

Non-woody life-form contribution to vascular plant species richness in a tropical American forest

Reynaldo Linares-Palomino · Victor Cardona · Ernest I. Hennig ·
Isabell Hensen · Doreen Hoffmann · Jasmin Lenzion · Daniel Soto ·
Sebastian K. Herzog · Michael Kessler

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Abstract We provide total vascular plant species counts for three 1-ha plots in deciduous, semi-deciduous and evergreen forests in central Bolivia. Species richness ranged from 297 species and 22,360 individuals/ha in the dry deciduous forest to 382 species and 31,670 individuals/ha in the

evergreen forest. Orchidaceae, Pteridophyta and Leguminosae were among the most species-rich major plant groups in each plot, and *Peperomia* (Piperaceae), *Pleurothallis* (Orchidaceae) and *Tillandsia* (Bromeliaceae), all epiphytes, were the most species-rich genera. This dominance of a few but very diverse and/or widespread taxa contrasted with the low compositional similarity between plots. In a neotropical context, these Central Bolivian forest plots are similar in total species richness to other dry

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R. Linares-Palomino (✉) · M. Kessler
Department of Systematic Botany, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany
e-mail: r.linaresp@yahoo.co.uk

V. Cardona
Herbario Nacional de Bolivia, Instituto de Ecología, Universidad Mayor de San Andrés, Casilla 10077, La Paz, Bolivia

E. I. Hennig
Department of Environmental Sciences, Institute of Terrestrial Ecosystems, ETH Zürich, Universitätstrasse 16, 8092 Zurich, Switzerland

I. Hensen · D. Hoffmann
Plant Ecology, University of Halle – Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany

J. Lenzion
Department of Plant Ecology and Ecosystem Research, Albrecht-von-Haller-Institute for Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

Present Address:
J. Lenzion
Institute of Botany and Landscape Ecology,
Ernst-Moritz-Arndt-University Greifswald,
Grimmer Str. 88,
17487 Greifswald, Germany

D. Soto
Herbario del Oriente Boliviano, Museo Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia

S. K. Herzog
Asociación Armonía – BirdLife International, Casilla 3566, Santa Cruz de la Sierra, Bolivia

Present Address:
M. Kessler
Institute of Systematic Botany, University of Zürich,
Zollikerstrasse 107, 8008 Zurich, Switzerland

deciduous and humid montane forests, but less rich than most Amazonian forests. Nevertheless, lianas, terrestrial herbs and especially epiphytes proved to be of equal or higher species richness than most other neotropical forest inventories from which data are available. We therefore highlight the importance of non-woody life-forms (especially epiphytes and terrestrial herbs) in Andean foothill forest ecosystems in terms of species richness and numbers of individuals, representing in some cases nearly 50% of the species and more than 75% of the individuals. These figures stress the need for an increased inventory effort on non-woody plant groups in order to accurately direct conservation actions.

Keywords Alpha diversity · Andean foothills forest ecosystem · Life-form diversity · Non-woody plants · Total species inventory

Introduction

Statements about the diversity of plant species in forest ecosystems are usually based on results from vegetation inventories that are mostly restricted to a certain plant subgroup. Woody species, usually trees and shrubs with diameter at breast height of ≥ 1 cm (e.g. the STRI 50-ha plots, Condit 1995), ≥ 2.5 cm (e.g. 0.1-ha transects, Gentry 1982) and ≥ 10 cm (e.g. Gentry 1988; Valencia et al. 1994; Smith and Killen 1998), are the most commonly studied plant groups. In contrast, herbs (e.g. Poulsen and Balslev 1991; Poulsen and Nielsen 1995), lianas (Pérez-Salicrup et al. 2001; Mascaro et al. 2004) and epiphytes (Ingram et al. 1996; Arévalo and Betancur 2004; Benavides et al. 2005; Krömer et al. 2005) are less commonly used to characterize the diversity of vegetation types. These non-woody life-forms, however, have been shown to be of importance in the few assessments of tropical plant alpha diversity in which all vascular plants were counted (Whitmore et al. 1985; Gentry and Dodson 1987; Duivenvoorden 1994; Balslev et al. 1998; Galeano et al. 1998; Langenberger et al. 2006). The scarcity of such studies can be attributed to the difficulties associated with identification of more (and usually less well known) plant groups (restricting inventories to some

life-form groups in the tropics is already a huge identification task) and the difficulty of collecting epiphyte specimens from the forest canopy. Whitmore and colleagues have undertaken the most comprehensive study of vascular plants to date in a Costa Rican rain forest. To accomplish their task of inventorying all species (including non-vascular plants), destructive sampling of a 10 m \times 10 m plot was required (Whitmore et al. 1985).

The few full tropical plant inventories performed to date have focused on a single and homogeneous vegetation type, usually tropical lowland rain forests. Although some of these studies (e.g. Duivenvoorden 1994; Langenberger et al. 2006) inventoried plots and transects along edaphic and physiographic gradients, only two have inventoried and compared different vegetation types using a uniform sampling methodology throughout. Álvarez et al. (2003) reported total vascular plant counts in three 0.1-ha plots in Amazonian, Chocóan and Andean forests in Colombia. This study, however, was not published formally, and epiphytes in the Amazonian plot were not sampled, restricting the total vascular plant count to the Chocó and Andean forest only. The other study by Gentry and Dodson (1987) compared three 0.1-ha plots in wet, moist and dry forests in Ecuador. The lack of standardized inventory methods hampers the quantitative comparison between both of these studies. The use of florulas could be an option to compare different forests (e.g. Gentry 1990), but the size of the areas studied and collection intensities are not uniform (Tobler et al. 2007).

