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DIPLOMARBEIT

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Diversity and Abundance of primary Hemiepiphytes in different Regions of Costa Rica

angestrebter akademischer Grad

Magistra der Naturwissenschaften (Mag. rer.nat.)

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Wien, im Dezember 2010

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an der
Fakultät für Lebenswissenschaften
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eingereicht von

Carina Lenotti

Wien, Dezember 2010

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Contents

1 Introduction

This master thesis is part of a survey on primary hemiepiphytes, their distirbution, abundance and diversity, in different regions of Costa Rica. The survey has been done in cooperation with David Bröderbauer, but we have examined different aspects in our seperate studies. I concentrate on diversity and general abundance of primary hemiepiphytes in different regions and on different sites (primary forests, secondary forests, and pastures), differing also between lowland and premontane sites, and Carribean- and Pacific-influenced regions. David, however, worked on „Spatial Distribution of Primary Hemiepiphytes in Different Costa Rican Rainforests“ and finished his work in his own master thesis 2008.

This thesis is formally constructed by two core chapters, which are drafts for papers and are intended to be published in the The Journal of The Marie Selby Botanical Gardens „Selbyana“, or a simillar magazine. Therefore these manuscripts are formated according to their preparation checklist. Preceding the manuscripts is an introduction consited of research aim and approach, general work flow, basic definitions, detailed description of the research sites and some detailed results, which are stripped-down to the basics in the papers itself. Postpositioned to the manuscripts is a Field Photo Guide to primary hemiepiphytes in Costa Rica and an abstract of the papers in geman language. As this theses consits of several parts, wich are intended to be used seperatly (the two manuscripts and the Field Photo Guide) some general information and phrases in introductions and methods may be redundant in the whole.

1.1 Approach

Primary hemiepiphytes (pHEs) are an important element of tropical rainforests, especially of wet lowland and montane forests (Gentry 1986; Williams-Linera & Lawton 1995). They are mostly woody plants, and more than 20 dicotyledonous families such as Moraceae, Clusiaceae and Araliaceae are known to contain species of the hemiepiphytic life form (Williams-Linera & Lawton 1995; Prosperi et al. 2001). But still there exits only few information on their abundance, diversitiy and distribution in different forest types, although pHEs are an important component of tropical moist forests (Todzia 1986; Orihuela & Waechter 2009). Often this information is only provided for a single genus such as *Clusia* and *Ficus* (Putz & Holbrook 1986), or pHEs are included in studies on holo-epiphytes (Kelly 1985; Ingram et al. 1996), but there they are only of less importance because of the comparatively smaller sample sizes within commensurate areas (Nieder et al 2001). Therefore there is a need for further investigations on diversity abundance and distribution of this life form (cf. Bröderbauer 2008).

1.2 Work flow

In this study we have examined the diversity and abundance of primary hemiepiphytes – their species, genera and families - in six different regions, different forest types in lowland and premontane sites, on 0.5 ha forest plots – primary and secondary forests – and on freestanding trees on pastures. The study is part of a survey on diversity and abundance of pHEs in Costa Rica (Bröderbauer, 2008). We have not focused on single species of pHEs, but have recorded all individuals within the sample areas.

Field work has been conducted during the dry season from January to May 2007 in six primary forest plots, two secondary forest plots and on six pastures together with David Bröderbauer. Whereas David Bröderbauer has examined the spatial distribution of primary hemiepiphytes, I have concentrated on their diversity and abundance.

Therefor I have calculated diversity, species richness and abundance of primary hemiepiphytes in seven different regions, different forest types in lowland and premontane sites, on 0.5 ha forest plots (one of 0.2 ha size) and on freestanding trees on pastures. Another question has been, if the sites are smilar to each other using different simmilarity measurements. Furthermore I have calulated Familiy Importance Value and Important Value Index of the families and species on all our sites, and I have examined the different generas and families in nonnumeric multidimensional scaling according to their location of their habitat. Detailed information on the methods used in field work and in data analysis are given in the papers. For the Filed Photo Guide I used photographs we have made of our vouchers and/ or the plants in the field. If photo and/ or voucher is from another resource it is marked and cited.

1.3 Definitions

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Whereas holo-epiphytes spend their whole life on top of other plants, or structures, without connections to the ground, hemiepiphytes also have an earth-bound phase in their life (Kress 1986). We can distinguish between primary hemiepiphytes and secondary hemiepiphytes. Primary hemiephiphytes, on the one hand, start their life epiphytically and send roots to the ground and so establish a connection to it later on (Schimper 1888). They are often woody dicots and could get treeshaped and treesized, sometimes they even kill their hosts by strangeling it. Secondary hemiepiphytes, on the other hand, germinate on the ground and climb onto a tree (or other structure). They loose their connection to the gound later on in their life circle, sometimes renewing it with new roots (i.e. the genus *Philodendron* of the family Araceae). Secondary hemiepiphytes mostly are herbaceaous, as the monocot aroids (Araceae), but are also found as woody plants like *Marcgravia* and *Sourobea* of the Marcgraviaceae (cf. Bröderbauer 2008, p. 1). In this thesis I focuse on primary hemiepiphytes, so if I don't reference to secondary hemiepiphytes explicitly, "hemiepiphyte" means primary hemiepiphyte.

1.3.1 Taxonomy

Over 800 species of primary hemiepiphytes and over 600 species of secondary hemiepiphytes are known. Putz and Holbrook (1986) even counted 2000 species in both growth forms. Data varies between 25 families and 59 genera (Williams-Linera & Lawton 1995) and 32 families (Prosperi et al. 2001). Due to the fact that many trees can grow accidentally hemiepiphytic and/ or that some species are able to establish as both – hemiepiphyte or tree – the species number is still unclear (cf. Bröderbauer 2008, p. 2 ff).

1.3.2 Distribution

Hemiepiphytes are mainly found in tropical wet forests (Benzing1990) and are absent in dry forests. There they are distributed from sea level up to 2500 m above sea level, their density increasing with increasing precipitation and humidity, and therefore hemiepiphytes are most abundant from premontane to montane forests (Williams-Linera & Lawton 1995). In tropical lowland forests they partly replace lianas (Gentry & Dodson 1987), which themselves are more abundant in moist and dry forests (Gillespie et al. 2000). "In general, primary hemiepiphytes are most abundant in undisturbed primary forests (Prosperi et al. 2001). In second growth forests hemiepiphytes are rare. Some of the reasons are limited time for colonization as well as differences in physical structure and microclimate (Williams-Linera & Lawton 1995)." (Bröderbauer 2008, p. 3).

1.3.3 Life circle

After Prosperi et al (2001) the life cycle of primary hemiepiphytes is consisted of following stages:

- seed dispersal and germination
- development of an ephemeral primary root system and slow growth
- establishment of ground contact by and adventitious, fast growing root system
- upward growth of the shoot system in the canopy
- flowering and fruiting

It is important that germination is on suitable sites on tree structures, whith humidity and fertile substrat, like the axils of large branches (Putz & Holbrook 1986). Therefore froot dispersial is essential for the primary hemiepiphyte, they are mostly dispersed by animals, mainly birds and bats, and other mammals (Serio-Silva & Rico-Gray 2002). Some species, i.e. *Cosmibuena valerii* (Rubiaceae) are also wind dispersed. Beside the dispersal, also vegetative propagation of the plants is essential. Besides sexual propergation hemiepiphytes can also propagate vegitative. “A high degree of root fusion is observed in stranglers like *Ficus*, *Clusia*, *Schefflera* or *Coussapoa* (Williams-Linera & Lawton 1995). Thus, individuals can fuse and propagate vegetatively. The vegetative propagation is facilitated by formation of suckers in the genus *Coussapoa* or layering in *Clusia* and *Ficus* (Prosperi et al. 2001).” (Bröderbauer 2008, p. 4)

For germination and growth nutrient supply is important. Primary hemiepiphytes do not need nutriens, wich are only found in terrestrical soil, but they do need permanent supply from the ground to grow (Wanek et al 2002a). For germination itself light and water play a more important role than nutrition supply (Laman 1993; Holbrook & Putz 1996a).

1.3.4 Evolution of hemiepiphytism

Taxonomy of primary hemiepiphytes indicates that this life form has evolved several times indipendently (Putz & Holbrook 1986). In evolution accidental hemiepiphytes, which are normaly ground growing plants and germinate and develop on trees accidently, could have been the first step. This is still common in tropical cloud forests, where many trees could be found as accidental epiphytes. This first step could lead through isolation and radiative adaption to specialization in hemiepiphytes, in particular in isolated syystems i.e. mountain forests (Williams-Linera & Lawton 1995). In this evolution the rooting system plays an important role. The ground connection leads to advantages in nutriation and water supply. Holo-epiphyts, without this connection to the ground have to cope with this problems, but have the same light ressource in the rainforest by settling in canopy layers (Williams-Linera & Lawton 1995). “Thus, hemiepiphytes can grow larger and compete with the trees for light. Meyer & Zotz (2004) found that primary hemiepiphytes of the Araceae were limited in the height of establishment by the growth rate of their roots. Thus, root growth is a key factor for establishmentl in the tree crowns.” (Bröderbauer 2008, p. 1f)

1.3.5 Hemiepiphytes and their hosts

Hemiepiphytes need their hosts for the structure they provide to them. Therefore they are often referd to as structural parasits. They compete with their hosts in other ressources, like nutrition and water, by having their root systems directly beside them, and some species (i.e. *Clusia rosea* or *Ficus nymphaeifolia*) also compete for light by overgrowing their host’s canopy. Hemiepiphytes do not acquire these resources directly from their hosts.

Many hemiepiphtes are not able to survive without the structure of their host, and therefore they do not to harm their host too much. Other species, in particular *Ficus* spp. or *Clusia* spp. could strangle their host and replace it. Some other species (i.e. *Clusia osaensis*) act similar as lianas as binder of tree crowns (Prosperi et al 2001).

Various studies examined that hemiepiphytes do not colonize trees randomly but prefer certain tree species as hosts (Todzia 1986; Michaloud & Michaloud-Pelletier 1987; Clark & Clark 1990; Daniels & Lawton 1991; Laman 1996a). Suitable hosts can provide the essential resources for hemiepiphytes: a stable site, humus, water and light. The different colinitation rate of tree species is due to animal dispersion of hemiepiphytes, because dispersers prefering tree species for roosting, feeding or as a shelter. Another factor of colinization on a tree are host tree attributes: its bark texture and the trunk physiognomy. They should be able to retain humus and therefore also humidity for proper germination sites (Todzia 1986). "Another important factor for colonization is the age of the host tree. According to Nieder et al. (2001), hemiepiphytic figs may colonize trees only after succession of other plants, so that host trees would have to be old enough to exhibit these successional stages. Nieder et al. (2001) conclude that forests have to be close to climax to offer suitable habitats." (Bröderbauer 2008, p. 7)

1.3.6 Physiological and morphological adaptations

Hemiepiphytes have a different moprphology and pysiology than trees, especially in their hydraulic architecture. After Zotz et al. (1994 & 1997) hemiepiphytes are having a higher specific conductivity and they invest less wood unit per leaf area. Detailed information on these differences and their implications are still unknown.

Among hemiepiphyteic species themselfes different adaptions in their physiology and morphology, like xeromorphic leaves, thick cuticula, depressed stomata and water accumulation in the hypoderm, could be explained to different ecology of the species (Putz & Holbrook 1986). Adaptions may even differ between juvenile plant in the epiphytic stage and adult plants (Putz & Holbrook 1989). "The main function of these adaptations is to protect the plant, especially in the epiphytic phase, from dehydration (…) Plants in their epiphytic phase had a higher specigic leaf area and a higher stomatal density than ground-rooted ones (Holbrook & Putz 1996b)" (Bröderbauer 2008, p. 8)

Other differences between hemiepiphytic species or different life stages in one species occour in utilization of water sources and photosyntethic adaptions. For example use epiphytic individuals of *Schefflera rodrigueziana* (abundant in cloud forests), water from mists, clouds and fog, but adult individuals use water in the soil (Feild & Dawson 1998). Photosynthetic adaptions are also importand factors to reduce water stress. Especially the genera *Clusia*, *Havetiopsis* and *Oedematopus* (Clusiaceae) are known to perform Crassulacean Acid Metabolism (CAM) in some species in response to the climatic conditions. They are also able to switch between C3 and CAM pathway (Zotz et al. 1999, Wanek et al. 2002b).

To adapt to environmental changes in the tree crown and to mantain the stable positon, like light stimulation, sequential reiteration of single architectural units is very important for hemiepiphytes (Prosperi et al 2001).

1.4 Basic geographical and climatic features

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1.4.1 Overview of selected regions of Costa Rica

"Costa Rica is a part of the Central American land bridge, lying between Nicaragua in the north and Panama in the south. The national territory covers 51.100 km² and is surrounded by the Carribean sea in the east and the Pacific ocean in the west. The Pacific region of Costa Rica includes two large peninsulas, the Peninsula de Nicoya in the north and the Peninsula de Osa in the south. The main mountain ranges that separate the Pacific and Atlantic lowlands are the Cordillera de Guanacaste, the Cordillera de Tilaran, the Cordillera Central and the Cordillera de Talamanca." (Bröderbauer 2008, S. 9)

Field work has taken place in six different regions of Costa Rica (Figure 1). We have observed seven primary forest plots, two secondary forest plots and six pasture plots in Costa Rica. Two primary forest plots and two pasture sites are at higher elevations about 1500 m above sea level (asl), on the Cordillera de Tilaran in the forest reserve of Los Alpes and on the Fila Costeña (Cordillera Costeña). Whereas our site in Los Alpes is influenced by Atlantic climatic patterns, Fila Costeña is influenced by Pacific climate. Another primary forest plot and a pasture site plot are at the lower Pacific slopes of the Fila Costeña at about 500m asl, nearby the village of San Miguel. Two adjoining lowland primary forest plots, a secondary forest plot and a pasture site are placed at the border of the Piedras Blancas National Park near the Tropenstation La Gamba, about 90m asl. This site is also on the Pacific slope of Costa Rica, not far of the Golfo Dulce (Pacific ocean), opposite to the Peninsula de Osa. Another pasture site is situated north of this region nearby the village Dominical, in Hacienda Baru. We have also placed one primary forest, a secondary forest plot and a pasture in the Carribean lowlands, close to Puerto Viejo de Sarapiqui. The primary forest site is at the research station of La Selva, the secondary forest and the pasture site are in Nogal, at the nature reserve of the Compañía Bananera del Atlántico Ltda. Some of our observations have been done in the primary forest of the National Park of Santa Rosa, in the North of Costa Rica on the Pacific slope.

1.4.2 Overall climatic patterns

The climate of Costa Rica is for the most part influenced by three atmospheric circulation patterns (Sanford et al. 1994):

- Intertropical Convergence Zone (ITCZ): in this zone southern and northern hemispheric trade winds come together in the equatorial trough. Therefore it is a zone of low pressure. It also is associated with intense solar radiation and heating (Clark et al. 2000). It therefore influences the seasonal cloud cover and rainfall. From Dezember to April it lies south of Central America and causes the dry season in Costa Rica. When it shifts over Central America in May the wet season begins.

- easterly waves embedded in the trade winds: this are low-depression troughs from West-Africa. They cause higher precipitation in September, especially in the Carribean region.

- northern trade winds from North America: These winds bring cold air and rain to Central America in the months November, December, January and in the beginning of February (Clark et al 2000). They are especially important for higher elevations in Costa Rica (Lawton & Dryer 1980).

The study has been carried out in five lowland and two premontane primary rainforests, two lowland secondary rainforests and four lowland and two premontane pastures (Table 1). Each forest plot was of 0.5 ha size, but the plot in Santa Rosa 0.2 ha. On each pastures 40 freestanding trees have been observed, but on Fila Costena 27 and in Baru 20.

