos.org).

Oligarch species were defined in terms of abundance and frequency (Arellano *et al.*, 2014; Macía & Svenning, 2005; Pitman *et al.*, 2001) as the dominant ones that contributed to the accumulated 50 percent of all individuals encountered in all plots together (ter Steege *et al.*, 2013) and were present in at least half (50%) of the plots (≥10 plots). Excluding oligarch ones, common species were defined with a threshold density ≥1 individual/ha (Pitman *et al.*, 2001) and with a frequency ≥25 percent of the plots (≥5 plots). Rare species were defined as those with mean densities < 1 individual per ha and/or frequency <25 percent of the plots. Those with only one individual sampled were defined as very rare species.

3.1.4.3 Statistical analysis

Canonical analysis of principal coordinates (CAP) was used to calculate the centroids of each forest type in the ordination space with all the species (Anderson & Willis, 2003). CAP performs a constrained ordination analysis in two steps as follows: (a) Computes a principal coordinate analysis (PCO) of the matrix of the abundance data (which was previously transformed using Hellinger transformation) and using Bray–Curtis as dissimilarity distance (Anderson & Willis, 2003; Borcard, Gillet & Legendre, 2018). Use of Bray–Curtis has been debated due to their sensitivity to density invariance (Jost, Chao & Chazdon, 2011), but we did not identify any significant differences in density within our plots, so we retained using this distance to analyze dissimilarity (Legendre & De Cáceres, 2013). (b) Runs a redundancy analysis (RDA) of the PCO

created above (which act as a response data) constrained by “forest type” as explanatory variable (Anderson & Willis, 2003; Borcard *et al.*, 2018; Oksanen *et al.*, 2017). For the CAP analysis, we used the function `capscale` of the `vegan` library under the R environment (R Development CoreTeam 2018); `capscale` uses all axes with positive eigenvalues, and axes are weighted by corresponding eigenvalues, so that the ordination distances are the best approximations of original dissimilarities (Borcard *et al.*, 2018; Oksanen *et al.*, 2017). This implementation makes CAP comparable to distance-based redundancy analysis (db-RDA; Oksanen *et al.*, 2017; Borcard *et al.*, 2018). Additionally, permutational multivariate analyses of variance or PERMANOVAs were used to quantify differences in community dissimilarity among forest types (Anderson, 2001). PERMANOVA analysis tests the null hypothesis that the centroids of the four forest types, as defined in the space by the abundance of trees, palms and lianas, are equivalent for all forest types (Anderson & Walsh, 2013). Thus, if null hypothesis were true, any observed differences among the centroids will be similar in size to what would be obtained under random allocation of individual sample units (plots) to the forest types (Anderson, 2001; Anderson & Walsh, 2013). A similarity percentage analysis, SIMPER, was used to decompose the Bray–Curtis dissimilarity and to estimate the contribution in percentage of each species to the average overall dissimilarity (Clarke, 1993). PERMANOVA and SIMPER were performed using the software PRIMER v7 (Clarke & Gorley, 2015).

A variation partitioning analysis was performed to examine the contribution of forest types and geographic distance among the plots to community composition (Bocard *et al.*, 1992; Legendre *et al.*, 2005, 2009). A redundancy analysis (RDA) was performed to determine the proportion of compositional variation explained by forest types and geographical coordinates. We integrated the geographic coordinates directly as explanatory variables in the RDA using trend surface regression methods (Legendre, 1990; Legendre *et al.*, 2005). To elucidate the effect of topography among the three primary forests, we repeated the variation partitioning analyses, first including all forest types and second excluding secondary forests. Significance of each fraction was based on 999 random permutations. Variation partitioning was analyzed with the `varpart` library under the R environment (R Development Core Team, 2018).

Differences in density and species richness among forest types were tested using one-way ANOVAs with site as block variable after testing for data normality. For ANOVA analyses, we used the `stats` library under the R environment (R Development Core Team, 2018).

3.1.5 Results

A total of 11,514 live trees were censused and measured. The 86.91 and 96.06 percent of all individuals were identified at the species and genera level, respectively. A significant part of trees (1.66%) identified at genus, but not at species level, belonged to the diverse genera *Inga* and *Pouteria*. We found a total of 485 species, 280 genera, and 77 families of trees with dbh ≥ 10 cm. Mean tree density was 575.65 ± 20.09 trees/ha (mean \pm SE), with no significant differences among sites and forest types. Mean richness was 96.3 ± 6.0 species/ha (mean \pm SE) and varied significantly among forest types ($df = 3$, $F = 13.64$, $p = 0.0004$) and sites (blocks; $df = 4$, $F = 21.72$, $p < 0.0001$); with the highest richness in slope and ridge primary forests (110.2 ± 12.0 and 103.6 ± 13.6 species/ha, respectively) and the lowest in secondary forests (73.0 ± 9.9 species/ha). No significant differences in mean richness were found among primary forests.