We chose Central Bolivia, a region where four major biomes occur in close proximity to each other (humid and moist vegetation from Amazonia, seasonal subtropical lowland vegetation from the Chaco, subtropical highland vegetation from the Andes and seasonal vegetation of the Chiquitanía (Ibisch et al. 2003)), as our study region. We established within this complex biogeographic setting three permanent 1-ha plots. We used a uniform methodology along a humidity gradient from deciduous to evergreen forest, inventorying all vascular plants present. Our main objective was to quantitatively assess the relative importance of different life-form groups and taxa within the different vegetation types we surveyed and to compare our results with similar studies in the neotropical region.

Methods

Study area

The study was carried out at the Refugio Los Volcanes in Santa Cruz, Bolivia. Los Volcanes is a private reserve of approximately 300 ha. It is located about 18°06' S and 63°36' E and is adjacent to the southern border of Amboró National Park, directly on the transition from the humid inner tropics to the seasonally dry subtropics (Fig. 1a). The substrate of the study area consists primarily of red sandstone and locally of loamy sedimentary rocks (lutite). These red sandstones form cliffs several hundred metres high and are intersected by narrow valleys providing the area with dramatic scenery. Annual precipitation is about 1200–1500 mm, with most of the rainfall from October/November to March/April, but with high temporal variability.

The general vegetation of the area has been classified as ‘subhumid to humid deciduous forest of southeastern Amboró’ (Navarro et al. 1996) and is usually found at 900–1100 masl. Among the dominant tree species are *Aspidosperma cylindrocarpon* (Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela lilloi* (Meliaceae), *Gallsia integrifolia* (Phytolaccaceae), *Pachystroma*

longifolium (Euphorbiaceae), *Pogonopus tubulosus* (Rubiaceae) and *Tabebuia lapacho* (Bignoniaceae) (Navarro et al. 1996). Locally, however, vegetation types are determined by differences in topography, aspect and precipitation regimes that lead to ecologically relevant differences in water availability within the study area. Consequently, the dominant zonal vegetation is semi-deciduous forest (about 30–50% deciduous trees) mainly found on shaded south-facing slopes. Steep, sunny and north-facing slopes are occupied by deciduous forest (70–90% deciduous trees), whereas flat, shaded valleys with groundwater supply support evergreen forest (10–20% deciduous trees) (Fig. 1b).

Vegetation sampling

A permanent plot of 1 ha was established in each forest type (deciduous, semi-deciduous and evergreen) between 2002 and 2003. Each plot was subdivided into 25 adjacent 20 m × 20 m subplots. Plots were laid out in such a way as to include only the forest type under study, avoiding other forest types, young secondary vegetation and non-forest vegetation (e.g. rock outcrops). Thus, our plots are not the traditional square 100 m × 100 m inventory plots but have rather irregular shapes (Fig. 1c).

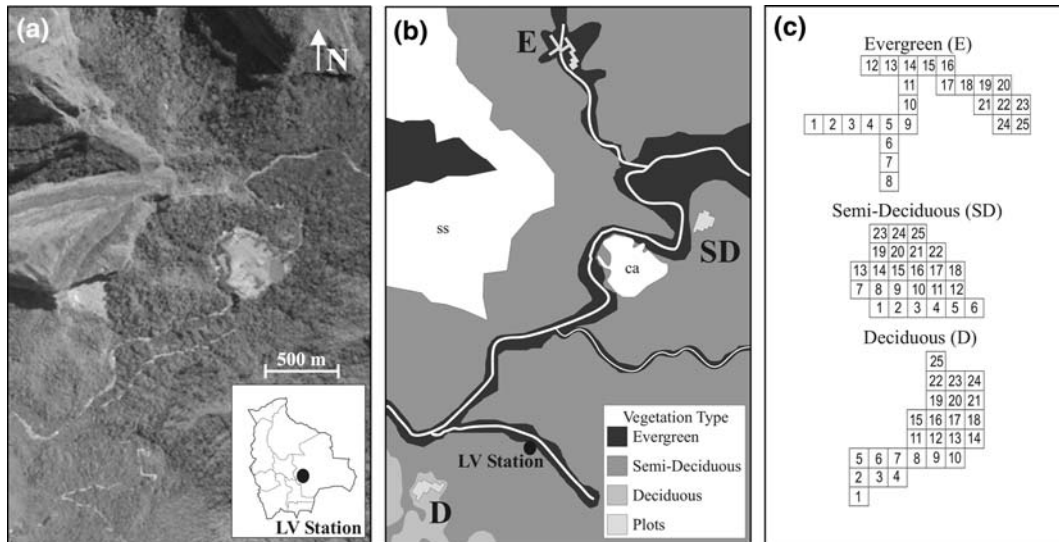


Fig. 1 Main vegetation types and plot shape and location in the study area. **a** Aerial photograph of the Refugio Los Volcanes area in central Bolivia, *inset* showing map of Bolivia and location of study area. **b** Schematic representation of the

major vegetation types and geographical characteristics of the area, showing plot locations and orientation (ss: sandstone, ca: cleared area, LV Station: Los Volcanes Research Station). **c** Shape of inventory plots, where numbers denote subplots