<u>Pacific-influenced region:</u>

Three forest sites – two primary forests and one secondary forest - and one pasture site (plots 1, 2 and 9) are located on the Southern Pacific slope of Costa Rica in the Golfo Dulce Region. Two primary forest sites and two pasture sites are located on the eastly adjoining Fila Costeña (plot 3, 4,10 and 11). Another pasture, also located on the Southern Pacific slope, has been observed in Baru, nearby Dominical, in the region of Peninsula de Osa (plot 14). On the Pacific slope, in the north of Costa Rica, a smaller forest plot has been examined in the Santa Rosa National Park (15).

Figure 1. The sample sites in Costa Rica: 1 – La Gamba in the Golfo Dulce region; 2 – Los Alpes on the Cordillera de Tilaran; 3 – La Selva and Nogal, in the Carribean lowlands; 4 – Fila Costeña and San Miguel on the Cordillera Costeña, 5 – Hacienda Baru, 6 – Santa Rosa. Detailed maps at the bottom of La Gamba, San Miguel and Fila Costena, Los Alpes and La Selva and Nogal (left to right)

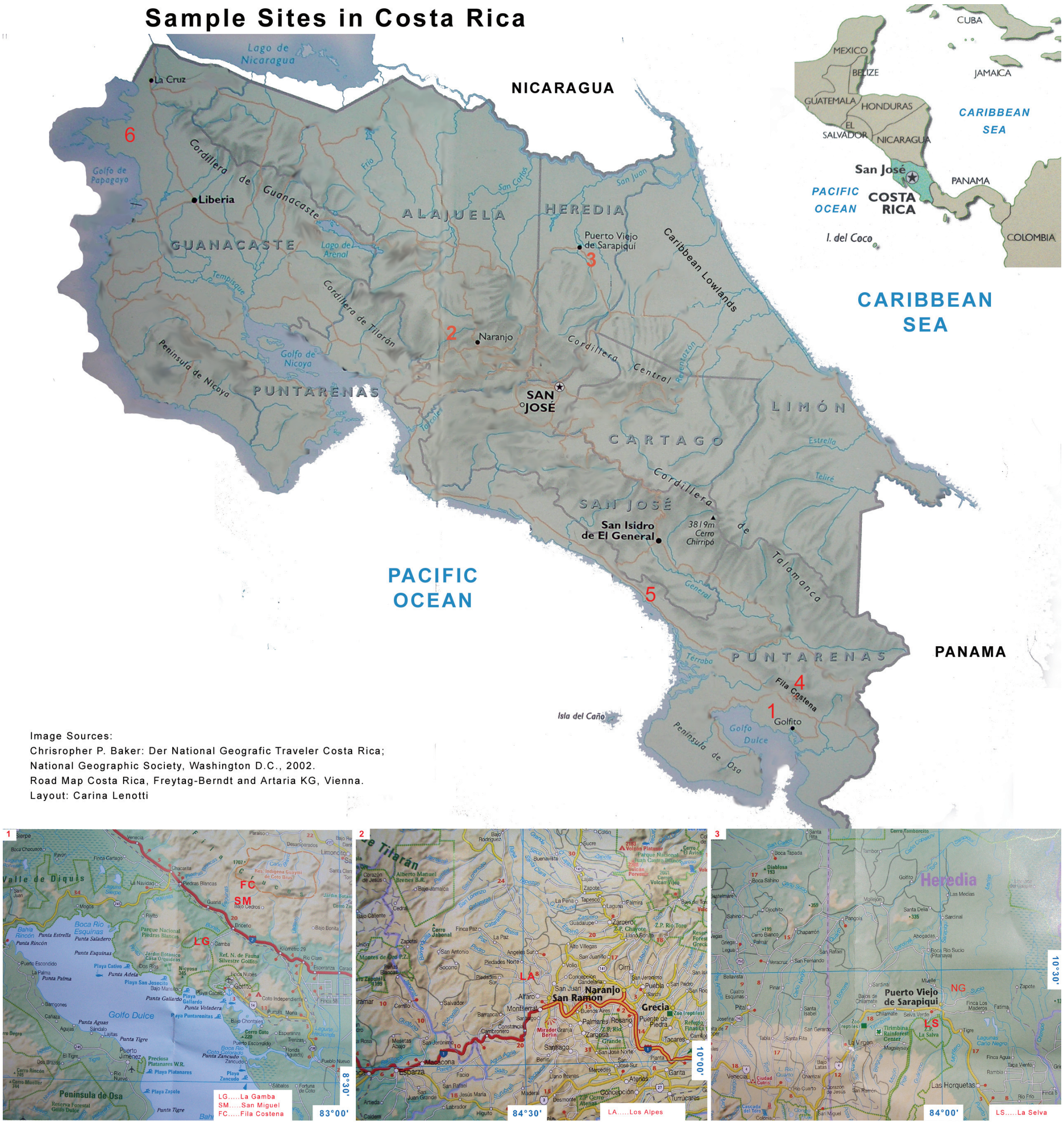

Image Sources:
Chrisropher P. Baker: Der National Geografic Traveler Costa Rica;
National Geographic Society, Washington D.C., 2002.
Road Map Costa Rica, Freytag-Berndt and Artaria KG, Vienna.
Layout: Carina Lenotti

Table 1. Description if the study sites.

	Site	Location	Altitude (m)	Mean Precipitation (mm/year)	Mean Temperature (°C/year)	Inclination (%)	Coordinates
1	La Gamba gorge	Lowland/ Pacific slope	90	6000	25.2	15	8°42’16”N, 83°12’15”W
2	La Gamba slope	Lowland/ Pacific slope	90	6000	25.2	20-30	8°42’16”N, 83°12’15”W
3	La Gamba secondary	Lowland/ Pacific slope	115	6000	25.2	0-20	8°41’57”N, 83°12’09”W
4	San Miguel	Lowland/ Pacific slope	500	~6000	No data	30	8°44’59”N, 83°9’40”W
5	Fila Costeña	Premontane/ Pacific slope	1450	~6000	17-22.5	10	8°47’25”N, 83°8’21”W
6	Los Alpes	Premontane/ Pacific slope	1480	2500	18-21	7	10°8’N, 84°34’W
7	La Selva	Lowland/ Carribean slope	50	4000	25.8	0-3	10°25’27”N, 78°38’23”W
8	Nogal	Lowland/ Carribean slope	50	4000	25-26	0	10°27’86” N 83°57’02” W
9	La Gamba pasture	Lowland/ Pacific slope	90	6000	25.2	0-7	8°42’20”N, 83°11’41”W
10	San Miguel pasture	Lowland/ Pacific slope	500	~6000	No data	0-5	8°45’15”N, 83°8’42”W
11	Fila Costena pasture (27 trees)	Premontane/ Pacific slope	1310-1400	~6000	17-22.5	0	8°47’12” N 83°8’28” W
12	Los Alpes pasture	Premontane/ Pacific slope	1480	2500	18-21	10	10°8’N, 84°34’W
13	Nogal pasture	Lowland/ Carribean slope	50	4000	25.8	0	10°27’6” N 83°57’26” W
14	Baru pasture (20 trees)	Lowland/ Pacific slope	0	4000	26	0	9°16’01” N 83°52’58” W
15	Santa Rosa (5 subplots)	Lowland/ Pacific slope	~0	1300	27-30	5	10°53’N 85°46’W

Atlantic-influenced region:

In addition, a forest plot and a pasture plot are placed on the Cordillera de Tilaran (6 and 12). A primary forest plot, a secondary forest plot and an additional pasture are located in the Carribean lowlands (7, 8 and 13).

1.4.3 Description of the research plots

Pacific-influenced regions - lowland:

La Gamba (LG): primary forest gorge, primary forest slope, secundary forest, pasture

Two lowland primary forests plots, a secondary forest plot and a pasture plot with 40 trees have been observed in LG. This is located at the border of the Piedras Blancas National Park, near the Tropical Research Station La Gamba. The national park is covered by tropical wet forest (after Holdridge et al. 1971), rainfall averages 6000 mm per year, with a short drier season from January to March (Weissenhofer & Huber 2001).

The two primary forest plots are directly adjoining plots, but differed in inclination and structure. The first one, the slope forest, has an average inclination of 15 %, whereas the second plot, the gorge forest, has inclinations between 20 and 30 %. Exposition is mostly SW to S and it is located around 90 m above sea level (asl). A small rill passes through the SW part of the gorge forest and there is a small gap at the SO part of the slope forest. Both plots are characterized by the high abundance of palms, especially *Socratea exorrhiza*. The forest consits of three canopy layers: an upper canopy from 25-35 m, a middle canopy of about 20 m and a subcanopy of 10-15 m. Single emergents are reaching heights of more than 40 m (cf. Bröderbauer 2008).

The secondary forest is located SW of the Tropical Research Station La Gamba. It is an about a 30 year old forest with an inclination between 5 % at the edge of the brook to 20 %, exposition is NW to N and it is about 115 m asl. This forest is characterized by two canopy layers (one at 10-15m and a second around 18 m, few trees reaching a height of more than 20 m), the tree *Vochysia* sp. and the liana *Doliocarpus* sp. are frequent.

40 freestanding trees have been observed for HEs on the pasture of LG. It is also adjoyning the Tropical Research Station La Gamba near the Piedras Blancas National Park. The pasture is about 90 m asl, an incination between 0-10 %. Trees are between 5 and 17 m high.

San Miguel (SM): primary forest, pasture

In SM we have had another primary forest site in the Golfo Dulce region, also classified as tropical wet forest (after Holdridge *et al*. 1971). It is located near the small village San Miguel, about 10 km east of the Tropical Research Station La Gamba at the basement of the Fila Costeña. It is on a plateau of at 500 m asl, an average inclination of 30 %, exposition SO, and at the botoom of the slope a brook limits our plot. As in our primary forest plots in LG, *Socratea exorrhiza* is very frequent here. Two canopy layers characterize this forest: the upper layer of 15-30 m, the lower of 10-15 m (cf. Bröderbauer 2008).

On the pasture of SM we have observed 40 freestanding trees between 5-17 m. The pasture is east of the forest 500 m asl, inclination between 0-10 %.

Hacienda Baru (BA): pasture

We have observed 20 freestanding trees at the way from the Hacienda Baru to the beach. These trees are standing beside the road in an alley and are between 5 and 23 m high. The Hacienda Baru is located nearby Dominical in the south of Costa Rica on the Pacific ozean, north of Peninsula de Osa influenced region. It is a reagion with tropical wet forests, an anueal rainfall of 4000 mm and a clear dry season up to 60 days from january to march (Kappelle 2002 and climatic information from Hacienda Baru).

Santa Rosa (SR): primary forest

In the Santa Rosa National Park we have observed a primary forest plot of 0.2 ha size about 500 m east of the Playa Naranja. This region in the province Guanacaste is characterised by an average rainfall of 1300 mm per year, with clear dry season from december to april (Janzen et al 1983). It is covered by and an tropical seasonal forest (after Holdridge *et al*. 1971), and in the dry season most of the trees drop their leaves. Our plot has an inclination between 3 and 10 %, exposition is W to SW. Lianas are frequent many trees branch out at the ground, some cactuses are in the understory.

Pacific-influenced regions – Premontane (pm):

Fila Costena (FC): primary forest, pasture

This site is also located in the south-west of Costa Rica directly on the Fila Costeña, which is part of the Cordillera Costeña, at 1450 m asl. It is classified as premontane rain forest (after Holdridge 1971). Here the climate is very wet, because of clouds that are coming from the Golfo Dulce and gather along the mountains. Annual rainfall for the region is probably more than 6000 mm (Werner Huber, pers. com.), with a short dry season from January to March (Weissenhofer & Huber 2001). The peak of the Fila Costena reaches 1700m asl, our plot in the primary forest is located on the pacific slope about 100 m below the crest surrounded by pasture land.

The primary forest plot itself consists of a 20 to 30 m tall canopy and a 10 to 15 m tall subcanopy, it has only few high trees and many gaps. Therefore, a great part of the sunlight reaches the dense understory (cf. Bröderbauer 2008). Inclination is between 5 and 10 %, exposition is S.

We have observed 27 freestanding trees on FC, on the pasture below our forest plot, these have been all trees we could find on that pasture, which is sourounded by a primary forest in the north, east and west. In the south the edge of the pasture is a gap. The pasture itselve is plain, but some trees are on a little lower level. So the trees are at between 1300 m asl and 1400 m asl. Some of the trees are broken (maybe through lightning) all are between 5 m and 18 m high.

Atlantic-influenced regions – lowland (al):

La Selva (LS)/ Nogal (NG): primary forest (LS), secundary forest (NG), pasture (NG)

These sites have been located in the Carribean lowlands of Costa Rica, that are mainly covered with tropical wet forests (after Holdridge et al. 1971). Here, annual rainfall averages 4000 mm with lowest precipitation from February to April (Sanford et al. 1994).

The primary forest plot is located at the La Selva Biological Station. It is 50 m asl, plain, only in the NE edge it is sloping down to a small rill. The plot is west of the Quebrada El Salto and north of the path CCL. The forest has three canopy layers at 20-30 m, 15-20 m and a subcanopy at 10 m. Some single trees are reaching heights up to 35 m. The plot includes several small gaps (cf. Bröderbauer 2008).

The secondary forest in the Carrebean Lowlands is located in Nogal, a village nearby Puerto Viejo de Sarapiqui, about 8 km from La Selva. It is a nature reserve of the Compañía Bananera del Atlántico Ltda. of 102 ha located between Río Sucio and a monoculture of bananas. In this area the disconected forest fragments are of different succession stages (Bogantes Montero 2006, Weithaeuser 2004). Our site is north of Rio Sucio in an about 30-year-old floodplain forest. Formerly a pasture, it is characterized by few mature old trees of about 30 m heigth. Part of it is in an early succession, with compact understory of *Heliconia spp.*. As in La Selva, the plot is plain. *Socrathea* sp.*, Asterogyne* sp. are frequent, canopy layers are at 20 m and a second at 10-15 m, some trees even smaller.

Our 40 freestanding trees we have observed on two located pasture plots nearby on even sites not far off the banana plantations. Trees are between 6 and 23 m heigh.

Atlantic-influenced regions – premontane (am):

Los Alpes (LA): primary forest, pasture

The second premontane site is situated in the southern part of the Cordillera de Tilaran 1480 m asl. It is part of a private rainforest reserve named “Reserva Los Alpes” covering 100 ha. Annual rainfall is about 2500 mm with a dry season from December to May (Haber et al. 2000). Following Holdridge (1971) Los Alpes is classified as premontane wet forest. Our site is located directly below the crest that forms the Continental Divide and, therefore, is influenced by the more humid Atlantic climate during the whole year.

The primary forest plot has an inclination of between 3 % and 10 %, exposition is W, and it is 1500 m asl. The forest is sparse, highly influenced by the Atlantic winds. On the part below the crest, canopy height is 10 to 15 m, whereas below canopy height is on average 20 m and subcanopy height 10 m (cf. Bröderbauer 2008).

On the pasture in the west of the forest we have observed 40 freestanding trees, inclination is around 12 %, exposition W. Trees are between 3 and 17 m heigh.

1. 5 Results on similarity of the research plots

The detailed results of the results in similarity of our research plots are excluded from the manuscript in paper one and presented here. In the manuskript there is a summary of the most importand results to keep it short and concise.

Methods. The Methodes to calculate similarity Jaccard, S∅rensen, Bray-Curtis and NESS Indices have been used. Jaccard, S∅rensen and Bray-Curtis have been calculated with EstimateS 8.0.0 (Colwell, 2005). Calculation of Normalized Expected Species Shared Index (NESS) has been carried out with an Excel Plug-In (Fiedler 2007). To adapt to the rare species the sampling parameter m has been set to m = 6 for comparison of the forest plots and to m = 3 for comparison of the pasture plots.

To compare the forests and the pasture plots according to their similarity in species composition of primary HEs, four indizes were calculated: the qualitative Jaccard and Sorensen and the quantitative Bray-Curtis and NESS (Normalized Expected Species Shared

Index). All indizes have values between 0 and 1. The closer the value comes to 1 the more compareably are the sites. Results are shown in table 4 for the forests and table 5 for the pastures in the manuscript of paper 1.

