

Diversity and composition of tropical forest plant communities in the Golfo Dulce region

Florian HOFHANSL, Eduardo CHACÓN-MADRIGAL, Albert MORERA, Fernando SILLA, Werner HUBER, Anton WEISSENHOFER & Wolfgang WANEK

The Golfo Dulce region located in southwestern Costa Rica represents one of the remnant global biodiversity hotspots containing the largest Pacific lowland tropical forest in Central America. Recent biogeographical analyses revealed a close relation of taxonomic tree species composition to northern South America. However, the underlying factors leading to the extraordinary taxonomic richness of the region have so far remained elusive. In this study, we analyzed the composition of tropical forest plant communities (trees, lianas and palms with a diameter at breast height ≥ 10 cm) occurring in one-hectare permanent forest inventory plots. To that end, we established 20 forest sites across the Golfo Dulce region, i.e. 5 geographic locations each comprising 4 forest habitat types in ridge, slope and ravine positions, as well as in secondary forest stands. Our study highlights the oligarchic dominance of tropical forest plant communities in the Golfo Dulce region, and further suggests that plant species composition is associated with topography, disturbance history and edaphic properties. The finding that oligarchic and rare species are affected by environmental filtering has important implications for assessment and modeling of important ecosystem functions, such as carbon storage and productivity, as well as nutrient cycling and trophic interactions and thus could potentially improve biodiversity conservation and management strategies.

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Die Golfo Dulce-Region im Südwesten von Costa Rica ist einer der letzten globalen Biodiversitäts-Hotspots mit dem größten verbliebenen tropischen Wald im pazifischen Tiefland in Mittelamerika. Jüngste biogeografische Analysen der taxonomischen Baumartenzusammensetzung zeigten eine enge Beziehung zu den Pflanzengesellschaften Südamerikas. Die zugrundeliegenden Faktoren, die zu dem außerordentlichen taxonomischen Reichtum der Region führten, sind jedoch bislang schwer fassbar. In dieser Studie haben wir die Zusammensetzung der tropischen Vegetation (Bäume, Lianen und Palmen mit einem Durchmesser in Brusthöhe ≥ 10 cm) auf 20 Inventarflächen von jeweils 1 ha Größe (5 geografische Standorte mit jeweils 4 Habitatstypen in Kamm-, Hang- und Schlucht-Position, sowie einem Sekundärwald) analysiert. Unsere Studie beschreibt die Dominanz häufiger tropischer Pflanzenarten und legt nahe, dass die Zusammensetzung der Vegetation mit der Topographie, der Störungsgeschichte und den edaphischen Eigenschaften zusammenhängt. Die Feststellung, dass die Zusammensetzung von sowohl häufig vorkommenden als auch eher seltenen, Großteils endemischen Arten von denselben Umweltfaktoren beeinflusst wird, birgt interessante Erkenntnisse über wichtige Ökosystemfunktionen wie die Kohlenstoffspeicherung und die Produktivität des Ökosystems und könnte somit helfen Strategien zur Erhaltung und Bewirtschaftung der Artenvielfalt in tropischen Ökosystemen zu entwickeln.

Keywords: Biodiversity, biogeography, Costa Rica, Golfo Dulce, tropical plant communities.

Introduction

Tropical forest ecosystems typically persist on strongly weathered nutrient-poor soils but comprise high species richness and store large amounts of carbon. Hence, tropical forest ecosystems provide crucial ecosystem functions, such as carbon sequestration from the

atmosphere via plant carbon metabolism (DUSENGE et al. 2018). However, despite their global importance in mitigating global warming, tropical ecosystems are still increasingly exploited by human activities, such as deforestation and logging, to support the increasing demands of global populations (Barlow et al. 2018). It is therefore of the utmost importance to understand how these important ecosystems function in order to derive and implement management plans that succeed in maintaining crucial ecosystem processes under projected future scenarios, while concomitantly providing ecosystem functions, such as continuous extraction of food and timber under realistic socioeconomic pathways.

Tropical tree communities are characterized by high species richness, often surpassing 100 species per hectare (VALENCIA et al. 1999). What drives this exuberant diversity has been a matter of scientific debate, but in general the number of co-occurring species depends on the number of available niches determined by local environmental factors, such as climate, parent material, topography and soil type (JUCKER et al. 2018). A structurally diverse environment was found to increase the available niche space and thereby enable a high diversity of co-occurring biota (FIGUEIREDO et al. 2018). As a result, distinct floristic communities with distinct functional properties may emerge on different parent material and soil types (PRADA & STEVENSON 2016). Both species diversity and taxonomic composition of tropical plant communities might therefore differ in association with geological substrate and topographic factors by affecting the availability of resources, such as light, water and nutrients along environmental gradients.

Topography strongly influences local-scale variability in soil chemistry, hydrology and microclimate (WERNER & HOMEIER 2015, JUCKER et al. 2018) thus being one of the main factors determining species-habitat associations in tropical forests (ZULETA et al. 2018). Due to subtle differences in elevation controlling soil chemistry and hydrology, such environmental filtering was found to profoundly influence forest-level patterns of community assembly by affecting diversity and composition of tropical tree communities (JUCKER et al. 2018). Furthermore, more diverse communities should have the potential to exploit available resources more efficiently due to niche complementarity and positive species interactions (TILMAN 1999). Therefore, it has been proposed that biodiversity positively affects ecosystem functioning in hyperdiverse tropical forests (POORTER et al. 2015). However, because a high proportion of biodiversity in tropical regions stems from closely related species, species diversity is not proportional to functional diversity (Safi et al. 2011), but higher levels of functional diversity imply larger numbers of functional types and therefore a greater breadth of functional response-spectra to climatic signals. Hence, it might not necessarily be species diversity of a location but rather species composition in a given environment, and particularly the functional composition of a given community, that will determine ecosystem functioning under future scenarios of projected environmental changes.

In this case study we examined tropical tree communities growing on nutrient-poor soils in a topographically heterogeneous environment located in southwestern Costa Rica. The study region is located in the largest remaining tropical rainforest in the Pacific lowlands of Central America (GILBERT et al. 2016), and constitutes one of the remnant global biodiversity hotspots. The region therefore is especially suited for studying biodiversity and species composition of tropical plant communities. We compiled a unique dataset comprising 10,007 individuals and 485 species recorded in twenty one-hectare permanent inventory plots established across five sites (differing in climate, parent material and soil type), each

one comprising four forest habitat types (differing in topographic position and disturbance regime). Based on this set-up we investigated the following hypotheses: (1) Plant species richness varies between sites, along spatial gradients in climate, soil parent material, landform and soil types; (2) plant species composition varies between forest habitat types, in association with local topography and disturbance regime and thus; (3) the abundance of hyperdominant plant species varies in relation to habitat preference among co-occurring plant species distributed across the Golfo Dulce region.