Considering the 20 plots, only 27 species, that is, 5.6 percent of all species, were classified as oligarch species. These oligarch species accounted for 37.4 percent of all individuals. 3.7 percent of species are distributed pantropical, 48.1 percent are widespread in tropical America, 33.3 percent are distributed in Mesoamerica and NW of South America, 7.4 percent are restricted to Mesoamerica, and 7.4 percent are endemics of Costa Rica and Panama (Table 1). In the primary forests, a subset of these oligarch species accounted for 31.3–40.6 percent of local abundance, whereas in the secondary forests, only 8 oligarch species were locally dominant with 22.0 percent of abundance (Figure 1). In the sampled sites, the oligarchs with local dominance showed some variation ranking between 23.6 and 42.8 percent of abundance (Figure 1). Local dominant species that were not classified as regional oligarch species contributed to 7.8–26.5 percent and 9.7–28.0 percent of the abundance across sites and forest types, respectively (Figure 1). The most abundant species was the palm *Iriartea deltoidea* (7.0% of all individuals, Tables 1 and Supporting Information Table S2), which was absent at the Piro site, but attained both the highest mean and maximum of abundance (Table 1). The oligarch *Brosimum guianense* was the unique species that appeared in all the 20 plots. On the other hand, 80.1 percent of the species (392 species) showed a mean density lower than 1 tree/ha and/or a frequency < 25 percent, with 98 species only represented by one individual in all the 20 plots (very rare species). These rare and very rare species contributed to ≈ 45 percent of the total abundance in each forest type (45.9–47.5%; Figure 1a) or site (41.2–46.9%; Figure 1b).