All vascular plants in each plot were inventoried between 2002 and 2004, mainly in the season following the summer rains (i.e. May–August). J. Lenzion inventoried herbs, shrub and tree seedlings, E. I. Hennig epiphytes, D. Hoffmann lianas and V. Cardona, D. Soto and S. K. Herzog woody plants. For the herb inventories, we recorded all species with stem diameter below 1 cm. Additionally, we recorded all Cactaceae, Bromeliaceae and Costaceae below 1 m height and epiphytes on fallen branches. For lianas, we recorded all individuals, including Araceae, with a diameter of >1 cm at 1.3 m above soil level. All epiphytes were observed and counted. Collections of epiphytes were made either with a clipper pole or with the help of rope-climbing techniques. Binoculars were used to aid identification when they were too inaccessible to collect. Finally, we recorded all woody plants, excluding lianas, with diameter at breast height (dbh) of >1 cm.

Voucher specimens of all species were collected for later determination and are deposited at USZ (Santa Cruz) and LPB (La Paz), with a small subset of samples at the Göttingen Herbarium (GOET) (herbarium acronyms follow Holmgren and Holmgren 1998). Several sterile specimens could not be fully identified and were sorted into morphospecies. The final stage of data production was completed at USZ (by R. Linares-Palomino) by cross-checking all collected vouchers in order to unify morphospecies delimitations.

Data analysis

We used a conservative approach in calculating species numbers by lumping highly similar morphospecies into one group instead of considering them as several distinct species. The herb inventory, which included life-forms other than herbaceous plants, was split into terrestrial herbs, tree seedlings, shrub seedlings and epiphytes. Thus, terrestrial herbs formed a life-form group by itself in subsequent analyses. The other three subgroups were cross-referenced with the tree, shrub and epiphyte inventories and merged accordingly. We follow the TROPICOS and Flora of Bolivia online databases for nomenclatural purposes (both available at <http://mobot.mobot.org/W3T/Search/vast.html> and http://www.efloras.org/flora_page.aspx?flora_id=40, respectively). Despite much progress in the

understanding of the phylogeny of extant ferns, familial composition and relationships are still unsatisfactorily solved (Smith et al. 2006; Schuettelpelz and Pryer 2007). We therefore refrained from assigning our collections to families and treated all ferns and fern allies as a single taxon Pteridophyta.

We computed species accumulation curves based on the 20 m × 20 m subplots using EstimateS (Colwell 2005). Similarity between forest plots was evaluated by subtracting the Bray–Curtis distance between two forest plots from unity. Pair-wise Bray–Curtis distances (D_{BC}) were calculated in the vegan package for R (Oksanen et al. 2006; R Development Core Team 2006) using presence/absence data by $D_{BC} = 2a/(2a + b + c)$, where a is the total number of species present in both forest plots, b is the number of species present only in the first forest plot, and c is the number of species present only in the second forest plot (Magurran 2004). In order to compare the species richness of the Los Volcanes plots with that of other forests in the neotropics, we searched for other published full plant, epiphyte, liana, terrestrial herb and tree/woody plant inventories (Appendix 1) and plotted species accumulation curves for each forest type at Los Volcanes against the species richness data of the other studies.

Results

Taxonomic diversity

We recorded 80,352 individual plants belonging to 670 species (including morphospecies) on the three plots (Appendix 2). We were able to completely identify 52% of our collections to species level (341 species), an additional 25% could be assigned to genus (172 morphospecies) and 14% to family (95 morphospecies). Nine percent (62 morphospecies) could not be assigned to a family or lower taxon.

The most species-rich plots were in the evergreen and semi-deciduous forest, both of which had an almost identical number of species (381 and 382, respectively). The deciduous forest had 297 species. Of the 273 genera, most were recorded in the evergreen and semi-deciduous forest (190 and 185, respectively) compared to 162 genera in the deciduous forest. Of the 92 families, 75 were found in the evergreen, 72 in the semi-deciduous and 60 in the

Table 1 Number of families, genera and species of three 1-ha plots in Santa Cruz, Central Bolivia (A: angiosperms, P: pteridophytes)

	Total from the three forest plots			Deciduous forest plot			Semi-deciduous forest plot			Evergreen forest plot		
	A	P	Total	A	P	Total	A	P	Total	A	P	Total
Families	80	12	92	55	5	60	64	8	72	65	10	75
Genera	245	28	273	149	13	162	168	17	185	166	24	190
Species	617	53	670	279	18	297	353	29	382	337	44	381
<i>Life-form</i>												
Epiphyte	142			67			80			109		
Hemiepiphyte	9			1			4			8		
Liana	153			64			86			44		
Shrub	97			45			49			57		
Tree, liana	1			1			–			1		
Tree, shrub	39			17			16			20		
Terrestrial herb	79			30			42			57		
Tree	148			71			105			84		
Other	1			–			–			1		
Parasite	1			1			–			–		

Life-form composition values show the number of species assigned to each plant group

deciduous forest. The contribution of ferns and lycophytes (“pteridophytes”) to species richness was higher in the evergreen forest than in the two other forest types (Table 1).