Material and Methods

The study was conducted in tropical lowland forests located between 50 and 450 m a.s.l. in the Área de Conservación Osa (ACOSA) at the Pacific slope of southwestern Costa Rica (08.6°N, 83.2°W). The region is considered a “hot spot” of biodiversity with 700 tree species among 2,369 species of ferns, fern allies and flowering plants recorded in total (QUESADA *et al.* 1997). The terrain is characterized by parent material originating from the Cretaceous, Tertiary and Quaternary (i.e. basalt, alluvium and sediment) and is divided into six different landforms (i.e. denudational, volcanic, alluvial, structural, littoral, tectonic) and four soil orders, i.e. Entisols, Inceptisols, Mollisols and Ultisols (LOBO 2016). The dominating, highly weathered, strongly acidic Ultisols on ridges and upper slopes are replaced by younger, moderately weathered Inceptisols in ravines and lower slopes and little-developed Mollisols in fluvial deposits (LOBO 2016). Daily climatologic data for temperature and precipitation (starting in 1997) are available from La Gamba field station; <https://www.lagamba.at/en/tropical-field-station/scientific-data-of-the-golfo-dulce-region/>. Mean annual precipitation for the period 1998–2017 accounted for 5892 mm with no month receiving less than 180 mm on average. The rainy season lasts from April to December, the driest months are January to March. Mean annual temperature for the period 1998–2017 was 28.0°C and ranged between 23.7°C and 33.7°C.

Study plot locations were selected based on a stratified sampling design (CLARK & CLARK 2000), i.e. the set of ecosystem types to be studied was pre-selected upon a thorough evaluation of the relative spatial contribution of different ecosystem types in the ACO-SA region. Dominant regional ecosystem types are broad-leaved evergreen well-drained lowland forests (38.3 %), dense tropical evergreen well-drained lowland (woody) herbland dominated by graminoids (pastures) (22.0 %) and dense tropical broad-leaved evergreen well-drained lowland shrubland with early to late successional re-growth (9.7 %). The old-growth lowland forests stock on narrow ridges (3.2 %), steep slopes (94.0 %) and valleys (2.8 %) passed by streams and small rivers (WEISSENHOFER *et al.* 2008). To account for the spatial variability of climate, parent material and soil types, permanent forest inventory plots were installed in replicates across five sites, i.e. La Gamba (LG), Riyito (RY), Agua Buena (AB), Rancho Quemado (RQ), and Piro (PR), each comprising four plots: three plots of old-growth forest in habitat types differing in topographic position, i.e. forest stands in hilltop (ridge), intermediate (slope) and valley bottom (ravine) positions and one plot in secondary re-growth forest stands. Plots were of 1-ha in size and subdivided into subplots of 10 × 10 m following the standards of ALDER & 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 ravine forest plots where subplots were situated along the small streams and adjacent terraces. For further information and an interactive map showing respective locations of forest plots includ-

ing numbers of surveyed tree individuals and identified taxonomic species please visit <http://www.univie.ac.at/bdef/>.

Plant species were identified in the field (Eduardo Chacon) and, where direct ID in the field was not possible, samples were collected for taxonomic identification and deposited in the herbarium of the Biology School of the University of Costa Rica (USJ, acronym). The number of species analyzed in this study was 485 species of trees, palms and lianas from a total of 11,786 individuals with a diameter at breast height ≥ 10 cm, of which only 11,514 represented live trees, 272 dead trees, and around 86 % were identified to species level (96 % at genus level), thus representing 10,007 individuals analyzed subsequently. Plot survey and data collection involved all live stems from individuals with a diameter above breast height larger than 10 cm (DBH ≥ 10 cm at 1.3 m), thus representing 485 species, 280 genera and 77 families of trees, palms and lianas recorded in the 2012–2015 census interval. To compare the diversity of species between locality and forest habitat types we used rarefaction analysis of Hill numbers based on the abundance of species (Hill 1973). We estimated the diversity of Hill numbers of order 0, 1 and 2, which represent the richness (number of species), the effective number of rare species and the effective number of abundant species (Hsieh et al. 2016), respectively. For each forest site we estimated the

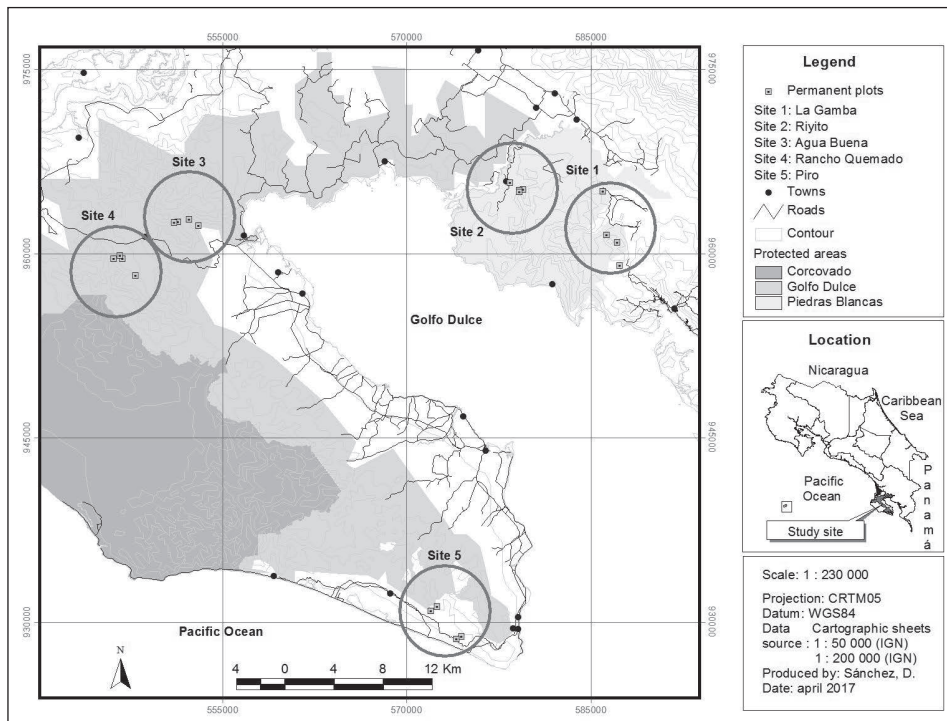


Fig. 1: Map of the study region showing the distribution of permanent plots surveyed per geographic location i.e. Site 1: La Gamba; Site 2: Riyito; Site 3: Agua Buena; Site 4: Rancho Quemado; Site 5: Piro, situated across the Golfo Dulce region in southwestern Costa Rica. – Abb. 1: Karte des Untersuchungsgebiets in der Golfo Dulce Region im Südwesten von Costa Rica inkl. Verteilung der geografischen Standorte, d. H. Standort 1: La Gamba; Standort 2: Riyito; Standort 3: Agua Buena; Standort 4: Rancho Quemado; Standort 5: Piro.