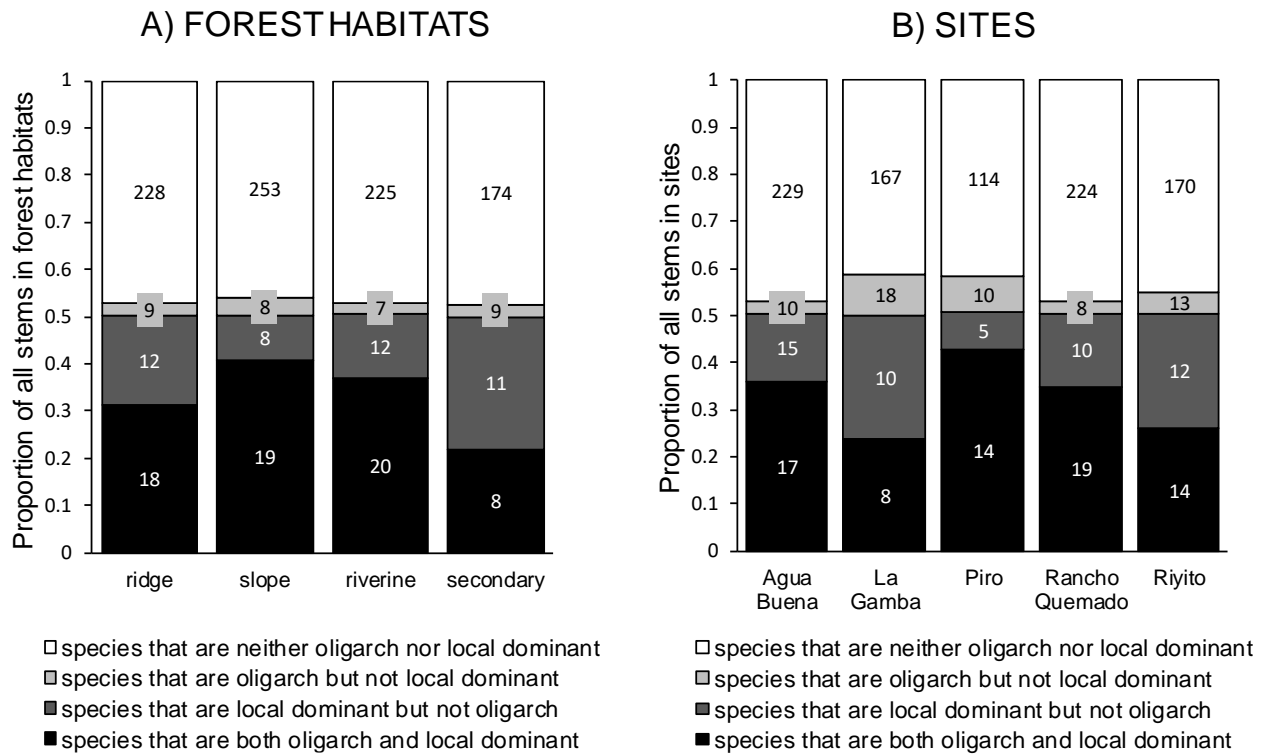


FIGURE 1 Proportions of abundance by forest type and site. (a) Proportions of stems in each forest type belonging to species that are oligarch, local dominant, or neither. (b) Proportions of stems in each forest type belonging to species that are oligarch, local dominant, or neither. Integers show the number of species in each compartment. Local dominants (oligarch or not) are species that contributed to the accumulated 50 percent of individuals encountered at that forest type or site. Oligarch are species that contributed to the accumulated 50 percent of individual in all plots and were present in at least half of the plots.

TABLE 1. List of the 27 most abundant palm and tree species in the study region, SW Costa Rica. Distribution of palms and trees was taken from Cornejo *et al.*, (2012) and www.tropicos.org

Species	Family	Distribution	% of trees	No of sites	No of forest types	No of plots	Mean density per ha \pm SE (max. density)
<i>Iriartea deltoidea</i>	Arecaceae	Widespread in Tropical America	6.97	4	4	16	40.15 \pm 8.84 (148)
<i>Otoba novogranatensis</i>	Myristicaceae	Mesoamerica/ NW South America	2.51	5	4	18	14.45 \pm 3.39 (46)
<i>Compsonera excelsa</i>	Myristicaceae	Costa Rica/ Panama	2.30	5	4	16	13.25 \pm 3.99 (60)
<i>Tetrathylacium macrophyllum</i>	Salicaceae	Widespread in Tropical America	2.08	5	4	18	12.00 \pm 2.09 (36)
<i>Symphonia globulifera</i>	Clusiaceae	Pantropical	1.97	5	4	18	11.35 \pm 2.01 (24)
<i>Carapa nicaraguensis</i>	Meliaceae	Mesoamerica/ NW South America	1.93	5	4	18	11.10 \pm 2.08 (32)
<i>Tapirira guianensis</i>	Anacardiaceae	Widespread in Tropical America	1.72	5	4	17	9.90 \pm 2.66 (41)
<i>Apeiba tibourbou</i>	Malvaceae	Widespread in Tropical America	1.61	5	4	14	9.25 \pm 3.95 (76)
<i>Castilla tunu</i>	Moraceae	Mesoamerica/ NW South America	1.44	5	4	13	8.30 \pm 4.42 (85)
<i>Perebea hispidula</i>	Moraceae	Mesoamerica	1.22	5	4	19	7.00 \pm 1.40 (24)
<i>Vochysia ferruginea</i>	Vochysiaceae	Widespread in Tropical America	1.02	5	4	11	5.85 \pm 2.43 (39)
<i>Socratea exorrhiza</i>	Arecaceae	Widespread in Tropical America	0.99	5	4	16	5.70 \pm 1.43 (24)
<i>Brosimum guianense</i>	Moraceae	Widespread in Tropical America	0.96	5	4	20	5.55 \pm 0.87 (13)
<i>Tetragastris panamensis</i>	Burseraceae	Widespread in Tropical America	0.92	5	4	14	5.30 \pm 1.86 (31)
<i>Sorocea pubivena</i>	Moraceae	Widespread in Tropical America	0.90	5	4	15	5.20 \pm 1.59 (27)
<i>Brosimum lactescens</i>	Moraceae	Widespread in Tropical America	0.86	5	4	16	4.95 \pm 1.50 (23)
<i>Cecropia insignis</i>	Urticaceae	Mesoamerica/ NW South America	0.86	5	4	14	4.95 \pm 1.64 (29)
<i>Chimarrhis parviflora</i>	Rubiaceae	Costa Rica/ Panama	0.83	5	4	11	4.75 \pm 1.45 (21)
<i>Virola sebifera</i>	Myristicaceae	Widespread in Tropical America	0.82	5	4	14	4.70 \pm 1.93 (33)
<i>Chimarrhis latifolia</i>	Rubiaceae	Mesoamerica	0.80	5	4	11	4.60 \pm 2.93 (45)
<i>Pourouma bicolor</i>	Urticaceae	Widespread in Tropical America	0.80	5	4	11	4.60 \pm 3.23 (51)
<i>Pleuranthodendron lindenii</i>	Salicaceae	Mesoamerica/ NW South America	0.77	5	4	14	4.45 \pm 1.98 (35)
<i>Marila pluricostata</i>	Calophyllaceae	Mesoamerica/ NW South America	0.68	4	4	11	3.90 \pm 1.18 (15)
<i>Virola surinamensis</i>	Myristicaceae	Widespread in Tropical America	0.68	5	4	19	3.90 \pm 0.62 (10)
<i>Lacmellea panamensis</i>	Apocynaceae	Mesoamerica/ NW South America	0.64	5	4	15	3.70 \pm 0.82 (14)
<i>Virola koschnyi</i>	Myristicaceae	Mesoamerica/ NW South America	0.58	5	4	18	3.35 \pm 0.57 (9)
<i>Vochysia gentryi</i>	Vochysiaceae	Mesoamerica/ NW South America	0.56	4	4	11	3.20 \pm 0.92 (10)