Of the 10 most species-rich families, seven were shared between all three plots, although with different ranking within each plot (Table 2). Taking all three plots together, the most species-rich families were Orchidaceae, pteridophytes, Leguminosae and Bignoniaceae. Orchidaceae, a family containing mostly epiphytic species, was by far the most species-rich in all plots. Pteridophytes, composed mostly of ground herbs, ranked second in the evergreen and semi-deciduous and fourth in the deciduous forest. Leguminosae, which was mainly composed of woody species in our plots, decreased in importance from the deciduous (second) to the evergreen forest (fourth). Absolute species numbers were similar in the evergreen forest and higher in the semi-deciduous forest as compared to the deciduous forest. Bignoniaceae (a family including liana, shrub and tree species), the third most important family in the deciduous forest, was the fourth most important family in the semi-deciduous forest (again with a higher species number) but was ranked only eighth in the evergreen forest. Only two other families were important in terms of species numbers, and these were shared by two forest

types: Apocynaceae (mostly trees) present in the deciduous and semi-deciduous forest and Rubiaceae (shrubs and trees) present in the semi-deciduous and evergreen forest.

In contrast to families, only five species-rich genera were common to all three forest plots (*Peperomia*, *Pleurothallis*, *Tillandsia*, *Acalypha* and *Eugenia*). Of these, the three most species-rich genera were *Peperomia*, *Tillandsia* and *Pleurothallis*, although ranking varied between forest plots (Table 2).

Two species of *Tillandsia* had the highest numbers of individuals on all three plots (Table 2): *T. bryoides* had highest numbers in the deciduous forest, whereas *T. tenuifolia* had most individuals in the semi-deciduous and evergreen forests. The 10 species with highest number of individuals in the deciduous forest included epiphytes and terrestrial herbs (three species each) and shrubs and trees (two species each). The contribution of non-woody plants increased in the semi-deciduous forest, including epiphytes (four species), terrestrial herbs (three species) and one species each of shrubs, trees and lianas. Non-woody plant contribution was highest in the evergreen forest with six species of epiphyte, two species of terrestrial herb and one hemiepiphyte species dominating. Only one shrub species was included among the top 10.

Table 2 Most species-rich families and genera (number of species in parentheses) and most abundant species (number of individuals in parentheses)

Deciduous	Semi-deciduous	Evergreen	Total
Families (Pteridophyta is considered as one family)			
Orchidaceae (34, e)	Orchidaceae (45, e)	Orchidaceae (60, e)	Orchidaceae (85, e)
Leguminosae (20, t)	Pteridophyta (29, h)	Pteridophyta (44, h)	Pteridophyta (53, h)
Bignoniaceae (19)	Leguminosae (26, t)	Bromeliaceae (20, e)	Leguminosae (39, t)
Pteridophyta (18, h)	Bignoniaceae (23)	Leguminosae (20, t)	Bignoniaceae (35)
Bromeliaceae (16, e)	Rubiaceae (16)	Piperaceae (16)	Bromeliaceae (26, e)
Euphorbiaceae (13, s,t)	Bromeliaceae (15, e)	Rubiaceae (14)	Rubiaceae (23)
Piperaceae (12)	Sapindaceae (13)	Euphorbiaceae (12, s,t)	Euphorbiaceae (21, s,t)
Acanthaceae (12, h)	Euphorbiaceae (12, s,t)	Araceae (9, e)	Acanthaceae (20, h)
Apocynaceae (10, t)	Apocynaceae (11, t)	Moraceae (9, t)	Apocynaceae (18, t)
Myrtaceae (9, s,t)	Piperaceae (11)	Asteraceae (8)	Piperaceae (18)
Cactaceae (9)		Bignoniaceae (8)	
		Lauraceae (8, t)	
		Melastomataceae (8)	
Genera			
<i>Peperomia</i> (9)	<i>Tillandsia</i> (11)	<i>Tillandsia</i> (13)	<i>Tillandsia</i> (15)
<i>Pleurothallis</i> (8)	<i>Peperomia</i> (8)	<i>Pleurothallis</i> (10)	<i>Pleurothallis</i> (14)
<i>Tillandsia</i> (7)	<i>Pleurothallis</i> (8)	<i>Peperomia</i> (9)	<i>Peperomia</i> (11)
<i>Acalypha</i> (6)	<i>Forsteronia</i> (6)	<i>Epidendrum</i> (8)	<i>Acalypha</i> (10)
<i>Forsteronia</i> (6)	<i>Acalypha</i> (5)	<i>Acalypha</i> (7)	<i>Epidendrum</i> (9)
<i>Acacia</i> (5)	<i>Eugenia</i> (5)	<i>Begonia</i> (7)	<i>Forsteronia</i> (9)
<i>Eugenia</i> (5)	<i>Machaerium</i> (5)	<i>Piper</i> (7)	<i>Begonia</i> (8)
<i>Machaerium</i> (4)	<i>Philodendron</i> (5)	<i>Eugenia</i> (6)	<i>Eugenia</i> (7)
<i>Epidendrum</i> (4)	<i>Psychotria</i> (5)	<i>Ficus</i> (6)	<i>Ficus</i> (7)
<i>Philodendron</i> (4)	<i>Randia</i> (5)	<i>Thelypteris</i> (6)	<i>Piper</i> (7)
<i>Ruellia</i> (4)	<i>Thelypteris</i> (5)		
Species (number of individuals)			
<i>Tillandsia bryoides</i> (2410, e)	<i>Tillandsia tenuifolia</i> (2008, e)	<i>Tillandsia tenuifolia</i> (5576, e)	<i>Tillandsia tenuifolia</i> (8059, e)
<i>Peperomia comarapana</i> (1654, h)	<i>Piper callosum</i> (1132, s)	<i>Racinaea parviflora</i> (1879, e)	<i>Peperomia tetragona</i> (2549, e)
<i>Rinorea ovalifolia</i> (1534, s)	<i>Paspalum humboldtianum</i> (972, h)	<i>Vriesea maxoniana</i> (1745, e)	<i>Racinaea parviflora</i> (2426, e)
<i>Petiveria alliacea</i> (1056, s)	<i>Olyra fasciculata</i> (932, h)	<i>Blechnum occidentale</i> (1058, h)	<i>Tillandsia bryoides</i> (2410, e)
<i>Peperomia tetragona</i> (1012, e)	<i>Peperomia tetraphylla</i> (925, e)	<i>Philodendron camposportianum</i> (837, e)	<i>Piper callosum</i> (2156, s)