Forests

Concerning all four indices it comes clear that the secondary forest of NG (al) has the least similiarity to all other forests, with a high number of zero values, and values that are very close to zero. First of all the secondary forest in LG (pl) shows a littly similarity to NG (al) in all indizes, second the primary forest in SM (pl) (also in all four indices), third (in Jaccard, Sorensen, and Bray-Curtis) is the gorge forest in LG (pl), with a very low value. The NESS index shows a higher similarity to LS (al), which has zero values in the other indizes, and on fourth place comes LGs (pl) gorge forest in NESS.

The highest similarity shows, in Jaccard and Sorensen, LGs (pl) primary slope forest with LGs (pl) secundary forest and, in Bray-Curtis, LGs (pl) primary slope forest with LS (al) primary forest. With NESS the two have high indizes, ranking the similarity of the two forests of LG (pl) first and this index also shows a high similarity of LS (al) and the secondary forest of LG (pl), even a little higher than the similarity of LS (al) and LGs (pl) slope forest.

The primary gorge forest in LG (pl) shows in all indices a high similarity to the other forests of LG (pl). In the qualitative indizes the seondary forest of LG (pl) is first, the slope forest second, both values in both indices are close toghether. In Bray-Curtis SM (pl) is in second place (which is on the qualitative in third) and the slope forest is in first, third is the secondary forest, each with a difference of 0.1. NESS ranks also the slope highest in similarity to the gorge forest, second the secondary forest again and before SM (pl) comes LS (al) in third place. The least similarity to the gorge forest in LG (pl) in all indizes show NG (al) and LA (am), in NESS LA (am) is behind NG (al), in the other three they have the same low values. FC (pm) has also a low value, but ranks higher than NG (al) and LA (am).

The primary slope forest in LG (pl) shows, as mentioned above, a high similarity to the secondary forest in LG (pl) (Jaccard, Sorensen, Ness in first place, in Bray-Curtis in forth), and to the forest of LS (al) (Bray-Curtis in first, NESS in second, in the qualitative indizes in third) and also a high similarity with a high value to the gorge forest in LG (pl) in all indizes (Jaccard, Sorensen, Bray-Curtis in second place, NESS in third place). Next in similarity to the slope forest in LG (pl) is SM (pl), and least again LA (am) and NG (al) with low values in all indizes, but LA (am) has a bigger value as NG (al) in three indizes.

The secondary forest in LG (pl) shows, as mentioned above, a high similarity to LGs (pl) slope forest, which ranks first in all indices. It is also very similar to LS (al) in NESS, in this index it is in second place in similarity as it is in Bray-Curtis. The qualitative indizes rank LS (al) in fourth place, behind the gorge forest in LG (pl) (second, and third in Bray-Curtis, forth in NESS) and SM (pl) (third, third also in Bray-Curtis and forth in NESS). NG (al) is in all indizes in fifth place in similarity, FC (pm) and LA (am) (in that order), are not very similar to the secondary forest in LG (pl).

The primary forest of SM (pl) shows high similarity to the forests of LG (pl) in all indizes. The ranking in similarity of the qualitative indizes is as follows: LG (pl) gorge forest, LG (pl) secondary forest and LG (pl) slope forest. FC (pm) lies pretty close to the LGs (pl) slope forest in forth place in that indizes. Bray-Curtis puts the slope forest of LG (pl) in first place, the gorge forest in second and the secondary forest in forth close behind the forest of LS (al). LS (al) is in the qualitative indizes in sixth place, in NESS in forth, behind the forests of LG (pl) (secondary, slope, then gorge). LA (am) has in all indice low values, also FC (pl) and NG (al) have low values in the quantitative indices.

The primary forest of FC (pm) shows very low values to all other forests in all indizes. The most similarity it shows to the forest of SM (pl) and the primary forests of LG (pl) in all four indizes. SM (pl) in first place in Jaccard, Sorensen and NESS, second in Bray-Curtis. The primary forests of LG (pl) equally in first in Bray Curtis, the slope forest second in NESS and third in the qualitative indizes, the gorge forest third in NESS and fifth in the qualitative indizes. Least similarity it shows to the secondary forests in NG (al) and in LG (pl). LA shows a realtivly high similarity to FC (pm) compared to the similarity of the other forests, in the qualitative (second place) and Bray-Curtis (third place), but a very low in NESS (sixth). LS (al) is in all four indizes in the middle of relative similarity.

The primary forest of LS (al) shows a high similarity to the forests of LG (pl) in the qualitative indizes (slope, gorge, secondary forests), and as mentioned above, in Bary Curtis and NESS it has a very high value to the slope forest of LG (pl), in NESS an even higher value to the secondary forest in LG (pl). SM (pl) shows a pretty high value too in NESS (forth place) and Bray-Curtis (second place), but the value in Jaccard and Sorensen is not that high. Still this forest is on forth place in similarity to LS (al) in these indizes. NG (al) has a very low value in all of the indizes, only in NESS it has got a higher similarity value than the forests of LA (am) and FC (am).

The primary forest of LA (am) is not very similar to all other observed forests, it shows low values in all of the indizes to all other forests. In Jaccard, Sorensen and Bray-Curtis it shows the most similarity to FC (pm), the least to NG (al). Bray-Curtis and especially NESS have many values in equal relative positions with values very close to zero. Relativly high similarity this forest has to LS (al), which is second in the qualitative indizes.

Pastures

The pastures are not very similar to each ohter, all indizes show very low values to all pastures compared to each other, many zero values as well. The most untypical pastures are in BA (pl) and NG (al). BA (pl) is only a little compareable to the pasture of LG (pl), in NESS it even has the highest value in similarity. NG (al) is only a little compareable to SM (pl), but there these pastures have relativly high values of similarity in the qualitative indizes. In Bray-Curtis and NESS, however, the value of SM (pl) to LG (pl) is a lot higher, and this value is not a big difference ot the one of SM (pl) and NG (al) in the qualitative indizes. Also SM (pl) and FC (pm) have a relativly high value of similarity.

LG (pl) is relativly similar to SM (pl) and BA (pl), not at all to NG (al).

LA (am) is relativly similar to FC (pm) and LG (pl), not to the other pastures.

FC (pm) is relativly similar to SM (pl), LA (am) (first in Bray-Curtis) and a little to LG (pl).

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2 Manuscript for paper 1:

LENOTTI: DIVERSITY OF HEMIEPIPHYTES

DIVERSITY AND ABUNDANCE OF PRIMARY HEMIEPIPHYTES IN DIFFERENT REGIONS OF COSTA RICA

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ABSTRACT We have compare the abundance and diversity of primary hemepiphytes in five lowland primary forest plots, two lowland secondary forest plots and two premontane primary forest plots of 0.5 ha size and additionally on six different pastures in Carribean- and Pacific-influenced regions of Costa Rica. We have found high abundances in all our primary forest plots from 6.6 to 12.8 individuals per 0.1 ha in lowland sites, up to 129.8 individuals per 0.1 ha in premontane forest sites. Different diversity indizes and species richness estimation has been carried out as well as the calculation of similarity of the plots to each other. Hs values reaching 2.36 to 2.74 in primary forests, 0.52 to 1.23 in secondary and high disturbed forests, and 1.01 to 2.16 on pastures. Species Richness extimation with ACE calculates values up to 38.30 in premontane primary forests, values around 17 in lowland primary forests and values up to 8.25 in secondary forests. Results are showing that abundance and diversity increase with the increase of altitude. They also indicate that hemiepiphyte diversity is a measurement of the disturbance in a forest and increases with wetter conditions. Forest plots show similarity, if the forest type is similar and are not only influenced by regional patterns. Whereas abundance per tree increases on freestanding trees species, diversity does not.

Key words: hemiepiphyte, abundance, diversity, similarity, species richness, Costa Rica, lowland and premontane diversity

INTRODUCTION

Primary hemiepiphytes (pHEs) are an important element of tropical rainforests, especially of wet lowland and montane forests (Gentry 1986; Williams-Linera & Lawton 1995). They start their life cycle as epiphytes on trees and send roots to the ground later on (Putz & Holbrook 1986). Most species are woody plants, belonging to more than 20 dicotyledonous families such as Moraceae, Clusiaceae and Araliaceae (Williams-Linera & Lawton 1995; Prosperi et al. 2001). Besides, Meyer & Zotz (2004) have also found pHEs in the Araceae, which mainly comprise secondary hemiepiphytes.

Whereas holo-epiphytes, which spend their hole life cycle epiphyticlly, are well-studied objects in tropical ecology, which is due to their high abundance, hemiepiphytes are often only included in these studies (Kelly 1985; Ingram et al. 1996), but they play a marginal role in analyses, because of the comparatively smaller sample sizes within commensurate areas (Nieder et al. 2001). Information on hemiepiphytes is often provided for single genera and species of primary woody hemiepiphytes such as *Clusia* and *Ficus* (Putz & Holbrook 1986) and species of the Araceae (Meyer & Zotz 2004). Informations on abundance and diversitiy and their distribution in different forest types are very rare, although pHEs are importand components of tropical moist forests (Todzia 1986; Orihuela & Waechter 2009). There is a need for further investigations (cf. Bröderbauer 2007).

In this study we have examined the diversity, species richness and abundance of primary hemiepiphytes in seven different regions, different forest types in lowland and premontane sites, on 0.5 ha forest plots (one on 0.2 ha size) and on freestanding trees on pastures. Another question has been if the sites are smilar to each other using different simmilarity measurements. The study is part of a survey on diversity and abundance of pHEs in Costa Rica (Bröderbauer et al., unpub. data). We have not focused on single species of pHEs, but have recorded all individuals within the sample areas.

METHODS

Study Sites

The study has been carried out in five lowland and two premontane primary rainforests, two lowland secondary rainforests and four lowland and two premontane pastures (TABLE 1). Each forest plot was of 0.5 ha size, but the plot in Santa Rosa 0.2 ha. On each pastures 40 freestanding trees have been observed, but on Fila Costena 27 and in Baru 20.

Pacific-influenced region

Three forest sites – two primary forests and one secondary forest - and one pasture site (plots 1, 2 and 9) are located on the Southern Pacific slope of Costa Rica in the Golfo Dulce Region. Two primary forest sites and two pasture sites are located on the eastly adjoining Fila Costeña (plot 3, 4,10 and 11). Another pasture, also located on the Southern Pacific slope, has been observed in Baru, nearby Dominical, in the region of Peninsula de Osa (plot 14). On the Pacific slope, in the north of Costa Rica, a smaller forest plot has been examined in the Santa Rosa National Park (15).

Atlantic-influenced Region

In addition, a forest plot and a pasture plot are placed on the Cordillera de Tilaran (6 and 12). A primary forest plot, a secondary forest plot and an additional pasture are located in the Carribean lowlands (7, 8 and 13).

Pacific-influenced regions – Lowland (pl)

La Gamba (LG). primary forest gorge, primary forest slope, secundary forest, pasture

Two lowland primary forests plots, a secondary forest plot and a pasture plot with 40 trees have been observed in LG. The sites are nearby the Piedras Blancas National Park, and the Tropical Research Station La Gamba. The national park is covered by tropical wet forest (after Holdridge et al. 1971), rainfall averages 6000 mm per year, with a short drier season from January to March (Weissenhofer & Huber 2001).

The two directly adjoining primary forest plots – a slope and a gorge forest - have an exposition of SW to S and are around 90 m above sea level (asl). The slope forest plot, has an average inclination of 0.15, the gorge forest, has inclinations between 0.2 and 0.3. Both plots are characterized by the high abundance of palms, especially *Socratea exorrhiza*, they consist of three canopy layers: 25-35 m, 20 m and 10-15 m. Single emergents are reaching heights of more than 40 m (cf. Bröderbauer 2008).

The secondary forest is an about a 30 year old forest with an inclination between 0.05 to 0.2, exposition is NW to N and it is about 115 m asl. This forest is characterized by two canopy layers (10-15m and 18 m, few trees reaching a height of more than 20 m), the tree *Vochysia* sp. and the liana *Doliocarpus* sp. are frequent.

40 freestanding trees have been observed for HEs on the pasture of LG The pasture is about 90 m asl, an incination between 0.0-0.1. Trees are between 5 and 17 m high.

San Miguel (SM). primary forest, pasture

This study sites are near the village San Miguel, about 10 km east of the Tropical Research Station La Gamba at the basement of the Fila Costeña, 500 m asl, in the Golfo Dulce region.

The primary forest site is classified as tropical wet forest (after Holdridge et al. 1971). It has an average inclination of 0.3, exposition SO, and *Socratea exorrhiza* is very frequent. Two canopy layers characterize this forest: the upper layer of 15-30 m, the lower of 10-15 m (cf. Bröderbauer 2008).

On the pasture of SM 40 freestanding trees between 5-17 m height have been observed. The pasture is east of the forest 500m asl, inclination between 0.0-0.1.

Hacienda Baru (BA). pasture

In BA we have observed 20 freestanding trees of a height between 5 and 23 m. The Hacienda Baru is located nearby Dominical in the south of Costa. This reagion is characterized by tropical wet forests, an anueal rainfall of 4000 mm and a clear dryer season from january to march (Kappelle 2002).

Santa Rosa (SR). forest

In the Santa Rosa National Park we have observed a forest plot of 0.2 ha size about 500 m east of the Playa Naranja. Inclination is between .0.03 and 0.1, exposition is W to SW. Average rainfall is of 1300 mm per year, with clear dry season from december to april (Janzen et al. 1983), it is covered by and an tropical seasonal forest (after Holdridge et al. 1971).

Pacific-influenced regions – Premontane (pm)

Fila Costena (FC). primary forest, pasture

This site at 1450 m asl is in the south-west of Costa Rica directly on the Fila Costeña, which is part of the Cordillera Costeña. It is classified as premontane rain forest (after Holdridge 1971). Here the climate is very wet, as clouds come from the Golfo Dulce and gather along the mountains. Annual rainfall for the region is probably more than 6000 mm (Werner Huber, pers. comm.), with a short dry season from January to March (Weissenhofer & Huber 2001).

The primary forest plot consists of a 20 to 30 m tall canopy and a 10 to 15 m tall subcanopy. A great part of the sunlight reaches the dense understory (cf. Bröderbauer 2008). Inclination is between 0.05 and 0.1, exposition is S.

We have observed 27 freestanding trees on FC, on the pasture below our forest plot. So the trees are at between 1300 m asl and 1400 m asl, the pasture is plain. Trees are between 5 m and 18 m high.

Atlantic-influenced regions – Lowland (al)

La Selva (LS)/ Nogal (NG). primary forest (LS), secundary forest (NG), pasture (NG)

These sites in the Carribean lowlands of Costa Rica are mainly covered with tropical wet forests (after Holdridge et al. 1971). Here, annual rainfall averages 4000 mm with lowest precipitation from February to April (Sanford et al. 1994).

The primary forest plot is located at the La Selva Biological Station. It is 50 m asl, plain. The forest has three canopy layers at 20-30 m, 15-20 m and a subcanopy at 10 m. Some single trees are reaching heights up to 35 m (cf. Bröderbauer 2008).

The secondary forest is in Nogal, a village nearby Puerto Viejo de Sarapiqui, about 8 km from La Selva. It is north of Rio Sucio in an about 30-year-old floodplain forest on a plain plot. Formerly a pasture (Bogantes Montero 2006; Weithaeuser 2004), it is characterized by few mature old trees of about 30 m heigth, canopy layers are at 20 m and a second at 10-15 m. Part of it is in an early succession, with compact understory of *Heliconia* spp., *Socrathea* sp., *Asterogyne* sp. are frequent.

Our 40 freestanding trees we have observed on two located pasture plots nearby on even sites not far off the banana plantations. Trees are between 6 and 23 m heigh.

Atlantic-influenced regions – Premontane (am)

Los Alpes (LA). primary forest, pasture

This site at 1480 m asl is situated in the southern part of the Cordillera de Tilaran. It is part of a private rainforest reserve named “Reserva Los Alpes” covering 100 ha. Annual rainfall is about 2500 mm with a dry season from December to May (Haber et al. 2000). Following Holdridge (1971) Los Alpes is classified as premontane wet forest.