The Arecaceae family, with 2 oligarch and 3 common species, was the most important component of abundance in our study area (11.1% of all individuals), followed by the Moraceae and the Myristicaceae (Table 2). The Myristicaceae with 5 oligarchs of a total of 8 species was the family with greater proportion of oligarch species. The most diverse family in terms of number of genera and species was the Fabaceae (the fifth most abundant family), showing no oligarch species, but eight common ones.

The dissimilarities among the centroids of the four forest types are shown in the CAP graph, where the two first axes explained 82.6 percent of the variation (Figure 2). PERMANOVA test confirmed statistically significant differences among forest types when all species were considered (df = 16, Pseudo-F = 1.8701, p = 0.003, permutations = 998). When pairwise tests with oligarch species were performed, secondary and ridge forest were the most dissimilar, with mean dissimilarities of 49.8 and 47.6% with the other forest types, respectively (Table 3, Figure 2). For all the species groups, ridge forest showed significant differences with ravine and secondary forest in community composition. Secondary forest also showed significant differences with slope forest (Table 3).

TABLE 2 Contribution of the top ten families to the number of trees, percentage of tree individuals, number of genera and species, as well as number of oligarch and common species. For reference, we also show the ranking of each family in the Amazon basin according to ter Steege *et al.*, (2013)

Family	ranking ¹	No. of trees	% of trees	No. of genera	No. of species	No. of oligarch species	No. of common species
1. Arecaceae	2	1274	11.07	9	9	2	3
2. Moraceae	8	1004	8.72	12	25	5	7
3. Myristicaceae	-	822	7.14	3	8	5	1
4. Malvaceae	5	722	6.27	15	26	1	5
5. Fabaceae	1	712	6.18	28	57	0	4
6. Euphorbiaceae	9	532	4.62	10	16	0	4
7. Clusiaceae	-	481	4.17	6	14	1	5
8. Salicaceae	-	410	3.56	5	13	2	0
9. Vochysiaceae	-	408	3.54	2	5	2	2
10. Meliaceae	-	396	3.44	23	30	2	0

¹This ranking is according to: ter_Steegen *et al.*, (2013)

Variation partitioning analysis showed that both spatial distance (geographical coordinates) and forest types explained significant differences in community composition within forest stands

when all, oligarch and common species were selected (Table 4). When all forest types were considered, spatial and forest types had similar weights in explaining community composition (Table 4). However when only primary forests were considered, spatial distance contributed with most of the explained variation for all species groups, except for oligarch species, where forest type contribution barely changed. Oligarch species was the component of community composition that best responded to spatial and forest type variables, with 42–43% of the explained variation in composition. Overall, the shared explained variation, the environmentally explained variation that is spatially structured, was between 12 and 16% of the total explained variation (Table 4).