diversity by extrapolation using rarefaction analysis to 3,500 individuals per site and for forest habitat type we estimated the richness by extrapolation using rarefaction analysis to 1,000 individuals for each forest habitat type in each site. Variation in species composition among forest plots was assessed using hierarchical cluster analysis and non-metric multi-dimensional scaling (NMDS) based on a double-standardized, square root-transformed species abundance Bray–Curtis dissimilarity matrix. To assess the relationships between tropical forest plant community composition, environmental variables and geographic distance we correlated the respective matrices of species composition, environmental variation and a matrix of three-dimensional Euclidean geographic distances calculated from GPS coordinates. Based on these parameters we performed variation partitioning among factors controlling variation of plant community composition (i.e. beta diversity) among twenty 1-ha permanent inventory plots established in the Golfo Dulce region, Costa Rica (Fig. 1).

Results and Discussion

Species richness (alpha diversity) of rare and abundant tropical plants

Tropical forests are characterized by extraordinary species richness, however, less is known about variation in species richness between rare and abundant species. We found that alpha diversity (species richness) varied throughout the study region (Fig. 1). However, while some regions, such as Rancho Quemado and Agua Buena, had high species richness with over 300 estimated species, other regions, such as Piro, hardly reached 200 estimated species based on extrapolation using rarefaction analysis (Fig. 2). Since all sites showed similar diversity of abundant species, the variation in alpha diversity was mainly due to differences in the number of rare species (Fig. 2). Within each region, plots in

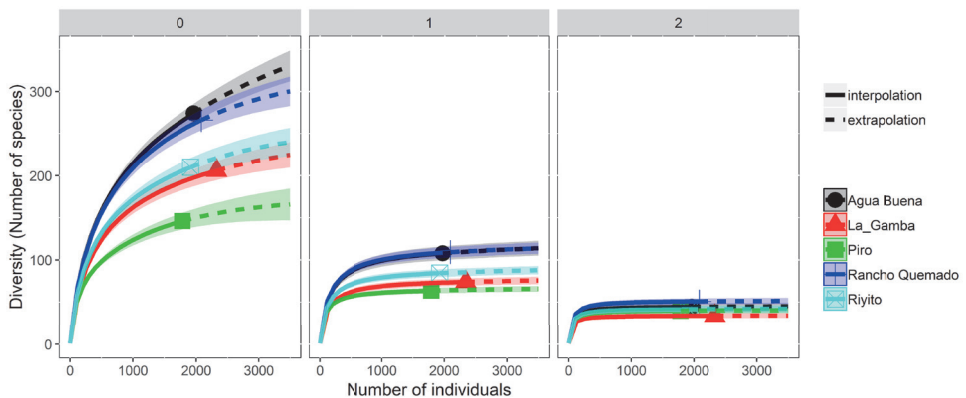


Fig. 2: Rarefaction analysis using Hill's numbers (0, 1, and 2) of the tree species by locality. The Hill's number 0 represents the species richness, the Hill's number 1 represents the effective number of rare species and the Hill's number 2 represents the effective number of abundant species. The solid lines represent the interpolation with the observed data and the dotted lines represent the extrapolation to 3,500 individuals. Shaded areas represent 95% confidence intervals. – Abb. 2: Rarefaction-Analyse unter Verwendung der Hill-Zahlen (0, 1 und 2). Die Zahl 0 steht für den Artenreichtum der Baumarten nach Lokalität, die Zahl 1 für die effektive Anzahl seltener Arten und die Zahl 2 für die effektive Anzahl häufig vorkommender Arten. Die durchgezogenen Linien repräsentieren die Interpolation mit den beobachteten Daten und die gepunkteten Linien repräsentieren die Extrapolation auf 3.500 Individuen. Schattierte Bereiche repräsentieren 95 % Konfidenzintervalle.