The primary forest plot has an inclination of between 0.03 and 0.1, exposition is W. The forest is sparse, highly influenced by the Atlantic winds. Canopy height is about 15 m and subcanopy height 10 m (cf. Bröderbauer 2008).

We have observed 40 freestanding trees on the pastur in the west of the forest. Inclination is around 0.12, exposition W. Trees are between three and 17 m heigh.

Field Methods

Field work has been conducted during the dry season from January to May 2007 in six primary forest plots, two secondary forest plots and on six pastures. The forest plots have been covering 0.5 ha, and have been divided into eleven 20 x 20 m and one 20 x 30 m subplots, their edges tagged every ten meters. The forest plot in SR has been covering 0.2 ha, in five 20 x 20 m subplots. In each subplot all trees with a diameter at breast height (dbh) ≥ 10 cm have been explored for primary hemiepiphytes (pHEs). On the pastures we have observed 40 freestanding trees in LG, LA, NG and SM, 27 freestanding trees in FC and 20 freestanding trees in BA. Observed trees on the pasture also have a dbh ≥ 10 cm. The dbh has been measured with tapes in mm and trees have been explored with binoculars (ESCHENBACH© trophy AS/D 10 x 50 und SWAROVSKI© Habicht SLC 7 x 42B).

Species of pHEs have been recorded, samples of each species have been collected and determined in the Herbario National of the Museo National de Costa Rica (CR). Vouchers have been deposited in the Museo Nacional in San José, Costa Rica, and in the Herbarium of the Institute of Botany, University of Vienna, Austria (WU).

Data Analysis

Descriptive statistic has been performed with SPSS 16.0. To estimate species richness Abundance-based Coverage Estimator (ACE), Michaelis-Menton richness estimator (MM) and rarefacion curves with Moa Tau have been calculated. To measure similarity of the plots Jaccard, S∅rensen, Bray-Curtis and NESS Indices have been used. ACE, MM, Jaccard, S∅rensen and Bray-Curtis have been calculated with EstimateS 8.0.0 (Colwell 2005). In rarefaction curves we ploted the number of species as a function of the number of individuals sampled. Calculation of Normalized Expected Species Shared Index (NESS) has been carried out with an Excel Plug-In (Fiedler 2007). To adapt to the rare species the sampling parameter m has been set to m = 6 for comparison of the forest plots and to m = 3 for comparison of the pasture plots. Shannon-Wiener and Simpson-Yule Diversity Indizes and Shannon-Wiener Evenness have been calculated using the formulae in TABLE 2 (Madsen & Ollgaard 1994). Tables have been constructed with Excel 11.5.1 for Mac and graphs with Plot 0.997.

RESULTS

We observed seven regions in Costa Rica, and distinguish Pacific- (p) from Atlantic- (a) influenced reagions, and loland sites (l) from premonane sites (m). Our sites:

Baru (BA, pl), Fila Costena (FC, pm), Los Alpes (LA, am), La Gamba (LG, pl), La Selva (LS, al)/Nogal (NG, al), San Miguel (SM, pl) and Santa Rosa (SR, pl).

There we have found in total 90 species of hemiepiphytes, within 22 genera and 12 families in our six primary forest plots of 0.5 ha (two different plots in LG (pl), none in Baru (pl)), two secondary forest plots of 0.5 ha in LG (pl) and NG (pl) and six pastures. In SR (pl) we have not found any primary hemiepiphytes in our 0.2 ha primary forest plot. For detailed information on distribution of the species in our plots and of the species accouding to databases for distribution data, see TABLE 3.

Hemiepiphyte Abundance of Study Sites compared

Descriptive results

We have found in premontane sites more pHE individuals in equal sized plots than in plots in the lowland, this result is valid for both: forests and pastures. Concerning primary forests we have found the most individuals in LA (am) (649) and and in LS (al) the fewest (33). In terms of our pastures there also are the most individuals in LA (am) (78), whereas on the pasture of NG (al) we have found the fewest number of individuals (18) compared to all other pasture sites with 40 trees.

Concerning the **primary forests** LA (am) has had the most number of individuals/0.1 ha (129.8), at FC (pm) we have found 60.6 individuals/0.1ha, SM (pl) at 500 m has 15.6 individuals/0.1 ha, LG (pl) primary forest plots at gorge and slope are very close to that number with 12.8 respectivly 11.2 individuals/0.1 ha, whereas in LS (al) we have only found 6.6 individuals per 0.1 ha. The two **secondary forests** in LG (pl) and NG (al) show compareable numbers with 13 individuals (2.6 ind/0.1 ha) in LG (pl) and 18 individuals (3.6 ind/0.1ha) in NG (al) (TABLE 4).

Primary hemiepiphytes per tree

The average number of pHE/tree, which is especially important for pastures, where hardly every tree has pHEs, also confirms that there are more pHEs in sites on higher sea level. FCs (pm) pasture has the most with 2.33 HEs/tree, in BA (pl) we have found the fewest with 0.3 HEs/tree. LA (am) has 1.95 pHE/tree on its pasture, which comes close to the pHEs/tree number in that primary forest (1.93). In all regions are more pHEs/tree on the pastures than in primary forests. The fewest pHE/tree where in the secondary forests, in LG (pl) 0.05 pHEs/tree, and NG (al) 0.14 pHEs/tree (TABLE 4).

Species Richness

The number of species, families and genera is also higher in the premontane sites than in the lowland sites. But in all sites the biggest species richness we find in primary forests, on pastures we find the fewest.

The **primary forests** of FC (pm) and LA (am) have a compareable number of species. FC (pm) has 26, within 15 genera and nine families, seven singletons. LA (am) has 25 species within 15 genera and 11 families, four singletons and one family with only one singleton. The most singletons in a primary forest we have found in SM (pl) – there are eight, but none family with only one singleton. The primary forest on the slope site in LG (pl) has the fewest number of species, even fewer than the secundary forest there. There are six species, in four families and genera, no singletons. Whereas in the **secondary forest** are eight species within four families, genera and singletons – which is more than in NG (al). In NG (al), however, is also a familiy with only one singleton and there are three species with singletons.

Concerning the **pastures** BA (pl) has the fewest number of species: three species, in one family and genera. The most number of species has LA (am) with 15 species, in 11 genera and ten families, with six singletons and three families with only one singletons (table 3). Species Richness togheter with singletons are shown in FIGURE 1.

Individuals per species

The average number of individuals per speciesis is hard to compare, because there is a great difference in the species number in different sites. But over all there is a similar tendence: the number of individuals per species is in premontane primary forest sites the greaters and in lowland secondary forest sites the fewest. Therefore it is in LA (am) the highest (26.0 in the primary forest, 5.2 on the pasture). Concerning pastures it is on FCs pasture (pm) it is a little higher with 5.7, but concerning the forests it is only 11.7. The lowest number of individuals/species we have found in LGs secondary forests (pl) with 1.6 (see TABLE 4).

Diversity

We have calculated two different indizes of diversity for all our sites and regions. Additionally to the Shannon-Wiener index as information index, we have calculated its evenness to evaluate the importance of the number of species in the sites. In the Simpson-Yule index as dominance index, we have used the complementary form, so that if diversity increases the index value increases too.

Shannon-Wiener Index (Hs) and Evenness

In terms of the **forest pots**, the plot with the highest Shannon diversity Index is LA (am) (2.74), close follow FC (pm) (2.51), SM (pl) (2.45) and the gorge plot in LG (pl) (2.36). LS (al) follows next and has with 2.13 a little lower index than the LG (pl) gorge plot. The plot in LGs slope (pl) has an index more off from the others (1.23) and comes closer to the secondary forest plots in NG (al) (0.56) and LG (pl) (0.52) than the other primary forest sites.

Regarding the evenness of the plots it appears, that high diverse sites have a high evennes as well. Most eye-cathing is, that the slope forest in LG (pl) has a higher evenness compared to its diversity than the other forests. The most even community is in LGs (pl) gorge forest (0.9), second is LA (am) (0.85), third LS (al) and SM (pl) (0.83). FC (pm) has only an index of 0.77, and, therefore, comes close in eveness with LGs (pl) slope site (0.69). The secondary forests have values of 0.31 (NG (al)) and 0.25 (LG (pl)).

Concerning the **pasture** plots, premontane sites have again higher Hs indizes. First is LA (am) with 2.16, second SM (pl) (1.89) and third FC (pm) (1.35), but with only 27 trees observed. Pastures of the lowland have lower indizes. LG (pl) has 1.66, NG (al) 1.35 and BA (pl) 1.01. Evenness is in all sites pretty close to 1, all are similar to the others, but pastures with lower Hs show high evenness: BA (pl) (0.92), LG (pl) and SM (pl) (0.86), NG (al) (0.84), LA (am) (0.8) and FC (pm) (0.78). See alsos TABLE 4 and FIGURE 2.

Simpson-Yule Index (Ds)

The Ds' (its complementary form) of the **forest sites** are closer toghether than the Hs'. First is again LA (am), but the secondary forest site in LG (pl) has the same value (0.92). Second is LGs (pl) gorge forest (0.9) close to FC (pm) and SM (pl), both with a Ds value of 0.89. LS (al) is a little off with 0.84, least are the sites of the slope in LG (pl) (0.79) and the site in NG (al) (0.72).

The Ds values of the **pasture sites** are not distiguished that hard too. Again the tendence shows higher diversity in premontane sites. LA (am) has 0.85, SM (pl) 0.84, LG (pl) 0.8 FC (pm) 0.79, NG (al) 0.75 and BA (pl) has 0.73.

See alsos TABLE 4 and FIGURE 2.

Rarefaction Curves

With the rarefaction method we have calculated the species richness for a given number of sampled individuals and plotted the number of species as a function of the number of individuals sampled in rarefaction curves. A steep slope indicates that if a bigger plot would be samled, it is likely to yield additional species. According to the huge difference of the number of individuals in premontane and lowland forets rarefaction curves are drawn according to their different background – regions, sea level or forest and pasture sites. Rarefaction curves are plotted in FIGURE 3.

Sites in La Gamba (pl)

These rarefaction curves show that the gorge site and the secondary forest in LG (pl) have a similar slope at the beginning. The steep slope at the end of the curve of secondary forest indicates that there is a high probability to find additional species in the site if a bigger plot would be observed. It is very similar to the slope of the gorge site, but here the plot size of 0.5 ha contains most species that could be expected in that site. Whereas the curve of the slope site soon flattens, so most species in that site are already found. The pasture has a higher slope than the slope forest but already flattens with the number of individuals we have observed.

Primary forests in La Gamba and San Miguel (pl)

Plotting the rarefaction curve of SM (pl) toghether with the primary forest plots in LG (pl) it shows that it has a higher slope as the sites on lower sea level in LG (pl), and although there are more individuals in SM (pl), it does not flatten as the curves in LG (pl) do. There could be more species expected with a higher sampling plot size.

Sites in Nogal and La Selva (al)

In these sites the primary forest in LS (al) shows the highest slope in its rarefaction curve, and it doesn't flatten at the edge. The pasture in NG (al) first has a higher slope than NG (al) forest, but flattens faster. The slope at the edge is not that high compared to the forest curve, but still some species would be discovered in a bigger sample size.

Lowland forests (LG, LS, NG)

Comparing the lowland forests in LG (pl), LS (al) and NG (al) we see that the slope forest in LG (pl) does not only has the lowest number of species, but this number has also a high saturation. The slope of the rarefaction curve of the secondary forest of NG (al) is a little higher but does not reach the other curves as well. The primary forest of LS (al), the gorge forest of LG (pl) and the secondary forest of LG (pl) show a similar slope. The gorge forest in LG (pl) is third, but has the highest density of individuals and species on the same area. The secondary forests of LG (pl) and NG (al) show a similar density of individuals but LG (pl) has a higher species richness and the curve indicates that in a bigger sample size would be even more species to find. LS (al) has a bigger density of both, individuals and species, than the secondary forests, but does not reach the one of LGs (pl) gorge forest, but also has a higher slope at the edge.

Forests on higher sea level (SM, FC, LA)

Concerning the forests of SM (pl), FC (pm) and LA (am) we see that the rarefaction curve of LA (am) shows a larger number of individuals and species in the 0.5 ha plot, but the curve flattens. SM (pl) and FC (pm) have a higher slope at the edge, SM (pl) even more than FC (pm).

Pasture sites on higher sea level (SM, FC, LA)

The pastures at higher sea level show a simmilar picture to the forest of SM (pl).

They have a similar slope at the beginning, but it decreases faster. The curves of the pastures of LA (am) and SM (pl) are very similar to each other, only that in SM (pl) there are less individuals on the same amount of trees. The pasture of FC (pm), although there where only 27 not 40 trees observed, flattens faster but has a higher density of individuals and species than SM (pl), but still lies below the curve of LA (am).

Lowland pastures

Lowland pasture curves are lying below the one of SM (pl) and also flatten much faster. The curve of LG (pl) is in the beginning very similar to the curve of SM (pl), and also reaches a similar amount of individuals, but at around 10 individuals the number of species begins to differ and the curve of LGs (pl) pasture flattens more than the curve of SM (pl). The pasture of NG (al) has a minor slope even in the beginning, similar to that of BA (pl). The curve of BAs (pl) pasture flattens the most and does not reach quite the number of individuals and species as the others do, but there are only 20 trees instead of 40. The slopes at the edge of all three lowland pasture curves are similar to each other and would indicate some more species on other trees in a bigger sample.

Species Richness Estimation

Abundance-based Coverage Estimator (ACE)

This Estimation is based on the abundance of rare species (between 1 and 10 individuals) adding on the number of more abundant species (Magurran 2004).

Concerning the **primary forests** this measurement of biological diverstiy and species richness shows that the forest of FC (pm) has the highest estimated species richness (38,30) followed by LA (am) (29.56) and SM (pl) (26,69). Concerning lowland primary forests LG (pl) gorge (17.75) and LS (al) (17.00) have similar values. LG (pl) slope has the lowest value (6.00) even under the **secondary forests** of LG (pl) (12.67) and NG (al) (12.00).

The highest value of the **pastures** have the premontane pastures as well, this time LA (am) (27.00) higher than FC (pm) (17.00). The value of LA (am) pasture is very similar to the primary forest in LA (am). SM (pl) (19.00) has a higher value than FC (pm). But there have been less trees on FC (pm) sampled than in LA (am). Concerning the lowland pastures LG (pl) (8.25) is before NG (al) (6.00) and Baru (pl) (4.00) (TABLE 3 and FIGURE 1).

Michaelis-Menton richness estimator (MM)

The functional extrapolation MM shows that species richness of the **primary forests** are closer toghether, LA (am) species richness value beeing apart from the other estimation value (ACE). It is only fourth in ranking with a value of 26.28. The highest MM has LS's (al) primary forest (32.33) also differing from ACE ranking. Next is FC (pm) (29.60), followed by SM (pl) (29.30), LG (pl) gorge (23.69) and LG (pl) slope (6.85), this is having again the lowest value. The **secondary forests** differ more than with ACE, but still LG (pl) has a higher species richness (27.89) than NG (al) (14.58). So in this index the secondary forest of LG (pl) has got a higher value than the primary forest in LA (am) and comes close to the forests of FC (pm) and SM (pl).

Pastures have more compareable values to ACE. With MM LA (am) pasture is on first place in species richness (28.86), and again this pasture has a similar species richness value than its primary forest. No other pasture shows that compared to the high diversity in the primary forests on the sites. FCs (pm) pasture is in second place (13.88) and a little higher than SMs (pl) pasture (13.09) even though the lower treenumber in FC (pm). Next follows LG (pl) (8.55), Baru (pl) (6.27) and NG (al) (5.95) (TABLE 3 and FIGURE 1).