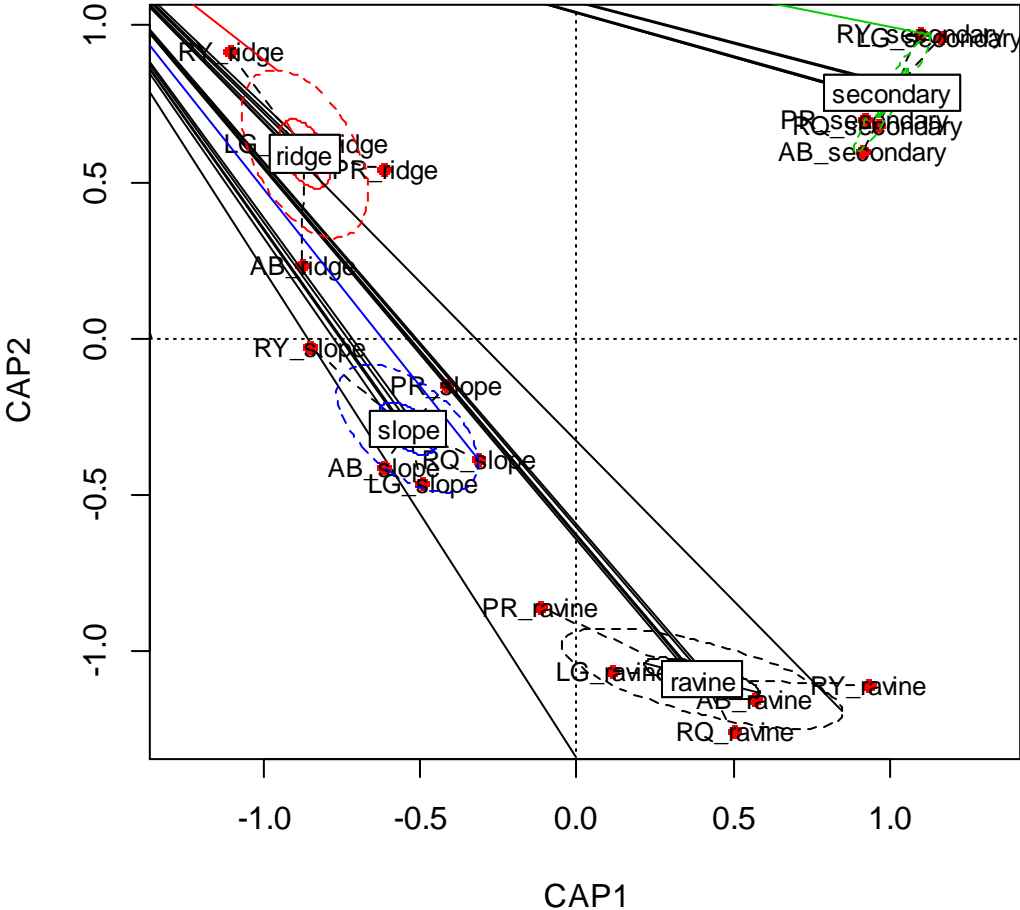


FIGURE 2 Canonical analysis of principal coordinates (CAP) showing the distances among the centroids of each forest type using the abundance data of all identified species. Striped lines of the ellipsoids indicate confidence interval limits at 95% of the centroids. Continuous lines of the ellipsoids indicate standard errors of the centroids. Dots indicate sampled plots. Site codes: AB (Agua Buena); LG (La Gamba); PR (Piro); RQ (Rancho Quemado); RY (Riyito) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Pairwise PERMANOVA tests of dissimilarity among forest types using oligarch, common and rare and very rare species.

Species	Groups	t	P(perm)	Unique permutations	Dissimilarity (%)
Oligarch	ridge/ ravine	1.882	0.043	998	48.63
	ridge/ secondary	1.862	0.008	997	55.08
	ridge/ slope	1.336	0.100	997	39.21
	ravine/ secondary	0.930	0.591	999	44.77
	ravine/ slope	1.146	0.227	999	37.67
	secondary/ slope	1.650	0.011	997	49.56
Common	ridge/ ravine	1.599	0.022	999	73.36
	ridge/ secondary	2.156	0.012	999	81.54
	ridge/ slope	0.652	0.903	999	56.05
	ravine/ secondary	1.280	0.090	999	67.80
	ravine/ slope	1.274	0.089	999	67.50
	secondary/ slope	1.928	0.007	998	76.36
Rare and very rare	ridge/ ravine	1.207	0.033	999	89.86
	ridge/ secondary	1.304	0.009	998	94.09
	ridge/ slope	0.846	0.872	998	82.91
	ravine/ secondary	1.061	0.282	999	90.66
	ravine/ slope	1.029	0.343	999	87.70
	secondary/ slope	1.209	0.010	999	93.38