Table 2 continued

Deciduous	Semi-deciduous	Evergreen	Total
<i>Olyra fasciculata</i> (986, h)	<i>Adiantum tetraphyllum</i> (800, h)	<i>Thelypteris dentata</i> (803, h)	<i>Vriesea maxoniana</i> (2120, e)
<i>Acacia polyphylla</i> (802, t)	<i>Peperomia tetragona</i> (789, e)	<i>Peperomia tetragona</i> (748, e)	<i>Olyra fasciculata</i> (2012, h)
<i>Commelina erecta</i> (777, h)	<i>Philodendron camposportanum</i> (745, e)	<i>Lomagramma guianensis</i> (741)	<i>Philodendron camposportanum</i> (2007, e)
<i>Tillandsia streptocarpa</i> (755, e)	<i>Piper amalago</i> (681, t)	<i>Peperomia aceroana</i> (735, e)	<i>Peperomia comarapana</i> (1678, h)
<i>Coursetia brachyrhachis</i> (522, t)	<i>Herreia montevidensis</i> (521, l)	<i>Piper callosum</i> (692, s)	<i>Commelina erecta</i> (1574, h)

The dominant life-form is indicated for families and individual species (e = epiphytic, h = terrestrial herb, s = shrub, t = tree, l = liana). Nomenclature follows TROPICOS and the Flora of Bolivia online databases (<http://mobot.mobot.org/W3T/Search/vast.html> and http://www.efloras.org/flora_page.aspx?flora_id=40, respectively)

Life-form composition

In the deciduous forest, trees, epiphytes and lianas contributed similar species numbers (22–24% of the total, Table 1). In the semi-deciduous forest, trees were slightly more species-rich than other life-forms (28%), followed by lianas (23%) and epiphytes (21%). The most species-rich life-form in the evergreen forest was epiphytes (29%), followed by trees (22%), shrubs (15%) and ground herbs (15%) (Table 1). Woody plants (including lianas and shrubs) contributed to approximately 66%, 57% and 54% of total species richness in the deciduous, semi-deciduous and evergreen forest plots, respectively. There was a highly significant statistical difference between the proportions of life-forms in the three studied forest types (G -test, $G = 28.34$, $P = 0.0004$, $df = 8$).

Pearson correlation analyses among life-form richness patterns within each forest plot showed that tree species richness patterns were positively and significantly correlated with total plant species richness: deciduous forest $r = 0.67$ ($P = 0.0002$), semi-deciduous forest $r = 0.54$ ($P = 0.0049$), evergreen forest $r = 0.59$ ($P = 0.0021$). No other significant correlation could be detected between trees and other life-forms, except with shrubs in the semi-deciduous forest ($r = 0.51$, $P = 0.01$) and with lianas in the evergreen forest ($r = 0.53$, $P = 0.0064$). Apart from trees, lianas were the only other life-form that showed similar levels of positive and significant correlations with total plant species richness across the three plots: deciduous forest $r = 0.63$ ($P = 0.0007$), semi-deciduous forest $r = 0.66$ ($P = 0.0003$), evergreen forest $r = 0.54$ ($P = 0.0051$). Other positive significant correlations were detected in the evergreen forest plot between total plant species richness and epiphytes ($r = 0.60$, $P = 0.0017$) and terrestrial herbs ($r = 0.69$, $P = 0.0001$).

Similarity among plots

Similarity among plots was 0.46 between deciduous and semi-deciduous (155 species shared), 0.37 between deciduous and evergreen (125 species shared) and 0.57 between semi-deciduous and evergreen (216 species shared). We recorded 106 species occurring in all three plots. One hundred and twenty-three species were recorded only in the deciduous

plot, 117 only in the semi deciduous plot and 146 only in the evergreen forest plot.