Similarity

To compare the forests and the plots according to their similarity in species composition of primary HEs, four indizes were calculated: the qualitative Jaccard and Sorensen and the quantitative Bray-Curtis and NESS (Normalized Expected Species Shared Index). All indizes have values between 0 and 1. The closer the value comes to 1 the more compareably are the sites. Results are shown in TABLE 5 for the forests and TABLE 6 for the pastures.

Forests

Concerning the least similarity of all four indices it comes clear that the secondary forest of NG (al) is not similar to all other forests. It has a high number of zero values, and values that are very close to zero. The highest similarity shows, in Jaccard and Sorensen, LGs (pl) primary slope forest with LGs (pl) secundary forest and, in Bray-Curtis, LGs (pl) primary slope forest with LS (al) primary forest. With NESS the two have high indizes, ranking the similarity of the two forests of LG (pl) first, second the primary forest of LS (al) and the secondary forest of LG (pl), third LS (al) and LGs (pl) slope forest.

The primary gorge forest in LG (pl) shows in all indices a high similarity to the other forests of LG (pl). The least similarity to LA (am) and the secondary forest of NG (al).

The primary slope forest in LG (pl) shows a high similarity to the other forests in LG (pl), and to the forest of LS (al). Next in similarity is SM (pl), and least LA (am) and the secondary forest of NG (al) with low values in all indizes.

The secondary forest in LG (pl) shows, as mentioned above, a high similarity to LGs (pl) slope forest, which ranks first in all indices. It is also very similar to LS (al), the gorge forest in LG (pl) and SM (pl). NG (al) is in all indices in fifth place in similarity, FC (pm) and LA (am), are not very similar to the secondary forest in LG (pl).

The primary forest of LS (al) shows a high similarity to the forests of LG (pl) in the qualitative indizes. SM (pl) shows a pretty high value too in NESS (forth place) and Bray-Curtis (second place), but the value in Jaccard and Sorensen is not that high. The secondary forest of NG (al) has a very low value in all of the indizes.

The primary forest of SM (pl at 500 m asl) shows high similarity to the forests of LG (pl) in all indizes (ranking: LG (pl) gorge forest, LG (pl) secondary forest and LG (pl) slope forest). LA (am) and and the secondary forest of NG (al) have in all indice low values, LS (al) has low values in the qualitatve indizes, FC (pm) has low values in the quantitative indizes.

The primary forest of FC (pm) shows very low values to all other forests in all indizes. The most similarity it shows to the forest of SM (pl) and the primary forests of LG (pl) in all four indizes. Least similarity it shows to the secondary forests in NG (al) and in LG (pl). LA (am) shows a realtivly high similarity to FC (pm) compared to the similarity of the other forests, in the qualitative (second place) and in Bray-Curtis (third place).

The primary forest of LA (am) is not very similar to all other observed forests, it shows low values in all of the indizes to all other forests. Some indizes show low similarity to FC (pm) and LS (al). It is ot at all similar to the secondary forest of NG (al).

Pastures

The pastures are not very similar to each ohter, all indizes show very low values to all pastures compared to each other, many zero values as well. Over all indizes, the pastures with the most zero values are BA (pl) and NG (al), and, therefore, are not similar to all others. If they show similarity the values are relativly high: NG (al) seems to be al little similar to SM (pl) and LG (pl), BA (pl) to LG (pl).

LG (pl) is relativly similar to SM (pl) and BA (pl), not at all to NG (al).

LA (am) is relativly similar to FC (pm) and LG (pl), not to the other pastures.

FC (pm) is similar to SM (pl), LA (am) (first in Bray-Curtis) and a little to LG (pl).

SM (pl) is similar to LG (pl), FC (pm) and NG (al), not to LA (am) and BA (pl).

DISCUSSION

Abundance of primary Hemiepiphytes

We have found in lowland primary forests six to 13 pHE individuals per 0.1 ha. The sites on the Pacific (p) influenced region (LG) have the higher value of individuals/ha than the site in LS, which is located in the Carrebean (a) lowland. This number lies far beyond the number of HEs, published by Todzia 1986 on BCI. On BCI there were only 11.1 HE individuals per hectare. Our secondary forests shows an abundance of circa three individuals per 0.1 ha, which comes closer to the value Todzia has found on BCI. Our premonane sites on about 1500 m asl are lying far beyond these valus with numbers of

60.6 (FC (p)) and 129.8 (LA (a)) individuals per 0.1 ha. The numbers of the pHE density in our lowland primary forest sites fits with the number Putz and Holbrook found in a palm savanna of Venezuela 141/ha (Wiliams-Linare and Lawton 1995).

Todzia has focused in her study on 20 species of primary hemiepiphytes in a similar method to ours, but she has excluded the small individuals (< 25 cm). Nevertheless, our study shows that pHEs are far more abundant in primary lowland forests, even more in greater heights above sealevel. BCI values come close to values in our secondary forests plots, but she has found that BCI values are also lower than abundance data in Venezuela (Todzia 1986). Also Gentry has found that BCI has less epiphytes than, for example, La Sleva (Gentry 1993). The low abundance in BCI may be a result of the drier clima, with a clear dry season of four months. In our site in Santa Rosa, a seasonal rain forest, we have not found any pHEs in our 0.2 ha forest plot. Another reason may be that the forests have another structure. Orihuela and Waechter 2009 have found that pHEs need larger canopy trres for establishment. This may be a reason for the lower pHE number in our secondary forests and in our disturbed sites.

Species Richness

The ranking of **forest sites** from highest species richness to lowest species richness S is the same like the abundanced based estimatd species richness ACE. The premontane forests are ranked on top of species richness: FC (pm) before LA (am), next is SM (pl), our site at 500 m asl. Lowland sites are behind them LGg (pl), LS (al), as primary forest plots, followed by the secondary forests of LGsec (pl) and NG (al), and the primary slope forest LGs (pl). The sites at about 1500 m asl FC (pm) and LA (am) are very close toghether in S, but ACE shows higher difference and is ranking LA (am) closer to the site in SM (pl) on 500 m asl. Lowland forest sites are ranked far behind them. LG (pl) gorge plot and LS (al) are similar to each other in both S and ACE, but again the Pacific-influenced site with minimal bigger values. Also in the secondary forest plots it is LG (pl) on the Pacific side before NG (al) in the Carrebean lowland, only with a minimal difference, but still well spaced out to the lowland primary plots. Only the primary forest on the slope in LG (pl) is ranked behind the secondary forests in all species richness values (S, ACE and MM), even though the general abundance fits with the other lowland primary forest sites, more over it is even grater as the abundance in LS (al). Also the rarefaction curve of the slope forest in LG (pl) shows that more species are not likely to be discovered.

The Michaelis Menton species estimation (MM) shows another ranking. Here LS (al) is even ranked before FC (pm) and SM (pl at 500 m asl), and the secondary forest of LG (pl) is ranked higher than LA (am), next comes LG (pl) gorge, NG (al) and LG (pl) slope. Magurran (2004) says that MM is very stable across sample sizes, which is important to the different number of pHE individuals in our sites, as premontane forests have a very high number of individuals and LS (al) and the secondary forests a relativly low number. Rarefaction curves of these sites indicate also a higher number of species if the plot size would be bigger. But MM increased also with the degree of patchiness (Magurran 2004), and low abundances of pHEs individuals, especially in the secondary forest in LG (pl), could be a reason of this MM value. For calculation rarefaction curves the individuals in the community have to be also randomly dispersed. Orihuela & Waechter (2009) have found out that concerning hemiepiphytes the species rarefaction indicates a stabilizing tendency after approximately 200 sampled individuals. This number we reach in only in our premontane sites. Therefore patchiness is still a factor in our data set. But also our premontane sites with individuals > 300 in FC (pm) > and 600 in LA (am) dont show a stabilization in the rarefaction curve yet. At least FC (pm) has still got a stee slope at the edge.

At the **pastures** the premonate sites are also ranked before lowland sites in S, ACE and MM. LA (am) is far off in first place in all three vlaues. The slope of the rarefaction curves of the pastures are very similar to each other, which means there could be some more species found if more trees were observed, only BA (pl) flattens faster. FC (pm) and SM (pl – at 500 m asl) are very close toghether, but more distant to the value of LA (am) in MM. At ACE SM (pl) lies higher as FC (pm), but in FC (pm) also less trees have been observed, this could cause a higher level to the S and MM value, because of greater patchiness. In lowland pastures it is LG (pl) before NG (al) and on last place BA (pl) in S and ACE, in MM BA (pl) is before NG (al) . But again here the MM value may be due to a low number of trees observed and a low individual abundance in general.

ACE is good in deducting the overall species richness, if there are many rare species in the sample (Magurran 2004). Considering that LS (al) and the secondary forest of LG (pl) have a high number of singeltons, compared to the other lowland sites, and even to the premonaten sites in relation to the overall abundance. Considering also the great difference in the estimated number of species in LS (al) (17 in ACE, 32.33 in MM) and LG sec. (pl) (12.67 in ACE, 27.89 in MM) it seems that ACE fits better for our data set.

Diversity

The Shannon Index also ranks premontane **forest** sites higher in diversity, but LA (am) before FC (pm) and SM (pl at 500 m asl). Concerning lowland forests, primary forests are higher in diversity (LG gorge (pl), LS (al), and LG slope (pl)) than the secondary forests in NG (al) and LG (pl). As our sites show a very different evenness, the sites with low evenness also show low values in Shannon index, which is effected by the number of species and the evenness. Therefore the secondary forest plots show, due to the low number of individuals and individuals per species, a low evenness and also a low Shannon index value. The slope forest in LG (pl) has a relative high evenness but still a low Shannon index value, this site is therefore low in diversity, as the species richness estimation sugests. The other primary forests lie close toghether in their Shannon index values. Premontane forests have indizes relativly high to their eveness than the forests in LG (pl) and LS (al). They therefore are a little higher in diversity.

The Simpson Index shows a different ranking, all sites are closer toghether in the values. LA (am) and the secondary forest in LG (pl) in equal position in frist place, followed by LG (pl) gorge forest, SM (pl) and FC (pm) each. LS (al) is in forth place, and the secondary forests are at the lower end, this time LG (pl) before NG (al). The Simpson index, as dominance index, shows the probability that two randomly selected individuals

belong to the same species (Korning et al 1990). It weights towards the abundance of the most common species. Therefore the sites with relativly few singletons have higher values, which may be the reason why the secondary forest of LG (pl) and the gorge forest of LG (pl) have higher diversity vlaues as FC (pm) and SM (pl), where we found many singletons although there was a high over all abundance of pHEs and a high species richness.
This shows that this index is inapprotiate to measure diversity in a species rich tropical rainforest (Madson and Ollgaard 1994) and this conclusion seems to be also valid for pHEs. The Shannon Index with its measuremnt of evenness gives the better information.

Concerning the **pasture** results of the two indizes, we see that they are more similar to each other. LA (am) and SM (pl) are on top in both. In the Shannon Index FC (pm) is in third place and LG (pl) in forth, in Simpson Index vice versa. At last there are NG (pl) and BA (pl). Again values of the Simpson Index lie closer togheter, in the Shannon Index Evenness on all pastures has similar values, but diversity is very different. Especially BA (pl) has a low value with a very high evenness, and therefore is lowest in diversity. NG (al) and LG (pl) have also clearly lower values as the premontane pastures and LA (am) has definitly the highest value.

Species Richness and Diversity Conclusions

Resutls therefore show, that not only the general abundance of primary hemiepiphytes increases from lowland to premontane sites, also the species richness increases. This goes in line with Wiliams-Linare and Lawton 1995 who suggest that density and diversity increases in premonaten and montane forests, in particular in midmontane cloud forests. This shows that the generally decline in species diverstiy with increase of sea level for plants (Homeier et al. 2002; Madson & Ollgaard 1994; Gentry & Dodson 1987) is not valid for primary hemiepiphyte diversity. Wattenberg & Breckle (1995) have shown in a lower montane rainforest in San Ramon (nearby LA) that plant biodiversity increases with increasing height. This may be due to the high annual rainfall in this area without a real dry season and may also explain our high diversity and species richness in the forest of LA (am) at 1500 m asl. FC (pm) and SM (pl) have even higher annual rainfall. Our lowland sides have this high amounts of rainfall too, but in our premontane sides at elevations about 1500 m asl are daily fogs and clouds, which cause additional wet conditions. Gentry & Dodson (1987) assumpt that there may be a mid-altitude bulge in diversity for epiphytes. This is may be correct according to our primary hemiepiphyte study. But to confirm this buldge we would need more data in even higher sealevels.

The pasture observation in Baru show that there is a decline – both in species number and individual abundance - in drier habitats with dry season. In Santa Rosa with a clear dry season and a seosonal tropical forest we see that the decline is even more explicit. There we have not found any hemiepiphyte in our forest plot. This phenomenon is typical for epiphytes (Gentry & Dodson 1987).

The low density and diversity in secondary forests could be due to the limited time for colonization on young trees (Wiliams-Linare & Lawton 1995) and the missing of adequat conditions for establishment and early development of pHEs fulfilled by larger trees (Orihuela & Waechter 2009). They could also be due to the other microclimate patterns and less canopy layers. In NG (al) for example there are some older trees because the secondary forest has been formerly a pasture, but still the density does not increase demonstratively. That HEs need more than light to establish in higher diversity is also indicated by the estimated species richness on pastures, which lies below the ones in the forest sites. Although the density per tree is greater on pastures than in forests, species richness is not. Specialisation on conditions like higher light, solar radation and/ or specialisation on animal froot dispersial may be the reason for lower species numbers on pastures. HEs therefore are not more likely to establish on pastures or more well-lit spots alone as Wiliams-Linare & Lawton (1995) suggest.

Our results show that the diversity and density of primary Hemiepiphytes are an indication for the disturbance of a forest plot. Secondary forests and high disturbed forests showing a significant decrease in diversity. Therefore the slope forest in LG, which is directly adjoining the gorge forest plot is more disturbed, maybe according to the greater inclination.

Similarity

There have been different similarity indizes chosen. Jaccard and Sorensen as qualitative measurements do not weight on abundance of species. Jaccard is independent from the total species number in the data set, whereas Soerensen weights total species number in both sites. Bray Curtis is the quantitative index, it is similar to Soerensen, but cares about abundances (Leyer & Wetsche 2007). NESS is less biased than other commonly used measurements and could be (with large m) more sensitive to less common species. It considers the probability of abundances in the data sets (Homeier et al 2002). Therefore NESS is the most reliable index for our data set.

There seems to be no significant difference in species richness and diversity between Pacific- and Atlantic-influenced plots. The similarity indizes show that there is not a difference of high significance ether. These data shows that there is higher similarity of the forests sites, if the forest type is similar, but for regional reasons. So the secondary forest of NG (al) shows the least similarity to all other forests, but if another forest is simillar it is the other secondary forest in LG (pl), not the primary forest in LS (al). LA (am) is a untypical forest in our data set as well. It shows little similarity to the other forests, but as it shows a relative high similarity in the three indizes but NESS to FC (pm), NESS shows higher similarity to LS (al).

Of course regional patterns influence these values as well, therefore all LG (pl) forests are similar to each other, but the directly adjoining primary forest plots show each a higher diversity to the secondary forests in most indizes but to each other. Only NESS measures this similarity between the adjoining plots.

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Table 1. Description of the study sites.