When oligarch species were used to identify the composition of ridge forests characteristic species were *Compsonera excelsa*, *Symphonia globulifera*, *Tapirira guianensis*, *Vochysia ferruginea* and *Pourouma bicolor* (Supporting Information Tables S1 and S2), whereas in ravine forest, *Otoba novogranatensis*, *Chimarrhis parviflora*, *Pleuranthodendron lindenii* and *Tetrathylacium macrophyllum* were the characteristic oligarch tree species (Supporting Information Tables S1 and S2). Although *I. deltoidea* was a common species in all forest types, it showed especially high abundance in the slope forest (Supporting Information Table S2). In fact, slope showed low dissimilarity with both ridge and ravine forests (Figure 2, Table 2) sharing high abundances of oligarch tree species such as *C. excelsa*, *S. globulifera*, *O. novogranatensis*, *T. macrophyllum*, *C. parviflora*, and *Sorocea pubivena*, in addition to *I. deltoidea*. Secondary forests were characterized by a lower number of oligarch species, such as *Apeiba tibourbou*, *Castilla tunu*, and *T. macrophyllum* (Supporting Information Tables S1 and S2).

TABLE 4 Variation partitioning analysis of community composition for all the species groups. Two variables were considered spatial (geographical position) and forest type. Shared variation is the amount of explained variation by forest type that is spatially structured. (a) All forest and (b) only primary forest types (excluding secondary).

	Variation explained (%)	All species	Oligarch	Common	Rare/very rare
(a) All forest types	Spatial	14.07	19.84	14.32	10.34
	F	2.727	3.820	2.780	1.680
	<i>p</i> (perm)	0.001	0.003	0.001	0.001
	Forest	11.56	15.76	18.45	3.75
	F	2.103	2.970	2.464	1.120
	<i>p</i> (perm)	0.001	0.001	0.030	0.215
	Shared	4.83	7.08	5.64	2.90
	Residual	69.54	57.32	61.59	83.01
(b) Only primary forests	Spatial	16.28	19.15	17.49	13.00
	F	2.534	3.820	2.650	1.680
	<i>p</i> (perm)	0.001	0.001	0.002	0.003
	Forest	5.67	16.15	7.52	1.04
	F	1.780	2.940	1.726	1.126
	<i>p</i> (perm)	0.017	0.003	0.04	0.195
	Shared	4.81	8.33	5.30	2.98
	Residual	73.23	56.37	69.68	82.98

3.1.6 Discussion

3.1.6.1 *Beta diversity and differentiation of community composition*

In tropical forests, changes in diversity of species assemblages across space have been explained by two main mechanisms that spatially structure tree species composition: a) the species-specific response to variation in environmental conditions across gradients or mosaics and b) the dispersion limitation of propagules over short distances (Harms *et al.*, 2001; Legendre *et al.*, 2005, 2009; Tuomisto & Ruokolainen, 2006). Although both mechanisms are not mutually exclusive, their relative contribution varies with spatial extent (de Cáceres *et al.*, 2012). At very local scales (<0.5 ha), neutral processes dominate community composition due to seed dispersal limitation leading to clumped structure of populations, whereas environmental factors linked to topographic and edaphic variation are more relevant with increasing plot size (de Cáceres *et al.*, 2012; Legendre *et al.*, 2009). However, at the landscape level, some studies have shown that geographical distance is the most important factor explaining composition dissimilarity due to dispersion constrains (Chain-Guadarrama *et al.*, 2012; Condit *et al.*, 2002; Duque *et al.*, 2009; Svenning *et al.*, 2004), whereas other studies have shown that this relationship loses significance when environmental factors are included (López-Martínez, Hernández-Stefanoni, Dupuy & Meave, 2013; Prada & Stevenson, 2016; Sesnie *et al.*, 2009). Our results show that both spatial

distance and environmental variation explain similar amounts of variation in species composition among tropical lowland forest types (Table 4). When secondary forests are excluded from analyses, forest type loses importance in explaining the variation in the dataset, highlighting the effect of successional status on forest species composition (Table 4). However, oligarch species were not affected by successional status and showed always the highest amount of variation explained in species composition (42–44% of total variation, Table 4), in response to both spatial and environmental variables. Topography is considered an indirect environmental variable, summarizing the observed match between species distribution and some environmental variables, as topographic features are correlated with soil drainage, water availability, soil depth, and nutrient availability, among others (de Cáceres *et al.*, 2012; Legendre *et al.*, 2009). Part of the residual variation is likely explained by environmental variables not assessed by our work, for instance, soil variables not related to topography (Baldeck *et al.*, 2013; Chain-Guadarrama *et al.*, 2012; Prada & Stevenson, 2016; Qiao *et al.*, 2015). Among primary forests, the greatest difference in community composition was between ridge and ravine forests. Slope forests represent a gradual change in community composition from more exposed hilltops on ridges to the bottom of the stream terraces and thus showed some similarities in species composition with both ridge and ravine forests.