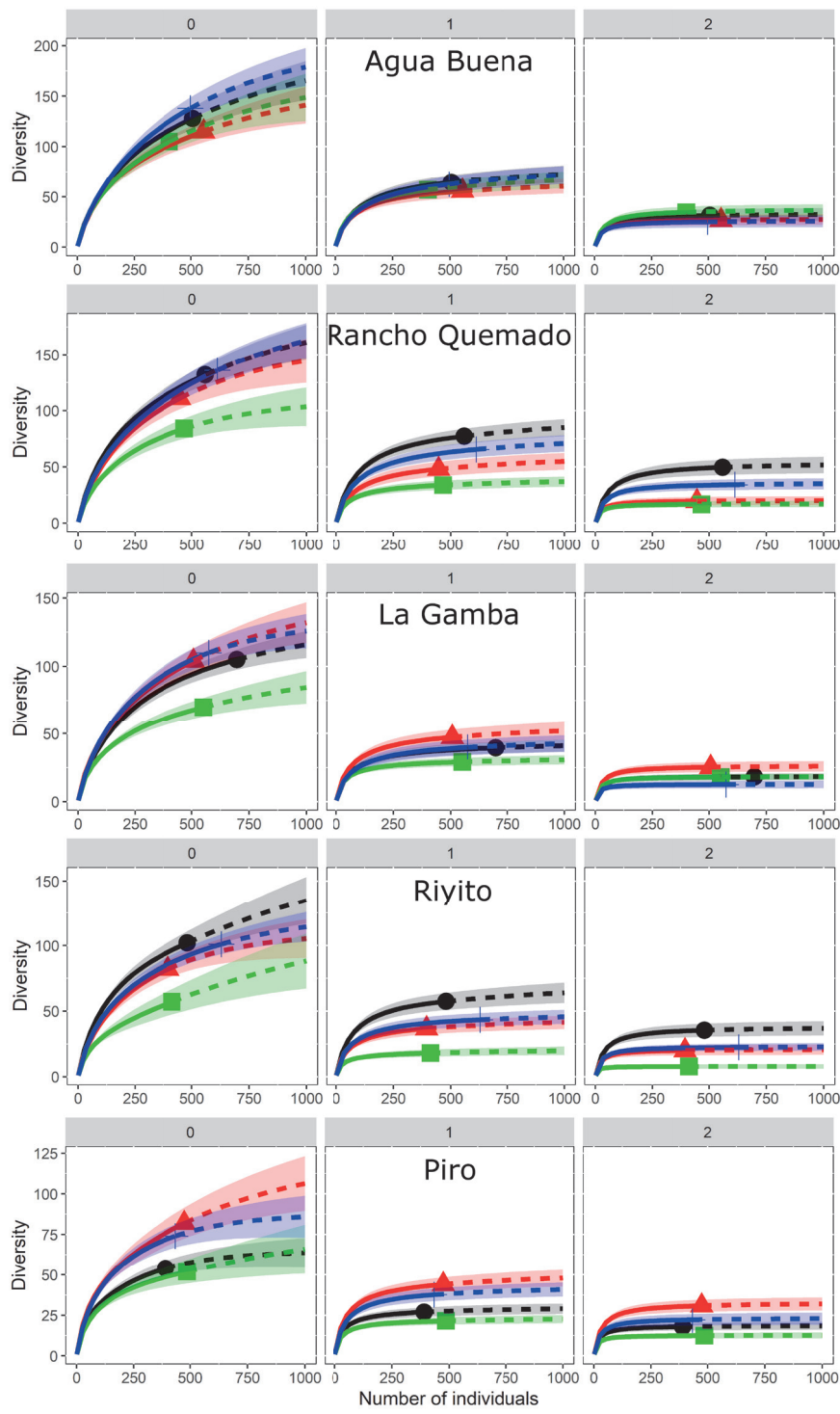


Fig. 3: Rarefaction analysis using Hill's numbers (0, 1, and 2) of the tree species by forest habitat type and locality. The Hill's number 0 represents the species richness, the Hill's number 1 represents the effective number of rare species and the Hill's number 2 represents the effective number of abundant species. The solid lines represent the interpolation with the observed data and the dotted lines represent the extrapolation to 3,500 individuals. Shaded areas represent 95% confidence intervals. – Abb. 3: Rarefaction-Analyse unter Verwendung der Hill-Zahlen (0, 1 und 2). Die Zahl 0 steht für den Artenreichtum der Baumarten nach Lebensraumtyp und Standort, die Zahl 1 für die effektive Anzahl seltener Arten und die Zahl 2 für die effektive Anzahl häufig vorkommender Arten. Die durchgezogenen Linien repräsentieren die Interpolation mit den beobachteten Daten und die gepunkteten Linien repräsentieren die Extrapolation auf 3.500 Individuen. Schattierte Bereiche repräsentieren 95% Konfidenzintervalle.

— interpolation
 ···· extrapolation

● Ridge Primary Forest
 ▲ Riverine Primary Forest
 ■ Secondary Forest
 ■ Slope Primary Forest

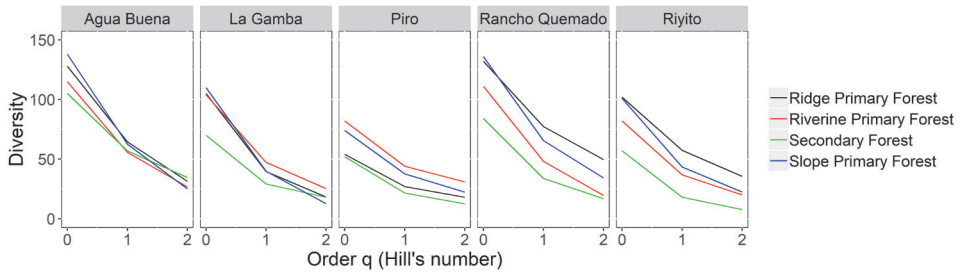


Fig. 4: Diversity of tree species observed for each Hill's number (0, 1, 2) in each locality and for each forest habitat type. The Hill's number 0 represents the species richness, the Hill's number 1 represents the effective number of rare species and the Hill's number 2 represents the effective number of abundant species. – Abb. 4: Diversität der Baumarten für die jeweilige Hill-Zahl (0, 1, und 2). Die Zahl 0 steht für den Artenreichtum der am jeweiligen Ort und für den jeweiligen Lebensraumtyp beobachtet wurden, die Zahl 1 für die effektive Anzahl seltener Arten und die Zahl 2 für die effektive Anzahl häufig vorkommender Arten.

secondary forest stands exhibited lower species diversity compared to old-growth forest plots (Fig. 3). However, this difference was less pronounced when only abundant species were considered (Fig. 3). Among old-growth forest stands within each region, there was no clear pattern of a particular forest habitat type association; however, the contribution of rare species to overall species diversity was higher for old-growth forests in slope position and lower for secondary forest stands (Fig. 4). The low alpha diversity and low contribution of rare species in more disturbed re-growth forest stands is likely a result of high colonization rates of opportunistic fast-growing species, taking advantage of high-light environments and thus attaining relatively high abundances. In contrast, high contribution of rare species to overall diversity in old-growth forests (especially in slope position) likely results from the fact that slope forests are situated between uphill ridges and downslope ravines, thus differing in edaphic properties and taxonomic species composition. Similar associations between rare species and edaphic conditions have been previously reported for other tropical regions (LAURANCE et al. 2010). Hence, our results indicate that the contribution of rare and abundant species to alpha diversity is affected by geological, topographic, and edaphic factors, as well as natural and anthropogenic disturbance regimes that in turn shape the distribution of species and determine the heterogeneity of habitats in the Golfo Dulce region.

Species composition (beta diversity) among forest plots

In tropical forest ecosystems the diversity of species assemblages across space and time has been explained by various theories (HUBBELL 1979, TILMAN 1999). Nonetheless, due to the spatial dependence of factors controlling plant species composition along environmental gradients, it might be impossible to separate contrasting theories explaining the high level of species co-existence in tropical forests (WRIGHT 2002, CHAVE 2004, CHISHOLM et al. 2013, CHASE 2014). While on a larger spatial scale intraspecific variability and functional equivalence of tropical plant species would indicate that species richness is maintained as a balance between immigration and extinction of species (HUBBELL 1979, GARZON-LOPEZ et al. 2014), on a smaller local-scale specialization of species to particular environmental conditions may better explain the co-existence and distribution of tropical tree commu-