	Site	Location	Altitude (m)	Mean Precipitation (mm/year)	Mean Temperature (°C/year)	Inclination (%)	Coordinates
1	La Gamba gorge	Lowland/ Pacific slope	90	6000	25.2	15	8°42’16”N, 83°12’15”W
2	La Gamba slope	Lowland/ Pacific slope	90	6000	25.2	20-30	8°42’16”N, 83°12’15”W
3	La Gamba secondary	Lowland/ Pacific slope	115	6000	25.2	0-20	8°41’57”N, 83°12’09”W
4	San Miguel	Lowland/ Pacific slope	500	~6000	No data	30	8°44’59”N, 83°9’40”W
5	Fila Costeña	Premontane/ Pacific slope	1450	~6000	17-22.5	10	8°47’25”N, 83°8’21”W
6	Los Alpes	Premontane/ Pacific slope	1480	2500	18-21	7	10°8’N, 84°34’W
7	La Selva	Lowland/ Carribean slope	50	4000	25.8	0-3	10°25’27”N, 78°38’23”W
8	Nogal	Lowland/ Carribean slope	50	4000	25-26	0	10°27’86” N 83°57’02” W
9	La Gamba pasture	Lowland/ Pacific slope	90	6000	25.2	0-7	8°42’20”N, 83°11’41”W
10	San Miguel pasture	Lowland/ Pacific slope	500	~6000	No data	0-5	8°45’15”N, 83°8’42”W
11	Fila Costena pasture (27 trees)	Premontane/ Pacific slope	1310-1400	~6000	17-22.5	0	8°47’12” N 83°8’28” W
12	Los Alpes pasture	Premontane/ Pacific slope	1480	2500	18-21	10	10°8’N, 84°34’W
13	Nogal pasture	Lowland/ Carribean slope	50	4000	25.8	0	10°27’6” N 83°57’26” W
14	Baru pasture (20 trees)	Lowland/ Pacific slope	0	4000	26	0	9°16’01” N 83°52’58” W
15	Santa Rosa (5 subplots)	Lowland/ Pacific slope	~0	1300	27-30	5	10°53′N 85°46′W

Table 2. Formulae applied.

Shannon-Wiener’s Diversity Measure	$H_S = - \sum_{i=1}^{S} p_i \ln p_i$
Evenness H_S	$E = H_S / H_{max} = H_S / \ln S$
Simpson-Yule’s Diversity Measure	$D_S = 1 - \sum_{i=1}^{S} (n_i^2 - n_i) / (N^2 - N)$
Hs .... Shannon-Wiener-Index Ds .... Simpson-Yule-Index E .... Evenness p_i …. relative ratio of species i on the total sample	S ………………………... total species number n_i …………………..…... individuals of species i N ……………………..…… total individuals number

Table 3. List of species we found in the six different regions. Page 1.

Family	Hemiepiphyte		LG	SM	FC	NG/LS	LA	BA	Distribution
Aquifoliaceae	*Ilex hemiepiphytica*	W. J. Hahn					P		Costa Rica
Araliaceae	*Oreopanax aff. striatus*	M. J. Cannon & Cannon			Fp; P				Costa Rica, Panama
Araliaceae	*Oreopanax capitatus*	(Jacqu.) Decne y Planch.			Fp		Fp; P		Peru and French Guiana to Mexico, incl. Dominican Republic
Araliaceae	*Oreopanax oerstedianum*	March.			Fp		Fp; P		no distribution found
Araliaceae	*Oreopanax sp.*					Fs			
Araliaceae	*Schefflera brennesii*	A. C. Smith		Fp	Fp; P				Costa Rica
Araliaceae	*Schefflera robusta*	(A. C. Smith) A. C. Smith			Fp; P		Fp; P		Costa Rica, Panama
Araliaceae	*Schefflera rodriguesiana*	Frodin ex M. Cannon & Cannon					Fp; P		Costa Rica, Panama
Asteraceae	*Neomirandea cf. parasitica*	(Klatt) R. King & H. Robinson					P		Costa Rica, Panama
Asteraceae	*Neomirandea cf. psoralea*	(B. L. Rob.) R. M. King & H. Rob.					Fp		Costa Rica, Panama
Asteraceae	*Neomirandea parasitica*	(Klatt) R. King & H. Robinson					Fp; P		Costa Rica, Panama
Asteraceae	*Neomirandea psoralea*	(B. L. Rob.) R. M. King & H. Rob.					Fp		Costa Rica, Panama
Asteraceae	*Neomirandea standleyi*	N. M. King & R. Hobl			Fp				Costa Rica, Panama
Cecropiaceae	*Cecropia peltata*	L.					Fp		Ecuador and Guyana to Mexico incl. Dominican Republic
Cecropiaceae	*Coussapoa glaberrima*	W. C. Burger	Fpg; P						Panama to Nicaragua
Cecropiaceae	*Coussapoa villosa*	Poepp. & Endl.		P		P			Bolivia to Honduras
Clusiaceae	*Chrysochlamys allenii*	(Maguire) Hammel					Fp		Costa Rica, Panama
Clusiaceae	*Clusia aff. flava*	Jaqu.				P			Costa Rica to Mexico
Clusiaceae	*Clusia aff. minor*	L.					Fp		Bolivia and Suriname to Mexico incl. Dominican Republic
Clusiaceae	*Clusia aff. multiflora*	Kunth					Fp		Bolivia to Mexico
Clusiaceae	*Clusia aff. palmana*	Standl.					Fp		Ecuador to Costa Rica
Clusiaceae	*Clusia amazonica*	Planch & Triana	Fpg; Fps; Fs	Fp		Fp			Bolivia and Brazil to Nicaragua
Clusiaceae	*Clusia cf. cylindrica*	Hammel				Fp			Columbia to Nicaragua
Clusiaceae	*Clusia cf. peninsulae*	Hammel -ined	Fpg						Costa Rica, Panama
Clusiaceae	*Clusia cf. stenophylla*	Standley		Fp					Ecuador to Mexico
Clusiaceae	*Clusia croatii*	D'Arcy			Fp; P				Panama to Nicaragua
Clusiaceae	*Clusia cylindrica*	Hammel	Fpg						Columbia to Nicaragua
Clusiaceae	*Clusia flava*	Jaqu.				Fs; P			Costa Rica to Mexico
Clusiaceae	*Clusia gracilis*	Standl.				Fp			Panama to Nicaragua
Clusiaceae	*Clusia minor*	L.					Fp		Bolivia and Suriname to Mexico incl. Dominican Republic
Clusiaceae	*Clusia multiflora*	Kunth					Fp; P		Bolivia to Mexico
Clusiaceae	*Clusia osaensis*	Hammel	Fpg						Costa Rica
Clusiaceae	*Clusia palmana*	Standl.					Fp; P		Ecuador to Costa Rica
Clusiaceae	*Clusia peninsulae*	Hammel -ined	Fps; Fs						Costa Rica, Panama
Clusiaceae	*Clusia quadrangula*	Bartlett				P			Panama to Mexico
Clusiaceae	*Clusia sp.*			Fp					
Clusiaceae	*Clusia stenophylla*	Standley			Fp; P				Ecuador to Mexico
Clusiaceae	*Clusia torresii*	Standl.					Fp		Panama to Nicaragua
Clusiaceae	*Clusia uvitana*	Pitt.				Fp; Fs; P			Panama to Nicaragua
Clusiaceae	*Clusia valerioi*	Standley	Fpg; Fps; Fs; P	P		Fp		Fp	Columbia to Nicaragua
Clusiaceae	*Clusiella isthmensis*	Hammel				Fp			Costa Rica, Panama
Ericaceae	*Cavendishia bracteata*	(Ruiz López & Pavón ex J. St. Hill.) Hoerold					Fp; P		Bolivia to Mexico
Ericaceae	*Cavendishia callista*	J. D. Smith		Fp; P	Fp; P				Ecuador and French Guiana to Guatemala
Ericaceae	*Cavendishia complectens*	Hemsl.					Fp; P		Peru to Nicaragua

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel; Fp = primary forest, Fs = secundary forest, g = gorge, s = slope
Sources for distributon data: http://www.gbif.org/, 22. 08. 2008; http://www.tropicos.org, 22. 08. 2008

Table 3. List of species we found in the six different regions. Page 2.

Family	Hemiepiphyte		LG	SM	FC	NG/LS	LA	BA	Distribution
Ericaceae	*cf. Satyria panurensis*	(Benth.) Benth. & Hook.			Fp				Peru and French Guiana to Mexico
Ericaceae	*Psammisia ramiflora*	Klotzsch			Fp		Fp		Columbia to Costa Rica
Ericaceae	*Psammisia williamsii*	A. C. Sm.					Fp		Costa Rica, Panama
Ericaceae	*Satyria panurensis*	(Benth.) Benth. & Hook.	Fpg; Fps; Fs	Fp; P		Fp	Fp		Peru and French Guiana to Mexico
Ericaceae	*Satyria warszewiczii*	Klotzsch			Fp; P				Peru and Venezuela to Mexico
Ericaceae	*Satyria/Psammisia panurensis/ramiflora*						Fp		
Gesneriaceae	*Drymonia alloplectoides*	Hanst.		Fp; P					Peru to Nicaragua
Gesneriaceae	*Drymonia conchocalyx*	Hanst.					Fp; P		Ecuador to Nicaragua
Gesneriaceae	*Drymonia macrantha*	(Donn. Sm.) D. N. Gibson		Fp	Fp				Costa Rica, Panama
Gesneriaceae	*Drymonia macrophylla*	(Oerst.) H. E. Moore			Fp				Peru to Nicaragua
Gesneriaceae	*Drymonia warscewicziana*	Hanst.		Fp					Costa Rica, Ecuador
Melastomataceae	*Blakea anomala*	Donn. Smith					Fp		Costa Rica
Melastomataceae	*Blakea cf. subpeltata*	Cogn.	Fpg						Costa Rica
Melastomataceae	*Blakea cf. tuberculata*	J.D. Smith					Fp; P		Costa Rica, Panama
Melastomataceae	*Blakea litoralis*	L. O. Williams	Fpg	Fp					Costa Rica, Panama
Melastomataceae	*Blakea scarlatina*	Almeda				Fp			Costa Rica, Nicaragua
Melastomataceae	*Blakea subpeltata*	Cogn.		Fp					Costa Rica
Melastomataceae	*Topobea maurofernandeziana*	Cogn.	Fpg; Fps	Fp; P	Fp; P	Fp			Panama to Nicaragua
Melastomataceae	*Topobea multiflora*	Triana			Fp				Bolivia to Costa Rica
Melastomataceae	*Topobea pittieri*	Cogn.			Fp; P				Ecuador to Costa Rica
Moraceae	*Ficus aff. colubrinae*	Standl.				Fs			Panama to Mexico
Moraceae	*Ficus americana*	Aublet						Fp; Fs; P	Brazil to Mexico incl. Dominican Republic
Moraceae	*Ficus cahuitensis*	C. C. Berg				Fp			Panama to Honduras
Moraceae	*Ficus cf. citrifolia*	Mill.	Fpg	Fp					Brazil to Mexico incl. Dominican Republic and Cuba
Moraceae	*Ficus cf. osensis*	C. C. Berg		Fp					Columbia to Costa Rica
Moraceae	*Ficus cf. pertusa*	L. f.				Fp			Brazil to Mexico
Moraceae	*Ficus citrifolia*	Mill.	Fpg; Fs; P	Fp				P	Brazil to Mexico incl. Dominican Republic and Cuba
Moraceae	*Ficus colubrinae*	Standl.	Fpg; Fs	Fp; P		P			Panama to Mexico
Moraceae	*Ficus costaricana*	(Liebm.) Miq.	Fpg; P	Fp					Ecuador to Mexico
Moraceae	*Ficus crassiuscula*	Warb. ex Standl.					Fp; P		Bolivia and Venezuela to Guatemala
Moraceae	*Ficus nympheifolia*	Miller	P	P					Brazil to Honduras
Moraceae	*Ficus obtusifolia*	Kunth						P	Brazil to Mexico
Moraceae	*Ficus pertusa*	L. f.	Fs	Fp; P		Fs			Brazil to Mexico
Moraceae	*Ficus sp0*				Fp				
Moraceae	*Ficus sp1*				Fp				
Moraceae	*Ficus sp2*				Fp				
Moraceae	*Ficus sp4*				Fp				
Moraceae	*Ficus sp5*		P						
Moraceae	*Ficus sp6*						Fp		
Rubiaceae	*Cosmibuena valerii*	Standl.					Fp; P		Costa Rica, Panama
Schlegeliaceae	*Schlegelia parviflora*	(Oersted) Monach.	Fpg; Fps; Fs; P	Fp	Fp; P		Fp; P		Peru and French Guiana to Mexico
Solanaceae	*Cestrum sp.*				Fp				
Solanaceae	*cf. Cuatresia riparia*	(Kunth) Huntz.			Fp				Ecuador and Venezuela to Guatemala
Solanaceae	*Lycianthes santaeclarae*	(Greenm) D'Arcy		Fp		Fs			no distribution found
Solanaceae	*Lycianthes synanthera*	(Sentn.) Bitter			Fp; P				Peru to Guatemala
Solanaceae	*Merinthopodium neuranthum*	(Hemsl.) Donn. Sm.			Fp	Fp	Fp		Panama to Belize

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel; Fp = primary forest, Fs = secundary forest, g = gorge, s = slope
Sources for distributon data: http://www.gbif.org/, 22. 08. 2008; http://www.tropicos.org, 22. 08. 2008

Table 4 Species Richness and Diverstiy Indize in the different Regions.

	Ind.	Ind/ 0.1ha	HE/tree	sp.	fam.	gen.	singl.	fam. singl.	Ind./ sp.	ACE	MM	Hs	E Hs	Ds
LG	155		0,29	17	6	7	3	0	9,1			2,46	0,87	0,90
LG prim gorge	64	12,8	0,24	14	6	7	3	0	4,6	17,75	23,69	2,36	0,90	0,90
LG prim slope	56	11,2	0,18	6	4	4	0	0	9,3	6,00	6,85	1,23	0,69	0,79
LG sec	13	2,6	0,05	8	4	4	4	0	1,6	12,67	27,89	0,52	0,25	0,92
LG pasture (40*)	22		0,55	7	4	4	2	0	3,1	8,25	8,55	1,66	0,86	0,80
LA	727		1,93	26	12	16	4	2	28,0			2,74	0,84	0,92
LA prim	649	129,8	1,93	25	11	15	4	1	26,0	29,56	26,28	2,74	0,85	0,92
LA pasture (40*)	78		1,95	15	10	11	6	3	5,2	27,00	28,86	2,16	0,80	0,85
LS/NG	69		0,18	19	8	11	5	2	3,6			2,52	0,86	0,90
LS prim	33	6,6	0,16	13	6	8	5	0	2,5	17,00	32,33	2,13	0,83	0,84
NG sec	18	3,6	0,14	6	4	4	3	1	3,0	12,00	14,58	0,56	0,31	0,72
NG pasture (40*)	18		0,45	5	3	3	2	1	3,6	6,00	5,95	1,35	0,84	0,75
FC	366		1,70	26	9	15	6	0	14,1			2,53	0,78	0,89
FC prim	303	60,6	1,61	26	9	15	7	0	11,7	38,30	29,60	2,51	0,77	0,89
FC pasture (27*)	63		2,33	11	6	8	3	1	5,7	17,00	13,83	1,86	0,78	0,79
SM	103		0,27	22	9	11	7	0	4,7			2,55	0,82	0,89
SM prim	78	15,6	0,23	19	8	10	8	0	4,1	26,69	29,30	2,45	0,83	0,89
SM pasture (40*)	25		0,63	9	6	7	4	1	2,8	19,00	13,09	1,89	0,86	0,84
BA pasture (20*)	6		0,3	3	1	1	1	0	2,0	4,00	6,27	1,01	0,92	0,73

*number of trees observed

BA = Baru; FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel; prim = primary forest, sec = secundary forest
Ind. = individuals; Ind/ 0.1 ha = individuals per 0.1 hectar; HE/ tree = hemiepiphytes per tree; sp. = species; fam. = families; gen. = genera
singl. = singletons; fam. singl. = families with only a singleton; Ind./ sp. = mean of individuals per species; ACE = Abundance-based Coverage Estimator
MM = Michaelis-Menton richness estimator; Hs = Shannon-Wiener-Index; E Hs= Evenness of Hs; Ds = Simpson-Yule-Index;

Table 5: Similarity Indizes of the Forests.