Discussion

Plot shape and its influence on species richness estimations

Spatial distribution patterns of plant species in tropical forests are influenced by niche assembly and/or random dispersal assembly processes acting at both local and landscape scales (Chave 2004; Gaston and Chown 2005; John et al. 2007), resulting in mostly clumped distributions (e.g. Condit et al. 2000). Within this scenario, plot shape has been documented to influence estimates of species richness, i.e. longer and narrower rectangular plots are prone to capture more species than square plots of similar area (Condit et al. 1996; Laurance et al. 1998). The differences, however, were found to be small and statistically non-significant in a study comparing tree species richness in 100 m × 100 m square plots versus 40 m × 250 m rectangular plots in Central Amazonia (Laurance et al. 1998). Given the patchy and fragmented nature of the deciduous and evergreen forests in our study area, it was impossible to survey the vegetation types in traditional square or rectangular plots. Rather, we tried to survey as environmentally homogeneous an area as possible, leading to our irregular plot shape design. There is little doubt that plot shape has influenced our results, especially those of the evergreen forest plot. The extent of this influence, however, seems to be small, since the species accumulation curves for all vascular plants together and for individual life-forms significantly decrease or level off when the hectare is completely surveyed, suggesting that sampling was representative in all three forest types.

Alpha diversity and plant density at Los Volcanes

Additional plant surveys across the entire Los Volcanes reserve (approx. 300 ha) have documented 65 species of pteridophytes (M. Kessler, unpublished data), of which 53 (82%) were recorded in the plots. The corresponding figures are 83% for Acanthaceae, 90% for Araceae, 84% for Bromeliaceae and 92% for Cactaceae. If these groups are considered to be

representative of the total flora, then our plots contain roughly 80–90% of the vascular plant flora of Los Volcanes reserve, which would then be estimated to be around 740–840 species, corresponding to about 6.4–7.2% of the Bolivian vascular plant flora (estimated at 11,600 species, Jørgensen et al. 2006). Species that were not encountered in the plots are either forest species that are patchily distributed or non-forest species occurring on sandstone walls of the area, secondary vegetation on landslides, rock falls or along streams.

The impressive number of individuals of *T. tenuifolia* and *T. bryoides* in the Los Volcanes plots is not unique to these forests. Both have been documented as the characteristic and dominant species of some seasonal forests of Central and Southern Bolivia (Navarro 2001). Likewise, Bonnet (2006) and Bonnet et al. (2007) reported high densities and wide regional distribution for *T. tenuifolia* in Paraná, Brazil. They attributed the success of this species in humid and seasonal semi-deciduous forests to its small size (ca. 25 cm long, Smith and Downs 1977), the presence of plumose wind-dispersed diaspores, CAM metabolism, its atmospheric nutrient acquisition strategy (i.e. species that have no form of absorptive root system, in which the tank habit is lacking and where epidermal trichomes cover the whole shoot system and are entirely responsible for nutrient and water uptake, cf. Griffiths and Smith 1983) and the fact that this species usually forms dense monospecific associations with no explicit preference for some position on the phorophyte. Most of these factors are also true for *T. bryoides*, in particular the small size of the plants (usually no longer than 5 cm), their plumose diaspores (Smith and Downs 1977) and the formation of dense monospecific populations (Navarro 2001).

Los Volcanes plots in a neotropical context

To our knowledge, there is only one other study (Balslev et al. 1998) that includes an inventory of all vascular plants in 1 ha of tropical forest and is therefore directly comparable to our study (although the mentioned study inventoried trees and shrubs of 1–5 cm dbh only in a 0.49-ha subplot). In the Amazonian terra firme rain forest of Cuyabeno, Ecuador, a perhumid area with 3555 mm of annual rainfall and no dry season, Balslev et al. (1998) found

942 species of vascular plants in 88 families. Our plots contained between 297 and 382 species in 60–75 families/ha for the three forest types studied. This is clearly much lower than the Cuyabeno plot, but lower rainfall and strong seasonality set the forests at Los Volcanes apart from the Amazonian site. There were further differences in the relative contribution of different life-forms to overall species richness at both sites. At Cuyabeno, trees (which made up 50% of species) were clearly the most species-rich group, distantly followed by epiphytes (making up 18% of species) and shrubs and lianas (both making up 11% of species). At Los Volcanes, trees were the most species-rich life-form in the deciduous and semi-deciduous forest but contributed only 32% of all species. Epiphytes (including hemiepiphytes) and lianas (23% and 22% in the deciduous forest, 22% and 23% in the semi-deciduous forest, respectively) followed them closely. Shrubs were less important in these forests, contributing 13% and 15% of all species in the deciduous and semi-deciduous forest, respectively, and having percentages only slightly

higher than terrestrial herbs (ca. 10%). The most striking difference is in the evergreen forest in which epiphytes (31%) were more species-rich than trees (27%).

For a more representative comparison of the Los Volcanes data with other neotropical sites, we constructed species accumulation curves for Los Volcanes that allowed comparisons with other surveys with plot sizes of up to 1 ha (Fig. 2). As Los Volcanes is found in a biogeographical transition zone and has high moisture variability between plots, our study plots cannot be easily assigned to any of the usual broad categories used for neotropical forests (lowland humid, montane humid, lowland dry, etc.). We therefore compared our richness counts with data from a wide range of other neotropical forest habitats.