nities (BROWN et al. 2013). Despite the fact that these theories emphasize different processes contributing to the maintenance of species diversity at the landscape-scale (QIAO et al. 2015), we found both significant effects of spatial distance and environmental factors (i.e. climate, parent material, soil type) on plant species composition across nearby lowland forest plots (Fig. 5). Our results suggest that both biotic and abiotic factors shape floristic community composition at the landscape-scale. Although residual variation was high (66 % unexplained variance), environmental factors, such as climate (4 %), soil type (6 %), parent material (11 %), and spatial autocorrelation (13 %) explained up to one third of the variation in species composition among lowland forest stands (Fig. 5). Similar levels of spatial autocorrelation have been observed by other authors in foregoing studies and have been attributed to multiple processes regulating forest structure and plant species composition across environmental gradients at the landscape-scale (e.g. TAYLOR et al. 2015). Furthermore, PRADA & STEVENSON (2016) reported that distinct floristic communities emerged on different parent materials and soil types, such that taxonomic species composition of tropical tree communities differed in association with topographic factors. Based on differences in geological substrates and soil types described across the Golfo Dulce region, we hypothesized that floristic community composition varies in relation to regional differences in geomorphology, topography and climate. Indeed, we found that each region, i.e. La Gamba, Riyito, Agua Buena, Rancho Quemado and Piro, exhibited its unique floristic community composition. For instance, whereas La Gamba was characterized by a high abundance of palms (33 % Arecaceae), Piro exhibited only a very small proportion of palm species (4 % Arecaceae) but much higher percentage of tree species (Fig. 6). Hence, our findings of regionally variable taxonomic composition might indicate that both large-scale abiotic factors (i.e. geomorphology, topography, climate) as well as local biotic processes (i.e. competition, dispersal, stochastic events of colonization and extinction) influence taxonomic community composition at the landscape-scale (CONDIT et al. 2002) and thus contribute to the extraordinary plant species richness of the Golfo Dulce region.

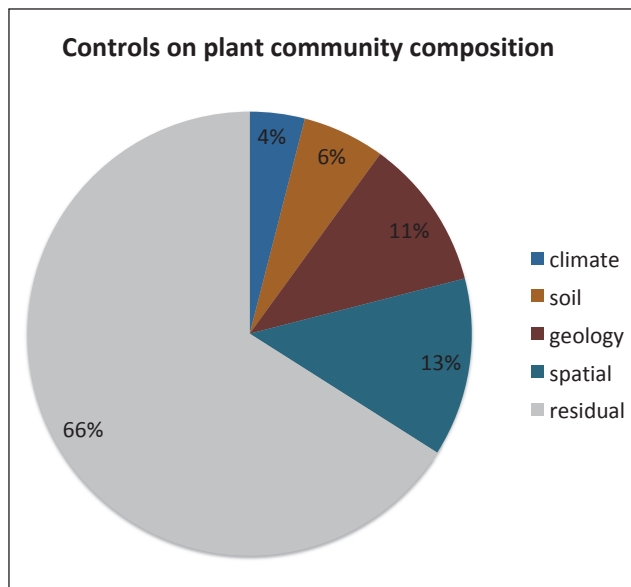


Fig. 5: Factors controlling beta diversity (i.e. variation of plant community composition) among permanent inventory plots established across the Golfo Dulce region, Costa Rica. Note the high amount of residual unexplained variation (66 %). – Abb. 5: Varianzanalyse der Faktoren, welche die Beta-Diversität (d. H. die Variation der Zusammensetzung der Pflanzengemeinschaft) in der Golfo Dulce-Region, Costa Rica steuern. Beachten Sie den hohen Anteil an ungeklärter Varianz (66 %).

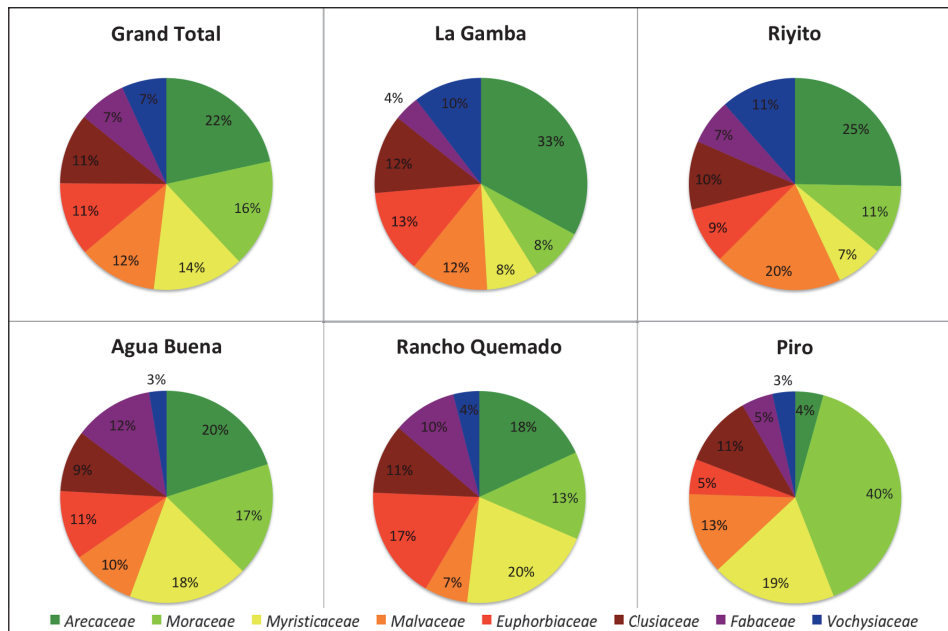


Fig. 6: Relative distribution (%) of dominant plant families (> 500 individuals) across different forest sites surveyed across the study region, i.e. for all forest sites (Grand Total), as well as for local clusters surveyed in La Gamba, Riyito, Agua Buena, Rancho Quemado and Piro, respectively. Note that most sites are dominated by palms (Arecaceae), but that every cluster exhibits a unique composition of tropical plant families (e.g. La Gamba dominated by Arecaceae; Piro by Moraceae, etc.). – Abb. 6: Relative Verteilung (%) der dominanten Pflanzenfamilien (> 500 Individuen) auf verschiedene Waldstandorte in der Golfo Dulce-Region, dh über alle Waldstandorte (Grand Total) sowie auf den lokalen Standorten La Gamba, Riyito, Agua Buena, Rancho Quemado und Piro. Beachten Sie, dass die meisten Standorte von Palmen (Arecaceae) dominiert werden, während jeder Cluster eine einzigartige Zusammensetzung tropischer Pflanzenfamilien aufweist (z. B. La Gamba, dominiert von Arecaceae; Piro von Moraceae usw.).