JACCARD	LG_Fp_g	LG_Fp_s	LG_Fs	SM_Fp	FC_Fp	LS_Fp	NG_Fs	LA_Fp
LG_Fp_g		0,429	0,467	0,375	0,081	0,25	0,053	0,053
LG_Fp_s	0,429		0,556	0,19	0,103	0,308	0	0,067
LG_Fs	0,467	0,556		0,286	0,063	0,188	0,167	0,063
SM_Fp	0,375	0,19	0,286		0,184	0,111	0,136	0,047
FC_Fp	0,081	0,103	0,063	0,184		0,088	0	0,156
LS_Fp	0,25	0,308	0,188	0,111	0,088		0	0,088
NG_Fs	0,053	0	0,167	0,136	0	0		0
LA_Fp	0,053	0,067	0,063	0,047	0,156	0,088	0	

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope

SORENSEN	LG_Fp_g	LG_Fp_s	LG_Fs	SM_Fp	FC_Fp	LS_Fp	NG_Fs	LA_Fp
LG_Fp_g		0,6	0,636	0,545	0,15	0,4	0,1	0,1
LG_Fp_s	0,6		0,714	0,32	0,188	0,471	0	0,125
LG_Fs	0,636	0,714		0,444	0,118	0,316	0,286	0,118
SM_Fp	0,545	0,32	0,444		0,311	0,2	0,24	0,089
FC_Fp	0,15	0,188	0,118	0,311		0,162	0	0,269
LS_Fp	0,4	0,471	0,316	0,2	0,162		0	0,162
NG_Fs	0,1	0	0,286	0,24	0	0		0
LA_Fp	0,1	0,125	0,118	0,089	0,269	0,162	0	

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope

BRAY-CURTIS	LG_Fp_g	LG_Fp_s	LG_Fs	SM_Fp	FC_Fp	LS_Fp	NG_Fs	LA_Fp
LG_Fp_g		0,4	0,2	0,3	0,09	0,23	0,02	0,02
LG_Fp_s	0,4		0,26	0,38	0,09	0,41	0	0
LG_Fs	0,2	0,26		0,2	0,02	0,23	0,12	0,01
SM_Fp	0,3	0,38	0,2		0,06	0,24	0,08	0,01
FC_Fp	0,09	0,09	0,02	0,06		0,03	0	0,05
LS_Fp	0,23	0,41	0,23	0,24	0,03		0	0,01
NG_Fs	0,02	0	0,12	0,08	0	0		0
LA_Fp	0,02	0	0,01	0,01	0,05	0,01	0	

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope

NESS (m=6)	LG_Fp_g	LG_Fp_s	LG_Fs	SM_Fp	FC_Fp	LS_Fp	NG_Fs	LA_Fp
LG_Fp_g		0,69	0,6	0,55	0,12	0,58	0,02	0,04
LG_Fp_s	0,69		0,88	0,58	0,11	0,83	0	0,05
LG_Fs	0,6	0,88		0,59	0,08	0,84	0,2	0,05
SM_Fp	0,55	0,58	0,59		0,18	0,54	0,17	0,02
FC_Fp	0,12	0,11	0,08	0,18		0,1	0	0,04
LS_Fp	0,58	0,83	0,84	0,54	0,1		0,12	0,05
NG_Fs	0,02	0	0,2	0,17	0	0,12		0
LA_Fp	0,04	0,05	0,05	0,02	0,04	0,05	0	

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope

Table 6: Similarity Indices of the Pastures

JACCARD	LG	LA	NG	FC	BA	SM
LG		0,048	0	0,059	0,111	0,143
LA	0,048		0	0,083	0	0
NG	0	0		0	0	0,167
FC	0,059	0,083	0		0	0,111
BA	0,111	0	0	0		0
SM	0,143	0	0,167	0,111	0	

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, NG = Nogal, SM = San Miguel

SORENSEN	LG	LA	NG	FC	BA	SM
LG		0,091	0	0,111	0,2	0,25
LA	0,091		0	0,154	0	0
NG	0	0		0	0	0,286
FC	0,111	0,154	0		0	0,2
BA	0,2	0	0	0		0
SM	0,25	0	0,286	0,2	0	

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, NG = Nogal, SM = San Miguel

BRAY-CURTIS	LG	LA	NG	FC	BA	SM
LG		0,04	0	0,047	0,071	0,213
LA	0,04		0	0,071	0	0
NG	0	0		0	0	0,093
FC	0,047	0,071	0		0	0,068
BA	0,071	0	0	0		0
SM	0,213	0	0,093	0,068	0	

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, NG = Nogal, SM = San Miguel

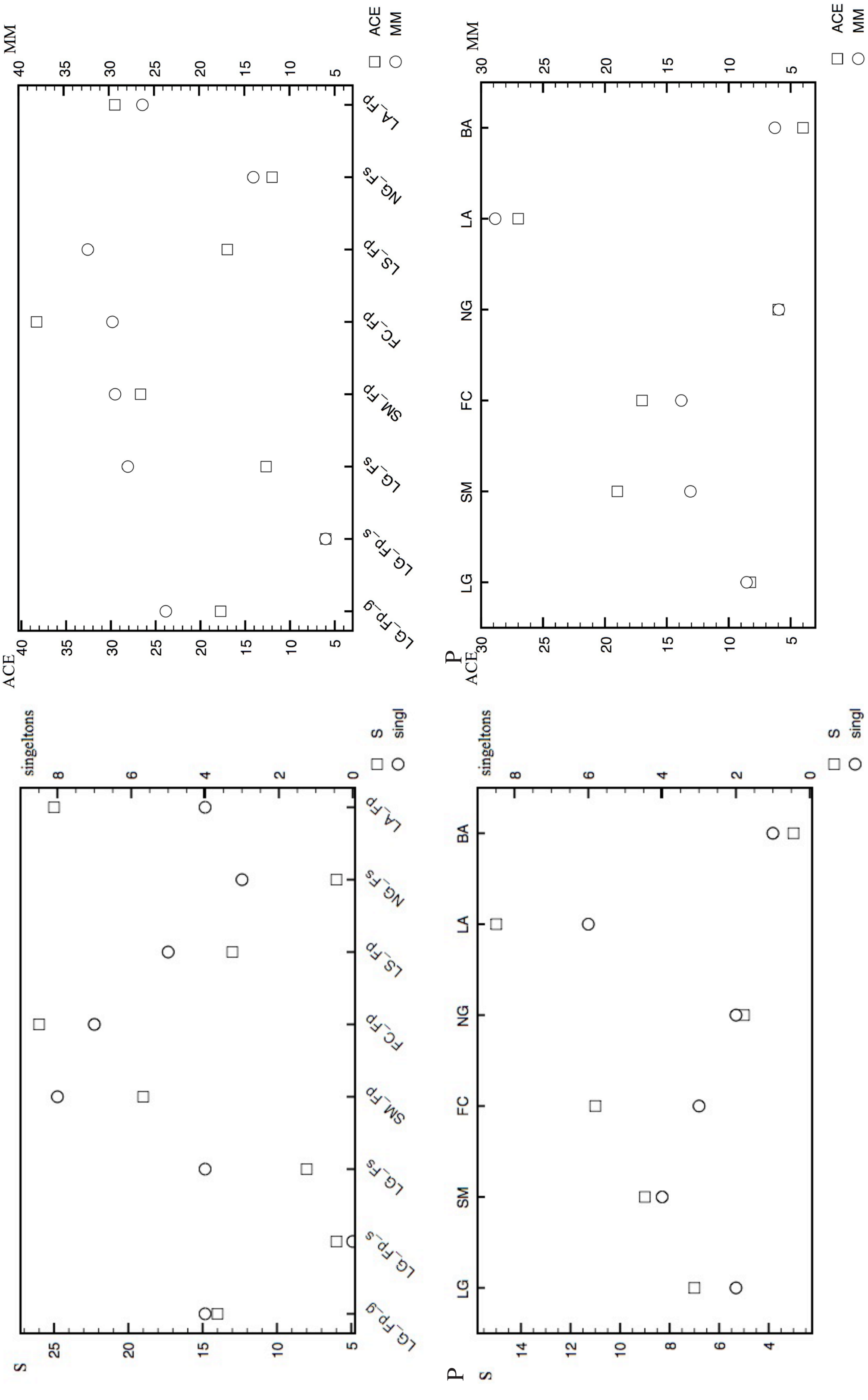
NESS (m=3)	LG	LA	NG	FC	BA	SM
LG		0,07	0	0,05	0,32	0,22
LA	0,07		0	0,05	0	0
NG	0	0		0	0	0,1
FC	0,05	0,05	0		0	0,16
BA	0,32	0	0	0		0
SM	0,22	0	0,1	0,16	0	

BA = Baru, FC = Fila Costena, LA = Los Alpes, LG = La Gamba, NG = Nogal, SM = San Miguel

Figure 1. Species Richness and singletons (left), ACE and MM (right) of forests (top) and pastures (bottom).

Species Richness

Species Richness (S) and singletons (singl); Abundance-based Coverage Estimator (ACE) and Michaelis-Menton richness estimator (MM)

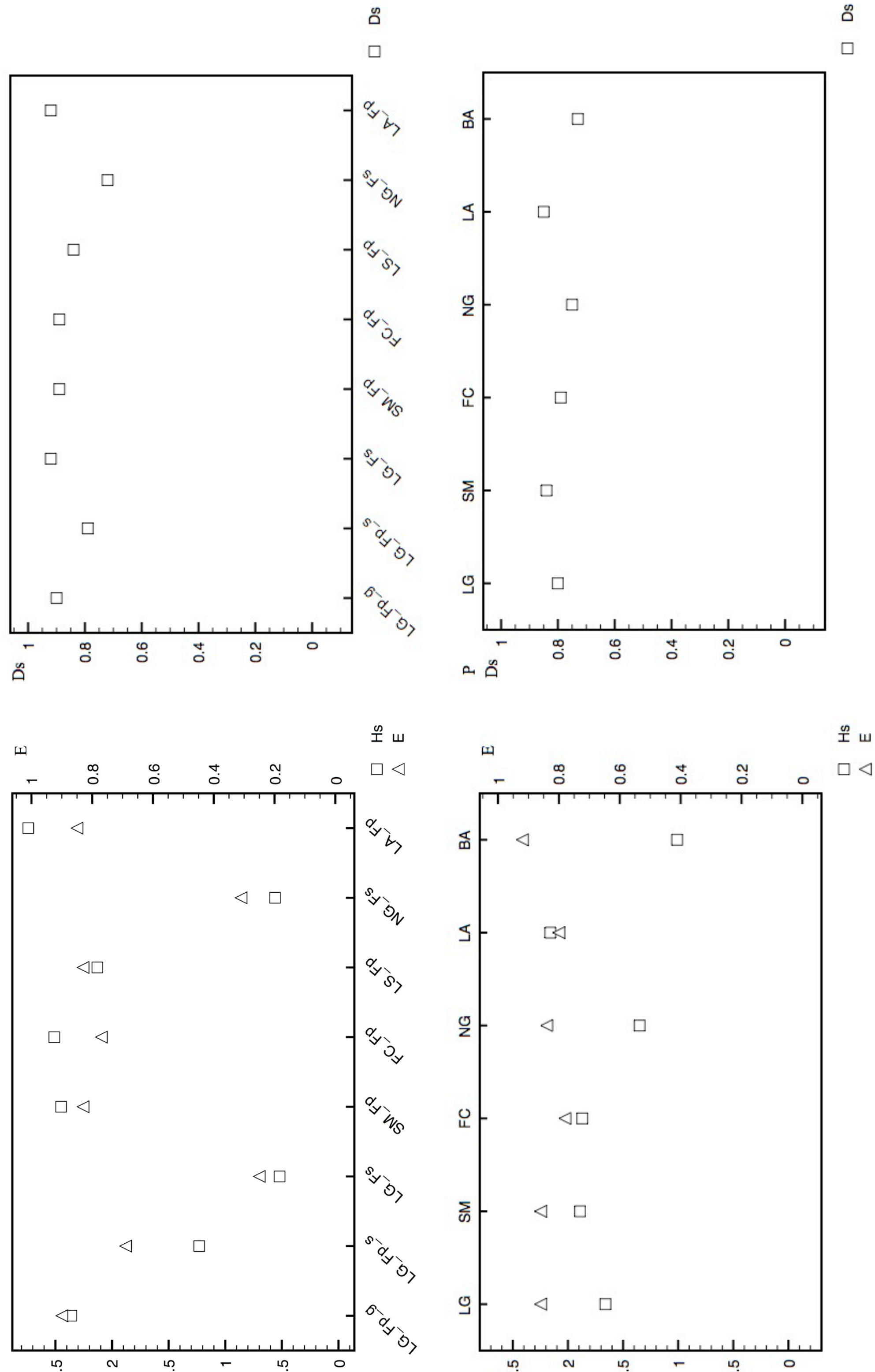


BA= Baru; FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel; Fp = primary forest, Fs = secundary forest, g = gorge, s = slope; P= pasture

Figure 2. Shannon-Wiener Index and Evenness (left), Simpson-Yule Index (right) of forests (top) and pastures (bottom).

Diversity

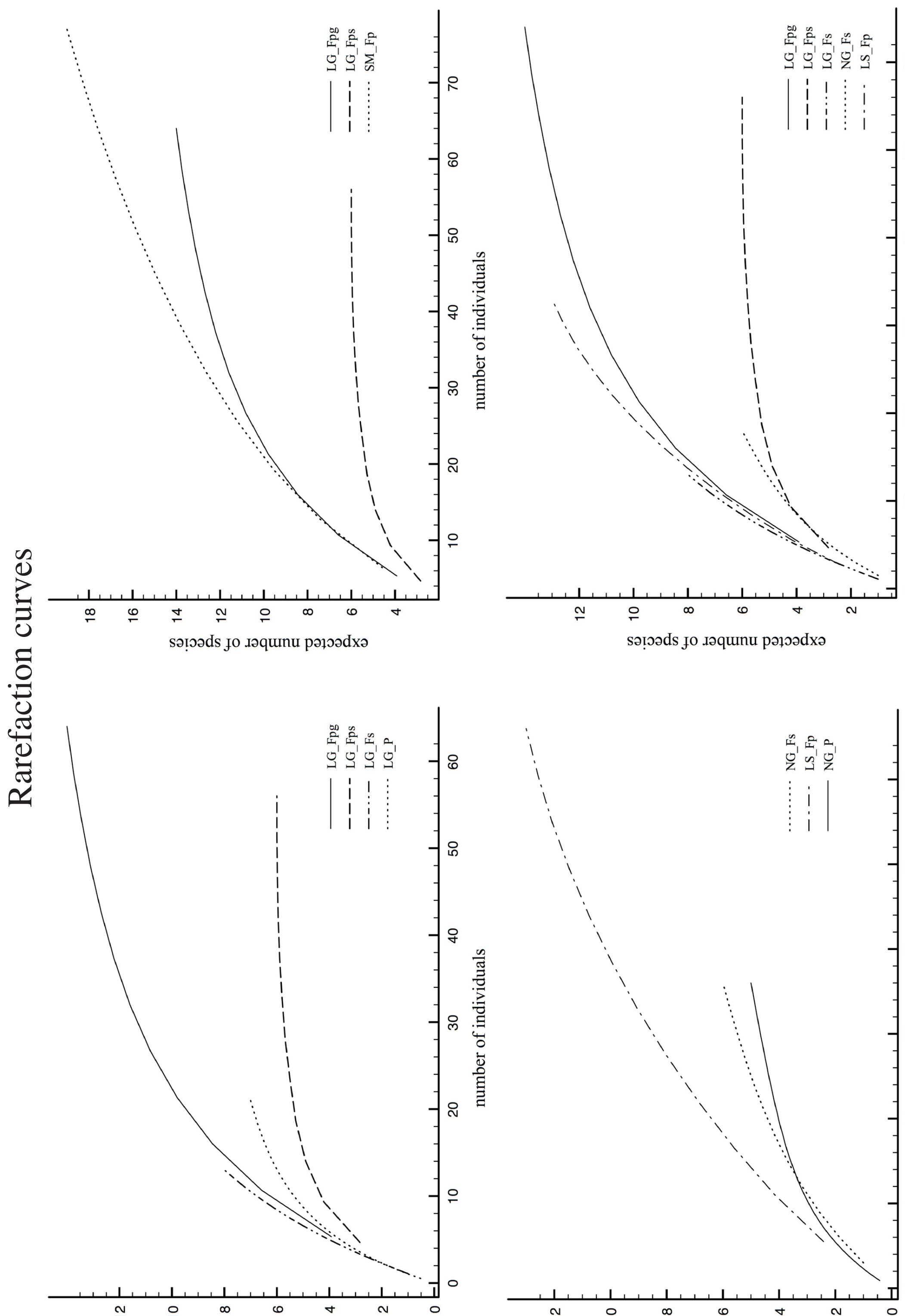
Shannon-Wiener-Index (Hs); Simpson-Yule-Index (Ds); Evenness (E) of Hs