Oligarch species have been reported to have relatively wider niche breadth than common species (Arellano *et al.*, 2014) and in our study were present in most of the plots (64% of oligarchic are present in at least 75% of all the plots), so differences in beta diversity of oligarch species among forest types were mainly attributed to differences in oligarchic abundance, rather than species identity. Wider niche breadth does not mean that oligarchic species can be defined as habitat generalists, conversely many of them can be considered as species with strong preferences for one or two types of habitats where they attain the highest abundances (Pitman, Terborgh, Silman & Núñez, 1999; Pitman *et al.*, 2013; ter Steege *et al.*, 2013). Only a few oligarch species, like *B. guianense*, *Virola koschnyi* or *V. surinamensis*, appeared as generalist species that barely contributed to the differentiation among the forest types (Supporting Information Table S1) and attained regionally high abundances with relatively local low densities in primary forests (Table 1). Conducting taxonomic complete (or almost complete) inventories in tropical forest ecosystems is a highly laborious and arduous task due to technical (climbing to get adequate plant samples) and taxonomic (uncomplete or partial knowledge of the tropical flora) problems (Balakrishnan, 2015; Gentry, 1988; ter Steege *et al.*, 2013). Oligarchic species are likely less susceptible to misidentification issues due to greater abundance (ter Steege *et al.*, 2013), allowing more confident characterization of beta diversity along environmental gradients (Arellano *et al.*, 2016).

All groups of species investigated allowed discrimination of secondary from ridge and slope forests. Gradual change from pioneer to late successional species is the most obvious explanation of differences in community composition, as secondary forests showed many oligarchic (*A. tibourbou*, *Castilla tunu* and *Cecropia insignis*), common (e.g., *Goethalsia meiantha*, *Hieronyma alchorneoides*, *Alchornea costaricensis*), and rare (e.g., *Hampea appendiculate*, *Margaritaria nobilis*) species with the typical pioneer habit (Clark & Clark, 2001; Gilman *et al.*, 2016; Guariguata, Chazdon, Denslow, Dupuy & Anderson, 1997; Healey & Gara, 2003; McClellan, Montgomery, Nelson & Becknell, 2018; Peña-Claros, 2003; Vandermeer, de la Cerda & Boucher, 1997; Wood, Lawrence & Wells, 2001). In contrast, secondary and ravine forests showed low dissimilarity in oligarch species composition. Although differences were not strictly significant ($p < 0.1$, Table 3), common species were better suited to differentiate secondary and ravine forests, due to the high abundance of pioneer species in secondary forest, such as *A. costaricensis*, *G. meiantha*, *Guatteria chiriquiensis*, *H. alchorneoides*, and *Spondias radlkoferi* (Supporting Information Table S1; Lieberman, Lieberman, Hartshorn & Peralta, 1985; Vandermeer *et al.*, 1997; Wood *et al.*, 2001; Healey & Gara, 2003; Peña-Claros, 2013; Gilman *et al.*, 2016).

3.1.6.2 Characterization of forest types with oligarch species

Slope and ravine forests showed the lowest dissimilarity in oligarch species composition due to the dominance of the two most abundant species that also most contributed to the differentiation from the ridge forest: *I. deltoidea* and *O. novogranatensis*. The palm *I. deltoidea* is also one of the most abundant plant species in the neotropics (Arellano *et al.*, 2014; Pitman *et al.*, 2001; Ruokolainen & Vormisto, 2000; ter Steege *et al.*, 2013). This species is ubiquitous in the sub-canopy domain, found across many soils and forest types (Clark, Clark, Sandoval & Castro, 1995; Ruokolainen & Vormisto, 2000), but is negatively affected by flooding in poorly drained habitats (Losos, 1995). Being considered a late successional species (Guariguata *et al.*, 1997), *I. deltoidea* is also found in secondary forests (Losos, 1995). Although *I. deltoidea* was common in all our forest types (Supporting Information Table S2), it was especially abundant in the steep slope and ravine plots, as demonstrated in another study in the same region (Huber, 2005). Stilt roots in palms such as *I. deltoidea* have shown to allow rapid height growth without loss of stability on steep slopes, allowing the early exploitation of light gaps (Avalos, Salazar & Araya, 2005; Dransfield, 1978; Hartshorn, 1983; Swaine, 1983), a factor that strongly limits *I. deltoidea* abundance at the seedling stage, but not at the mature palms (Svenning, 1999). On the other hand, *O. novogranatensis* is associated to moist but well-drained soils in low altitude locations (Lieberman *et al.*, 1985). Although *O. novogranatensis* is considered a late successional mid-canopy tree (Cole, Holl, Keene & Zahawi, 2011), it was relatively common in almost all our