Species composition and relative abundance of plant functional groups

We found that local small-scale heterogeneity of environmental and topo-edaphic factors promotes tropical plant species richness in the Golfo Dulce region. Previous studies reported that variation in tree species composition across forest plots was highly correlated to gradients in resource availability (PRADA & STEVENSON 2016), due to feedbacks between edaphic properties, disturbance and floristic community composition (PRADA et al. 2017). Indeed, we found that topographic forest habitat types, i.e. forest plots established in hilltop (ridge), slope and valley bottom (ravine) positions, showed a distinct pattern in plant species composition and relative abundance. We found that ridge and slope forests exhibited a higher abundance of palms (i.e. *Iriarte*, *Welfia*) and certain tree species (e.g. *Mabea*, *Compsoeura*), while ravine forests were dominated by other taxa (e.g. *Otoba*), and that secondary re-growth forests were characterized by a distinct taxonomic species composition (Fig. 7). The latter finding for re-growth forest stands indicates differences in successional stage and disturbance regime between forest habitat types, whereas the variation among old-growth forest stands points to variability in edaphic properties, in turn

affecting species diversity and community composition between forest stands. It has been proposed that physical and chemical properties of forest soils determine local community composition via positive feedback mechanisms (QUESADA et al. 2012). According to this theory, in relatively stable environments on flat terrain, low clay content and nutrient availability favor a rather slow-growing tree community, whereas in highly disturbed systems on steep terrain, high clay content and nutrient availability support a fast-growing community in competition for resources (QUESADA & LLOYD 2016). This would suggest that local resource availability affects forest structure and function, such that distinct floristic communities emerge in different topographic forest habitat types. Accordingly, we found that *I. deltoidea*, a fast growing palm, was especially abundant in slope forests, as its characteristic stilt roots allow for early exploitation of light gaps without loss of stability on steep slopes (HUBER 2005, HUBER et al. 2008). In contrast, *O. novogranatensis*, a late-successional mid-canopy tree, was associated with moist but well-drained soils in ravine forests (LIEBERMAN et al. 1996) but can be successfully introduced into early stages of succession (COLE et al. 2011). *Apeiba tibourbou* and *Goethalsia meiantha* were present in high densities in tree inventories of secondary re-growth forest stands, with juvenile stages associated with canopy gaps (CLARK & CLARK 2001). In contrast, *Mabea occidentalis* and *Compsoeura excelsa* were almost exclusively found at ridges and slopes in moderate to high densities, with the endemic *C. excelsa* being restricted to the very humid forests of Costa Rica and west Panamá (CORNEJO et al. 2012). As a result, such differences in habitat preference between co-occurring plant species and associated differences in abundance across environmental gradients caused differences in floristic dominance between forest habitat types in the Golfo Dulce region (Fig. 7).

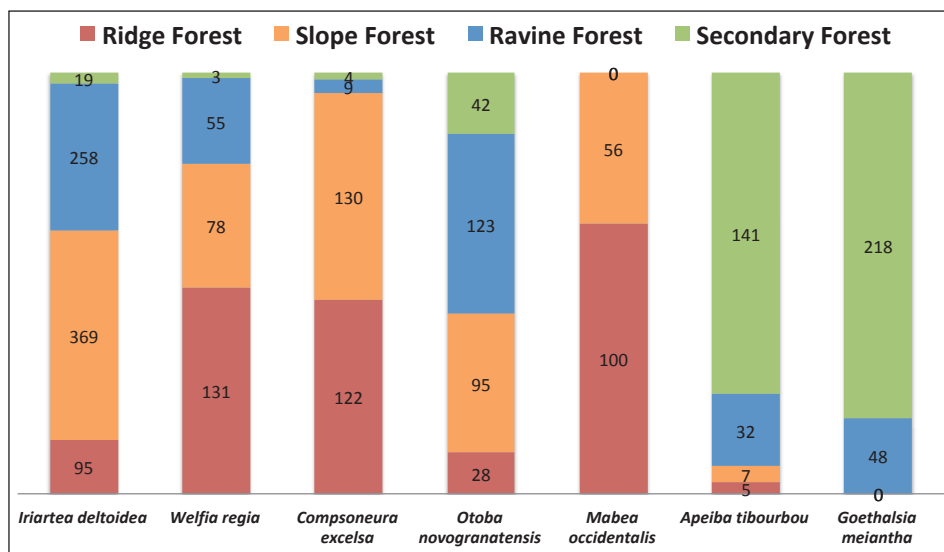


Fig. 7: Most abundant (> 100 individuals) plant species per habitat type, i.e. ridge forest, slope forest, ravine forest and secondary forest surveyed across the Golfo Dulce region, SW Costa Rica. – Abb. 7: Die am häufigsten vorkommenden Pflanzenarten (> 100 Individuen) pro Lebensraumtyp, d. H. Kammwald, Hangwald, Schluchtenwald und Sekundärwald, in der Golfo Dulce-Region, Costa Rica.

Hyperdominance in the Costa Rican plant flora

Tropical forests are characterized by extraordinary species richness and scientists still debate how many tree species might occur in the Amazon or how many will go extinct in the course of climate change (HUBBELL et al. 2008). However, it may not be so important to know the exact number of species, as it has been proposed that only a few abundant tropical plant species make up a large proportion of tree stems found in the Amazon (TER STEEGE et al. 2013). Accordingly, it was reported that only about 1 % of Amazon tree species are responsible for 50 % of carbon storage and productivity (FAUSET et al. 2015). Hence, knowledge about patterns in floristic dominance might be crucial for understanding ecosystem functioning and associated responses of tropical forests to changing climatic signals. Previous studies on nearby forest plots in the Golfo Dulce region found that the climate sensitivity of tropical forest productivity was affected by local topography and disturbance history (HOFHANSL et al. 2014). This suggests that ecosystem resistance to projected global changes might be strongly related to local site characteristics, while ecosystem resilience might depend on the potential of the local species pool to adapt to these novel conditions. Hence, hyperdominant plant species could determine local responses of tropical forest ecosystems due to their abundance in certain habitat types. Nonetheless, the most species-rich plant families in a given region must not necessarily coincide with the most abundant plant families. For instance, while Fabaceae, amounting to approx. 7 % of flowering plant species, represent the most diverse plant family found in tropical rainforests, the palm *I. deltoidea* is reportedly one of the most abundant plant species in the Neotropics (PITMAN et al. 2001, TER STEEGE et al. 2013, ARELLANO et al. 2014). Accordingly, we found that although Fabaceae represented the most species-rich plant family, Arecaceae was the most abundant plant family in the Golfo Dulce region, followed by Moraceae, Myristicaceae and Malvaceae (Fig. 8), which is a pattern reported similarly for other forests in the Neotropics (GENTRY 1990). Nonetheless, our study further highlighted that floristic plant species composition and diversity was related to landscape heterogeneity and local topographic properties, thus allowing for characterization of hyperdiverse forest communities and potentially improving our understanding of tropical ecosystem processes and associated crucial ecosystem services, such as carbon storage in tropical forest ecosystems

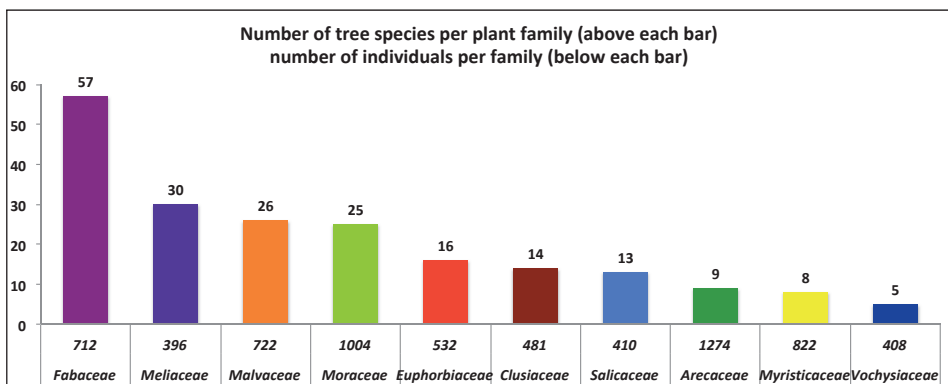


Fig. 8: Most species-rich plant families in the region (N above each bar). Most abundant plant families in the region (N below each bar). – Abb. 8: Die artenreichsten Pflanzenfamilien der Golfo Dulce-Region (N über jedem Balken), sowie am häufigsten vorkommende Pflanzenfamilien in der Region (N unter jedem Balken).