Most inventories in lowland humid forests (mostly in Amazonia) have higher vascular plant, epiphyte, liana and terrestrial herb counts than any of the plots at Los Volcanes (Fig. 2). In contrast, plots inventoried in dry deciduous or humid montane forests have similar levels of species richness (Fig. 2). For example,

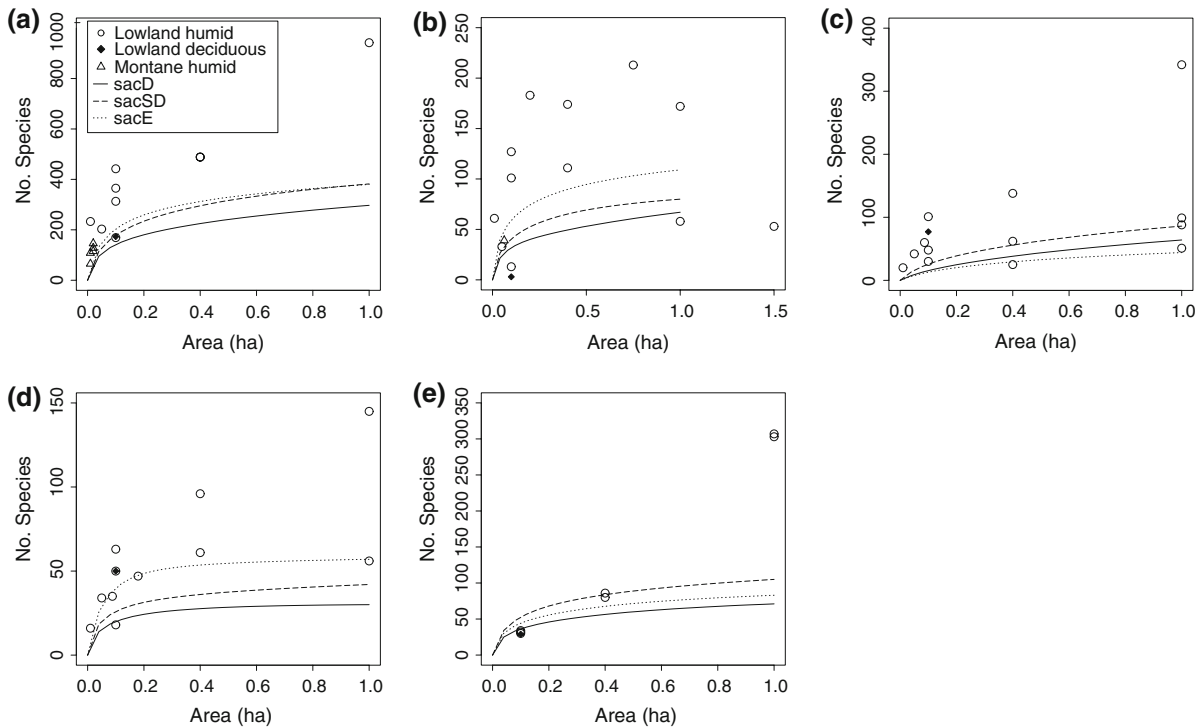


Fig. 2 Species accumulation curves (sac) for each forest type at Los Volcanes (D = deciduous, SD = semi-deciduous, E = evergreen) against species richness data of: **a** vascular plant counts, **b** epiphyte inventories, **c** liana inventories, **d**

terrestrial herb inventories and **e** woody plant inventories in the neotropics. Symbols described in the *legend* apply to the entire figure. Note the different scales of the x and y axes. (Values for individual sites are provided in Appendix 1)

vascular plant counts at Los Volcanes are similar to those in the humid mountains of the Carrasco National Park (Ibisch 1996) and those in the deciduous forest of Capeira and moist forest of Jauneche in Ecuador (Gentry and Dodson 1987), at least at small plot sizes (Fig. 2a). Epiphytes are perhaps the best represented group at Los Volcanes. They are more diverse here than a humid forest plot in Ecuador (Jauneche, Gentry and Dodson 1987) and at least as diverse as the humid forest plots in French Guyana (Sinamary, Bordenave et al. 1998), Venezuela (Surumoni, Nieder et al. 2000) and interestingly also as the Chocoan forests in Caquetá (Colombia, Duivenvoorden 1994). They also have higher species richness than other deciduous forests and similar species richness as montane forests (Fig. 2b). Lianas have similar levels of species richness to several humid forests in Ecuador (Yasuní, Nabe-Nielsen 2001; Burnham 2004), Colombia (Niqui and Coqui, Galeano et al. 1998) and Bolivia (Oquiriquia, Pérez-Salicrup et al. 2001). In contrast, the deciduous forest of Capeira in coastal Ecuador (Gentry and Dodson 1987) has a much higher species richness of lianas in smaller plots (Fig. 2c). Terrestrial herb counts are similar to other humid forests from Costa Rica (Whitmore et al. 1985), Panama (Royo and Carson 2005), French Guyana (Bordenave et al. 1998), Colombia (Galeano et al. 1998), Ecuador (Gentry and Dodson 1987; Poulsen and Balslev 1991) and Brazil (Costa 2004). The deciduous forest in Capeira (Gentry and Dodson 1987) again has a higher count of terrestrial herbs than any plot at Los Volcanes (Fig. 2d).