secondary plots, and it was shown that the large-seeded tree *O. novogranatensis* can be successfully introduced into early stages of succession (Cole *et al.*, 2001).

The oligarchs *C. excelsa* and *S. globulifera*, that are common in both ridge and slope forests with moderate to high densities, exemplify contrasting life-history traits and biogeographic patterns. *Compsonera excelsa*, a mid-canopy tree (up to 25-m height in our study sites) with unknown ecology, is an endemic species restricted to the very humid forests of Costa Rica and west Panama (Cornejo *et al.*, 2012; Jiménez, 2007). *Symphonia globulifera*, in contrast, has an exceptionally large geographic distribution from Mexico to Brazil and also occurs in tropical West Africa. It grows in a range of habitats, from swamps (van Andel, 2003; Scarano, Ribeiro, de Moraes & de Lima, 1997) to flat plateaus and well-drained sites (Carneiro, Sebbenn, Kanashiro & Degen, 2007; Hartshorn, 1983), which has led some authors to suggest that what is treated as a single species may in fact be at least two species distinguished by morphological and ecological features (Loubry, 1994). In our plots, *S. globulifera* is a tree of the upper canopy (up to 46 m height), which contrasts with data from other studies where it was usually considered a sub-canopy tree (Hammel, 1986; Gill, Fowler & Mori, 1998; but see Hartshorn, 1983). Nonetheless, only a few oligarch species, *V. ferruginea* and *P. bicolor*, contributed to the differentiation of the community composition of the ridge plots. *Vochysia ferruginea* showed high abundance on ridges in other studies in the Golfo Dulce region (Huber, 2005) and interestingly was also an abundant species recorded in secondary forests (Guariguata *et al.*, 1997; Letcher & Chazdon, 2009; Wood *et al.*, 2011), as was also corroborated by our study. Snapping due to wind exposure and clumps of standing dead trees after lightning storms are very common disturbances on ridges (Gale 2006, Weissenhofer, 2005), likely creating recruitment opportunities for *V. ferruginea*, which rapidly grow into canopy gaps via a gap mode of regeneration (Vandermeer *et al.*, 1997).

Secondary forests showed the lowest species richness, as is common in tropical forests (Guariguata *et al.*, 1997; Peña-Claros, 2013), with stem abundance strongly dominated by pioneer tree species. Only three typical pioneer species are so frequent to be considered as oligarchs: *A. tibourbou*, *Castilla tunu*, and *C. insignis*. These species usually are present in the tree inventories of secondary but also in primary forests (Clark & Clark, 2001; Li, Aguilar & Berkov, 2017; Oliveira-Filho, Curi, Vilela & Carvalho, 1998), with juvenile stages associated with canopy gaps (Clark & Clark, 2001). Only some tree species characteristic of primary forest (Cole *et al.*, 2001; Webb, 1999) such as *T. macrophyllum*, *Carapa nicaraguensis*, and *O. novogranatensis* were able to recruit in significant numbers in these secondary forests.

3.1.7 Conclusions

Tropical tree and palm species responded to topographic variation among tropical lowland forest stands, thus contributing to variation in beta diversity across the landscape. Although secondary forest species composition was well reflected by common species, characterization of tropical primary forests was best captured by oligarch species composition as these species showed the greatest response to spatial and environmental variables. The ubiquity of oligarchic patterns in neotropical plant communities has led to the powerful concept of hyperdominance to study and model important ecosystem functions, such as carbon storage and productivity, nutrient cycling and trophic interactions by focusing on a subset of species (Fauset *et al.*, 2015; ter Steege *et al.*, 2013). Our results corroborate the utility of the hyperdominance concept and extend the concept to the analysis of beta diversity allowing for characterization of hyperdiverse forest communities across tropical landscapes.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6d8p7j1> (Morera-Beita *et al.*, 2019).

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SUPPORTING INFORMATION (See Appendices)

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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