(TER STEEGE et al. 2013, FAUSET et al. 2015). Eventually, we conclude that our findings of local hyperdominance in the Costa Rican plant flora could provide useful information for biodiversity conservation and management strategies by focusing on a subset of the most abundant plant species in the Golfo Dulce region (Tab. 1, Tab. 2).

Tab. 1: List of the 20 most abundant plant species in the Golfo Dulce region, SW Costa Rica. – Tab. 1: Liste der 20 häufigsten Pflanzenarten in der Golfo Dulce Region, SW Costa Rica.

Species	Family	Distribution	% of re- corded in- dividuals DBH>10cm	Mean den- sity ha-1	Standard error	Max. density
<i>Iriartea deltoidea</i>	Arecaceae	Widespread in Tropical America	6,97	40,15	± 8,84	148
<i>Otoba novogranatensis</i>	Myristicaceae	Mesoamerica/ NW South America	2,51	14,45	± 3,39	46
<i>Compsonura excelsa</i>	Myristicaceae	Costa Rica/ Panama	2,3	13,25	± 3,99	60
<i>Tetrathylacium macrophyllum</i>	Salicaceae	Widespread in Tropical America	2,08	12	± 2,09	36
<i>Symphonia globulifera</i>	Clusiaceae	Pantropical	1,97	11,35	± 2,01	24
<i>Carapa nicaraguensis</i>	Meliaceae	Mesoamerica/ NW South America	1,93	11,1	± 2,08	32
<i>Tapirira guianensis</i>	Anacardiaceae	Widespread in Tropical America	1,72	9,9	± 2,66	41
<i>Apeiba tibourbou</i>	Malvaceae	Widespread in Tropical America	1,61	9,25	± 3,95	76
<i>Castilla tunu</i>	Moraceae	Mesoamerica/ NW South America	1,44	8,3	± 4,42	85
<i>Perebea hispidula</i>	Moraceae	Mesoamerica	1,22	7	± 1,4	24
<i>Vochysia ferruginea</i>	Vochysiaceae	Widespread in Tropical America	1,02	5,85	± 2,43	39
<i>Socratea exorrhiza</i>	Arecaceae	Widespread in Tropical America	0,99	5,7	± 1,43	24
<i>Brosimum guianense</i>	Moraceae	Widespread in Tropical America	0,96	5,55	± 0,87	13
<i>Tetragastris panamensis</i>	Burseraceae	Widespread in Tropical America	0,92	5,3	± 1,86	31
<i>Soroea pubivena</i>	Moraceae	Widespread in Tropical America	0,9	5,2	± 1,59	27
<i>Brosimum lactescens</i>	Moraceae	Widespread in Tropical America	0,86	4,95	± 1,5	23
<i>Cecropia insignis</i>	Urticaceae	Mesoamerica/ NW South America	0,86	4,95	± 1,64	29
<i>Chimarrhis parviflora</i>	Rubiaceae	Costa Rica/ Panama	0,83	4,75	± 1,45	21
<i>Virola sebifera</i>	Myristicaceae	Widespread in Tropical America	0,82	4,7	± 1,93	33
<i>Chimarrhis latifolia</i>	Rubiaceae	Mesoamerica	0,8	4,6	± 2,93	45
<i>Pourouma bicolor</i>	Urticaceae	Widespread in Tropical America	0,8	4,6	± 3,23	51
<i>Pleuranthodendron lindenii</i>	Salicaceae	Mesoamerica/ NW South America	0,77	4,45	± 1,98	35
<i>Marila pluricostata</i>	Calophyllaceae	Mesoamerica/ NW South America	0,68	3,9	± 1,18	15
<i>Virola surinamensis</i>	Myristicaceae	Widespread in Tropical America	0,68	3,9	± 0,62	10
<i>Lacmellea panamensis</i>	Apocynaceae	Mesoamerica/ NW South America	0,64	3,7	± 0,82	14
<i>Virola koschnyi</i>	Myristicaceae	Mesoamerica/ NW South America	0,58	3,35	± 0,57	9
<i>Vochysia gentryi</i>	Vochysiaceae	Mesoamerica/ NW South America	0,56	3,2	± 0,92	10

Tab. 2: Top 30 species (O: oligarch/ C: common/ R: rare; total number of individuals) per forest habitat type, i.e. ridge forest, slope forest, ravine forest and secondary forest surveyed across the Golfo Dulce region, SW Costa Rica. – Tab. 2: Die 30 häufigsten Arten (O: oligarchen / C: häufig / R: selten; Gesamtzahl der Individuen) nach Waldlebensraumtyp, d.H. Kammwald, Hangwald, Schluchtwald und Sekundärwald, der Untersuchungsflächen in der Golfo Dulce-Region, Costa Rica.

Ridge Forest	Slope Forest	Ravine Forest	Secondary Forest
<i>Welfia regia</i> (C; 131)	<i>Iriartea deltoidea</i> (O; 369)	<i>Iriartea deltoidea</i> (O; 258)	<i>Goethalsia meiantha</i> (C; 218)
<i>Compsonura excelsa</i> (O; 122)	<i>Compsonura excelsa</i> (O; 130)	<i>Otoba novogranatensis</i> (O; 123)	<i>Apeiba tibourbou</i> (O; 141)
<i>Mabea occidentalis</i> (C; 100)	<i>Otoba novogranatensis</i> (O; 95)	<i>Tetrathylacium macrophyllum</i> (O; 71)	<i>Hieronyma alchorneoides</i> (C; 91)