Tree species richness at Los Volcanes is similar to several other forest types in the neotropics. If only trees with $\text{dbh} \geq 10$ cm are considered, the plots at Los Volcanes are similar to other deciduous forests in Bolivia and reach the lower end of species richness of 1-ha plots in humid and montane forests (Figs. 2e, 3). If we compare the overall richness of trees on the Los Volcanes plots (including those with $\text{dbh} < 10$ cm) with several forest types inventoried by A. Gentry (0.1-ha transects using the exploded quadrat method, available at <http://www.mobot.org/MOBOT/research/gentry/transect.shtml>), the studied plots have higher species richness values than most dry deciduous forests in the neotropics. They have also values similar to the average species richness of humid montane forests but only reach the lower end of the species richness values of humid lowland forest (Fig. 3).

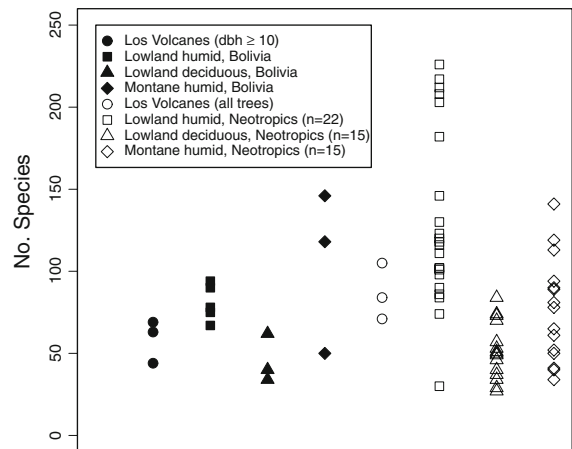


Fig. 3 Species richness values of woody plants and trees at Los Volcanes (LV) with $\text{dbh} \geq 10$ cm compared against species richness data of other woody plant inventories (1 ha, $\text{dbh} \geq 10$ cm) in Bolivia (filled symbols), and all trees inventoried at Los Volcanes compared to species richness data of woody plant inventories (0.1 ha, $\text{dbh} \geq 2.5$ cm) in the neotropics (empty symbols)

Contribution of non-woody plant groups to overall plant species richness

Non-woody plants, and specifically epiphytes, have been highlighted by Gentry and Dodson (1987) as the most important plant group in terms of species richness and individual numbers in wet tropical rain forests in Ecuador, whereas tree species with $\text{dbh} \geq 10$ cm were more or less equally well represented in dry, moist and wet forest. In the wet forest sampled by them, 35% of the species and 49% of the individuals were epiphytes. At Los Volcanes, epiphytes (including hemiepiphytes) included ca. 30% of the species and nearly 60% of the individuals in the evergreen forest plot. If terrestrial herbs are included, non-woody life-forms represent 45% of the species and more than 76% of the individuals. In the semi-deciduous and deciduous forest plots, figures are somewhat lower but still impressive. Epiphytes (including hemiepiphytes) comprised 22% and 23% of the species and 36% and 31% of the individuals on the semi-deciduous and deciduous forest plots, respectively. If terrestrial herbs are included, the figures are ca. 32% of the species in both forests and 58% and 52% of the individuals, respectively. Non-woody life-forms showed a consistent pattern across the different forest types and represented an important component of neotropical forests. This is

certainly overlooked when plots are only sampled for trees. In contrast, trees with dbh ≥ 10 cm represented only 14%, 18% and 16% of the species and 2.4%, 2.5% and 1.7% of the individuals on our deciduous, semi-deciduous and evergreen forest plot, respectively.

Despite these facts, species richness and floristic data arising from tree inventories are often used (for want of better and more complete, but also usually more work-intensive, information) to characterize all the surrounding vegetation because they are the major structural element (e.g. ter Steege et al. 2000a; La Torre-Cuadros et al. 2007). While this may be enough to identify the major forest types, and indeed some studies in tropical forests do confirmed a positive correlation between the richness of the woody component of a forest and its accompanying non-woody component (e.g. Webb et al. 1967), there is also evidence that this is not a consistent pattern (Duivenvoorden and Lips 1995 in Colombia; ter Steege et al. 2000b in Guyana; Williams-Linera et al. 2005 in Mexico; Tchouto et al. 2006 in Cameroon). Our own data indicate that there is no consistent correlation between tree species richness and the other life-forms studied at Los Volcanes. The comparisons of inventories across the neotropics discussed above also show that forests with higher tree species richness do not necessarily contain higher species richness in non-woody life-forms. In a neotropical context, the forests at Los Volcanes may be poor in terms of tree species richness, but they do show remarkable species richness of lianas, terrestrial herbs and, especially, epiphytes, challenging even those of the most diverse forests of the continent, the Colombian Chocó.

We have shown that tree species richness alone does not always correlate with species richness patterns in other life-forms (although it consistently did so with total species richness across the three forest types studied, as did the species richness patterns of lianas). We thus advocate that more effort be put into non-woody plant inventories in order to better assess the biodiversity of an area and to allow more informed conservation decisions to be made.

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