Tab. 2 continued

Ridge Forest	Slope Forest	Ravine Forest	Secondary Forest
<i>Symphonia globulifera</i> (O; 99)	<i>Symphonia globulifera</i> (O; 81)	<i>Welfia regia</i> (C; 55)	<i>Castilla tunu</i> (O; 90)
<i>Iriartea deltoidea</i> (O; 95)	<i>Welfia regia</i> (C; 78)	<i>Pleuranthodendron lindenii</i> (O; 51)	<i>Alchornea costaricensis</i> (C; 88)
<i>Qualea paraensis</i> (C; 86)	<i>Tetrathylacium macrophyllum</i> (O; 70)	<i>Carapa nicaraguensis</i> (O; 50)	<i>Tetrathylacium macrophyllum</i> (O; 85)
<i>Tapirira guianensis</i> (O; 72)	<i>Carapa nicaraguensis</i> (O; 64)	<i>Goethalsia meiantha</i> (C; 48)	<i>Iriartea deltoidea</i> (O; 81)
<i>Vochysia ferruginea</i> (O; 64)	<i>Chimarrhis latifolia</i> (O; 58)	<i>Sorocea pubivena</i> (O; 41)	<i>Spondias radlkoferi</i> (C; 81)
<i>Carapa nicaraguensis</i> (O; 62)	<i>Tapirira guianensis</i> (O; 56)	<i>Symphonia globulifera</i> (O; 40)	<i>Gmelina arborea</i> (R; 67)
<i>Pourouma bicolor</i> (O; 61)	<i>Mabea occidentalis</i> (C; 56)	<i>Socratea exorrhiza</i> (O; 40)	<i>Guatteria chiriquiensis</i> (C; 51)
<i>Perebea hispidula</i> (O; 58)	<i>Sorocea pubivena</i> (O; 49)	<i>Chimarrhis parviflora</i> (O; 40)	<i>Carapa nicaraguensis</i> (O; 46)
<i>Marila laxiflora</i> (C; 56)	<i>Qualea paraensis</i> (C; 45)	<i>Virola sebifera</i> (O; 39)	<i>Miconia trinervia</i> (C; 44)
<i>Pausandra trianae</i> (C; 52)	<i>Castilla tunu</i> (O; 43)	<i>Calatola costaricensis</i> (C; 36)	<i>Otoba novogranatensis</i> (O; 43)
<i>Socratea exorrhiza</i> (O; 48)	<i>Marila pluricostata</i> (O; 35)	<i>Eschweilera biflora</i> (C; 35)	<i>Luehea seemannii</i> (C; 43)
<i>Brosimum guianense</i> (O; 44)	<i>Pausandra trianae</i> (C; 33)	<i>Apeiba tibourbou</i> (O; 32)	<i>Cecropia insignis</i> (O; 42)
<i>Tetragastris panamensis</i> (O; 44)	<i>Brosimum guianense</i> (O; 31)	<i>Cleidion castaneifolium</i> (C; 31)	<i>Tapirira guianensis</i> (O; 40)
<i>Brosimum lactescens</i> (O; 41)	<i>Tetragastris panamensis</i> (O; 30)	<i>Tapirira guianensis</i> (O; 30)	<i>Ficus tonduzii</i> (C; 40)
<i>Lacmellea panamensis</i> (O; 33)	<i>Perebea hispidula</i> (O; 29)	<i>Perebea hispidula</i> (O; 30)	<i>Hampea appendiculata</i> (C; 39)
<i>Guarea pterorhachis</i> (C; 32)	<i>Brosimum lactescens</i> (O; 29)	<i>Chrysoschlamys glauca</i> (C; 30)	<i>Vochysia ferruginea</i> (O; 36)
<i>Euterpe precatória</i> (C; 30)	<i>Cecropia insignis</i> (O; 26)	<i>Ocotea rivularis</i> (C; 30)	<i>Platymiscium curuense</i> (C; 31)
<i>Otoba novogranatensis</i> (O; 28)	<i>Lacmellea panamensis</i> (O; 26)	<i>Tetragastris panamensis</i> (O; 29)	<i>Inga oerstediana</i> (C; 30)
<i>Calophyllum brasiliense</i> (C; 28)	<i>Chimarrhis parviflora</i> (O; 25)	<i>Brosimum utile</i> (C; 28)	<i>Jacaranda copaia</i> (C; 28)
<i>Vochysia gentryi</i> (O; 25)	<i>Batocarpus costaricensis</i> (C; 24)	<i>Virola surinamensis</i> (O; 26)	<i>Chimarrhis parviflora</i> (O; 25)
<i>Virola sebifera</i> (O; 21)	<i>Marila laxiflora</i> (C; 23)	<i>Brosimum lactescens</i> (O; 25)	<i>Terminalia amazonia</i> (C; 25)
<i>Marila pluricostata</i> (O; 21)	<i>Virola surinamensis</i> (O; 23)	<i>Cecropia insignis</i> (O; 25)	<i>Trattinnickia aspera</i> (C; 24)
<i>Cassipourea elliptica</i> (C; 21)	<i>Guarea pterorhachis</i> (C; 23)	<i>Peltogyne purpurea</i> (C; 23)	<i>Perebea hispidula</i> (O; 23)
<i>Garcinia madruno</i> (C; 20)	<i>Pourouma bicolor</i> (O; 21)	<i>Cryosophila guagara</i> (C; 23)	<i>Vochysia allenii</i> (C; 23)
<i>Calophyllum longifolium</i> (C; 20)	<i>Protium pecuniosum</i> (C; 20)	<i>Brosimum guianense</i> (O; 21)	<i>Terminalia oblonga</i> (C; 22)
<i>Castilla tunu</i> (O; 18)	<i>Aspidosperma spruceanum</i> (C; 20)	<i>Marila pluricostata</i> (O; 21)	<i>Virola sebifera</i> (O; 19)
<i>Aspidosperma spruceanum</i> (C; 18)	<i>Protium glabrum</i> (C; 19)	<i>Virola koschnyi</i> (O; 21)	<i>Virola koschnyi</i> (O; 19)

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Addresses:

Dr. Florian HOFHANSL, IIASA International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria. E-Mail: hofhansl@iiasa.ac.at

Dr. Eduardo CHACÓN-MADRIGAL, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica. E-Mail: edchacon@gmail.com

Dr. Albert MORERA, Laboratory of Applied Tropical Ecology, National University of Costa Rica, Costa Rica. E-Mail: amorerabeita@gmail.com

Dr. Fernando SILLA, Area of Ecology, Faculty of Biology, University of Salamanca, Spain. E-Mail: fsilla@usal.es

Dr. Werner HUBER, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria. E-Mail: werner.huber@univie.ac.at

Dr. Anton WEISSENHOFER, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, 1030 Vienna, Austria. E-Mail: anton.weissenhofer@univie.ac.at

Univ.-Prof. Dr. Wolfgang WANER, Department of Microbiology and Ecosystem Science, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria.
E-Mail: wolfgang.waner@univie.ac.at

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