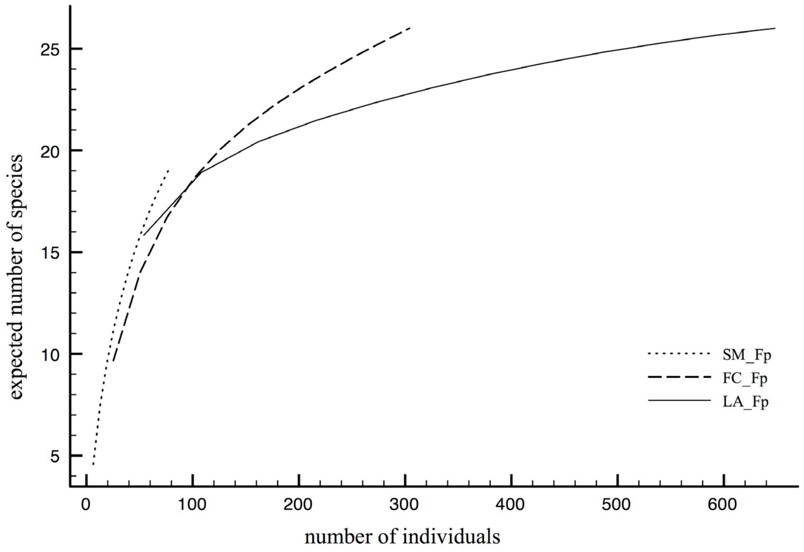


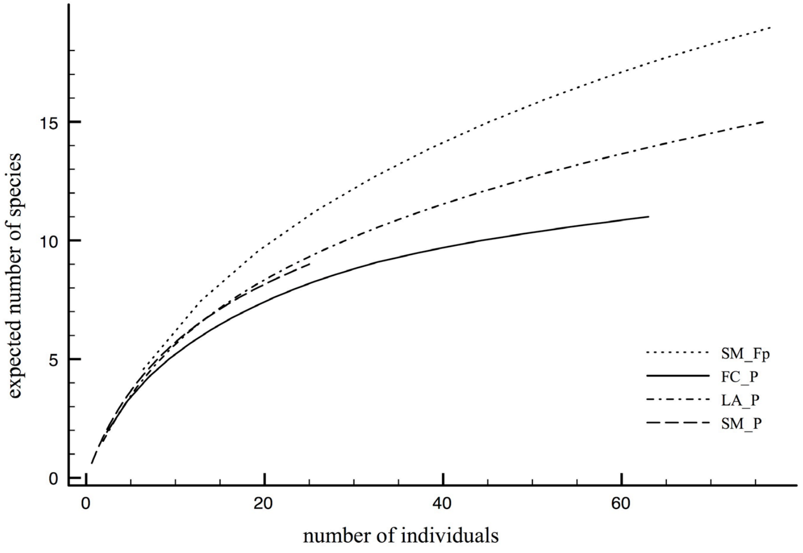
BA= Baru; FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel; Fp = primary forest, Fs = secundary forest, g = gorge, s = slope; P= pasture

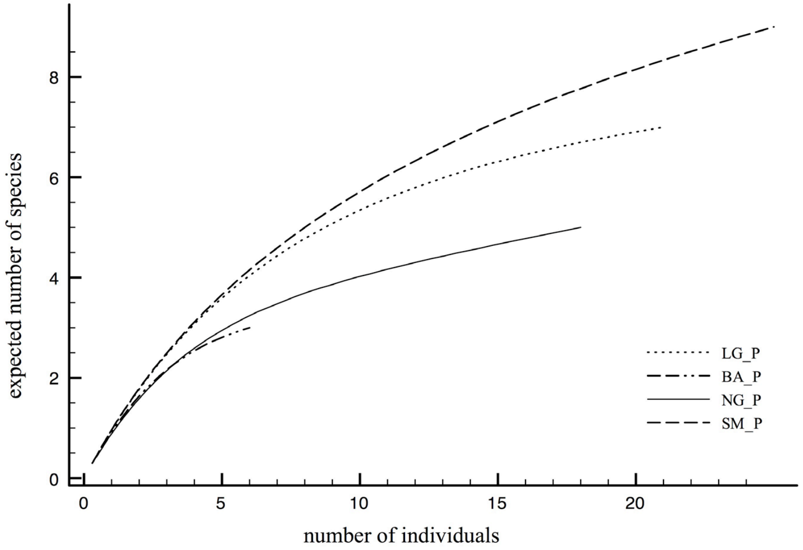
Figure 3. Rarefaction curves in order of placement (left to right): Sites in LG, Primary forests in LG and SM, Sites in NG and LS, Lowland forests in LG and LS/NG.

Next paige. premontane forests and SM forest, premontane pastures and SM pasture, Lowland pastures.









Rarefaction curves in order of placement:

Sites in La Gamba
Primary forests in La Gamba and San Miguel
Sites in Nogal and La Selva
Lowland forests in LG and LS/NG

Premontane forests and SM
Premontane pastures and SM
Lowland pastures

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope; P= pasture

3 Manusscript for paper 2:

LENOTTI: SPECIES ABUNDANCE OF HEMIEPIPHYTES

Species abundance and family importance of primary Hemiepiphytes in different study sites, forests and pastures, in Costa Rica

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Abstract We have compared the species abundance and family importance of primary hemepiphytes in four lowland primary forest plots, two lowland secondary forest plots and two premontane primary forest plots of 0.5 ha size and additionally on five different pastures in Carribean- and Pacific-influenced regions. We have found that there are different species and families of importance, calculated FIV and IVI of the forest plots and general abundance of pastures and regions. Beside the importance of Clusiaceae, and Moraceae there are many other families of importance, like Melastomataceae and Ericaceae. We have also found that some species prefer regional and or ecological parameters to more light on freestanding trees. Species of the families Cecropiaceae and Moraceae show high importances on lowland pastures, whereas Araliaceae and Rubiaceae are of high importance in premontane primary forests. Moreover the families Schlegeliacea and Cusiaceae are of higher importance in the lowland in general, whereas beside Araliaceae, also Asteraceae and Gesneriaceae are of higher importance in premontane sites.

Key words: hemiepiphyte, species abundance, FIV, IVI, NESS, MDS, Costa Rica, lowland and premontane, primary forest, secondary forest, pasture

INTRODUCTION

This study is part of a survey on diversity and abundance of primary hemiepiphytes (pHEs) in different regions in Costa Rica. In a previous paper titled “Diversity and Abundance of Primary Hemiepiphytes in Costa Rica” we found that pHEs, as an important element of tropical rainforests (Gentry 1986; Williams-Linera & Lawton 1995) have high abundances in primary forest plots from 6.6 to 12.8 individuals per 0.1 ha in lowland sites, up to 129.8 individuals per 0.1 ha in premontane forest sites. Species Richness extimation with ACE calculates values up to 38.30 in premontane primary forests, values around 17 in lowland primary forests and values up to 8.25 in secondary forests. This shows that diversity and abundance increases with higher altitudes and decreases with invreasing disturbance of the forests.

This paper now gives more information on species, genara and families - in six different regions in Costa Rica, observing also different forest types in lowland and premontane sites, on 0.5 ha forest plots and on freestanding trees on pastures. Besides calculating Familiy Importance Value and Important Value Index of all our sites, we have examined the different generas and families in nonnumeric multidimensional scaling according to their location of their habitat.

Therefore this paper intends to give, toghether with other work in this survey on spatial distripution by David Bröderbauer 2008, more information data on the very rare information about primary hemiepiphytes. We have not focused on single species of pHEs, but have recorded all individuals within the sample areas.

METHODS

Study Sites

The study has been carried out in four lowland and two premontane primary rainforests, two lowland secondary rainforests and three lowland and two premontane pastures (TABLE 1). Each forest plot was of 0.5 ha size. On each pastures 40 freestanding trees have been observed, but on Fila Costena 27. The study sites go in line with our sites in the other work on “Diversity and Abundance of Primary Hemiepiphytes in Costa Rica” ecept the sites in Santa Rosa and Baru, which are excluded from this work. Therefore site description of all other plots is the same, and could be read in the previous paper. We distinguish between:

- Pacific influenced lowland sites: two primary forests plot, a secondary forest plot and a pasture in La Gamba (LG), a primary forest and a pasture plot in San Miguel (SM) on 500 m above sea level (asl).
- Pacific influenced premontane sites: a primary forest plot and a pasture plot on the Fila Costena (FC)
- Atlantic influenced lowland sites: a primary forest plot in La Selva (LS), a secondary forest plot and a pasture plot in Nogal (NG)
- Atlantic influenced premontane sites: a primary forest and a pasture in the Reserva Los Alpes (LA)

Field Methods

Field work has been conducted during the dry season from January to May 2007 in five primary forest plots, two secondary forest plots and on five pastures and also goes in line with the filed mehtods of the whole survey. As in the previous paper the forest plots have been covering 0.5 ha, and have been divided into twelve subplots. In each subplot all trees with a diameter at breast height (dbh) ≥ to 10 cm have been explored for primary hemiepiphytes (pHEs). On the pastures in La Gamba, Los Alpes, Nogal and San Miguel 40 and on the Fila Costeña 27 freestanding trees with a dbh greater ≥ to 10 cm have been observed. The dbh has been measured with tapes in mm and trees have been explored with binoculars (ESCHENBACH© trophy AS/D 10 x 50 und SWAROVSKI© Habicht SLC 7 x 42B).

Species of pHEs have been recorded, samples of each species have been collected and determined in the Herbario National of the Museo National de Costa Rica (CR). Furthermore, the sizes of the pHEs have been determined through the estimation of the percentage of the host canopy shaded by the primary hemiepiphyte. The pHEs have been assigned to five classes: 0) < 5 percent, 1) 5-25 percent, 2) 26-50 percent, 3) 51-75 percent, 4) 75-100 percent (following Todzia, 1986).

Vouchers have been deposited the Museo Nacional in San José, Costa Rica, and in the Herbarium of the Institute of Botany, University of Vienna, Austria (WU).

Data Analysis

Descriptive statistic has been performed with SPSS 16.0, calculating species abundance, relative species abundance, cumulated species abundance and relative cumulated species abundance in genera and families. Important Value Index (IVI) and Family Index Value (FIV) have been calculated using the formulae in TABLE 2 (Madsen and Ollgaard, 1994). Calculation of density, dominance, frequency and diversity has been done as follows: 1) density: individuals per 0.1 hectar, 2) dominance: sum of the values of the five size classes of the pHEs, 3) frequency: relative abundance in the 12 subplots and 4) diversity: species per family (following Wattenberg & Breckle, 1995).

Nonmetric Multidimensional Scaling (NMDS) of genera and families has been carried out with Statistica 6 on the basis of Normalized Expected Species Shared Index (NESS) to adapt to the matrix with many zero values. NESS has been calculated with an Excel Plug-In (Fiedler 2007) and a sampling parameter m of 5. If the abundance of genera or families is limited to a single sample site, this genera or family has been excluded. NESS is less biased than other commonly used measurements and could be (with large m) more sensitive to less common species. It considers the probability of abundances in the data sets (Homeier et al. 2002).

RESULTS

In six regions, Fila Costena (FC), Los Alpes (LA), La Gamba (LG), La Selve (LS)/Nogal (NG) and San Miguel (SM), we have observed six primary forest plots of 0.5 ha (two different ones in LG), two secondary forest plots of 0.5 ha in LG and NG and five pastures. On these we have found in total 90 species of primary hemiepiphytes, in 22 generas and 12 families. Of these regions we have calculated the abundance and relative abundance of the HEs, of the forests and pastures we also have calculated density (individuals per 0.1 ha), relative density (which therefore goes in line with the relative abundance presented), dominance (dominance per size classes observed), relative dominance, frequency (relative abundance in the 12 subplots), relative frequency, diversity (species per family), relative diversity, Important Value Index (IVI) and Family Index Value (FIV).

TABLE 5 in the appendix shows the abundance and cummulated abundance of all species, genera and families in the different regions and sites, whereas TABLE 6 in the appendix shows density, relative denisty, dominance, relative dominance, frequency, relative frequency, diversity, rlative diversity, IVI and FIV of all species in the different sites.

Regions

Pacific-influenced region (p) – lowland (l)

On the two primary forest plots - gorge and slope -, the secondary forest plot and the pasture in LG (pl) we have found in total 155 individuals of pHEs, within 17 species, seven generas and six families. Of three species we have only found singletons. Most abundant are *Clusia amazonica* and *Schlegelia parviflora* with 0.1548 each, followed by *Topobea maurofernandeziana* with 0.129 and *Satyria panurensis* (0.1097). The abundance of the other species is under 0.10 (not more than 13 individuals). Most abundant genera and family are *Clusia* and Cusiaceae (0.3097 cumulative).

In SM (pl), in the primary forest and the pasture, we have found in total 103 individuals of pHEs, within 22 species, 11 generas and nine families. Of seven we have only found singletons. Most abundant is *Drymonia alloplectoides* (0.2718), and in a bigger interval, *Satyria panurensis* (0.1268) and *Clusia amazonica* (0.1068). All other species are far below 0.10, a lot with less than five individuals. The most abundant genera is therefore *Drymonia* and the most abundant family is Gesneriaceae with an abundance of 0.2913, highly characterized by *D. alloplectoides*.

Pacific-influenced region (p) – premontane (p)

On the FC (pm), in the primary forest and on the pasture, we have found in total 366 individuals of pHEs of 26 species, 15 generas and nine families, with six singletons. Most abundant, with a relative abundance higher than 0.10, are *Topobea pittieri* (0.1803), *Schefflera brennesii* (0.153), *Clusia stenophylla* (0.1448) and *Cavendishia callista* (0.1393). The most abundant genera is *Topobea* with 0.2240, followed by *Clusia* (0.1803) and *Schefflera* (0.1776). The most abundant family is Ericaceae with 0.2459.

Atlantic-influenced region (a) – lowland (l)

In the primary forest of LS (al) and the secondary forest and on the pasture of NG (al) we have found in total 69 individuals of pHEs of 19 species, 11 generas and eight families, five species with singletons. Most abundant are *Clusia flava* (0.2174), *Satyria panurensis* (0.1884) and *Clusia quadrangula* (0.1014). All other species have a relative abundance lower than 0.10. The most abundant genera is therefore *Clusia* with 0.5072 and the most abundant family Clusiaceae with a relative cumulative abundance of 0.5217.

Atlantic-influenced region (a) – premontane (p)

In the primary forest and on the pasture of LA (am) we have found in total 727 individuals of pHE of 26 species, 16 generas, 12 families and four singletons. The species

Blakea anomala (0.1486) and *Clusia palmana* (0.1431) have a relative abundance higher than 10 %. Most abundant genera are therefore *Blakea* (0.2242) and *Clusia* (0.1994), most abundant families are Melastomataceae (0.2242), Clusiaceae (0.2008) and Ericaceae (0.1939).

Primary forests

The most abundant or important species per site are presented, mostly with a relative abundance higher than 0.10. IVI with relative density, relative dominance and relative frequency of the species with the highest values are presented in TABLE 3. FIV of the families with the highest values are presented in TABLE 4.

Primary gorge forest of LG (pl). There we have found 64 individuals of pHEs in 14 species, seven generas and six families, three singletons. This is a density of 12.8 HEs per 0.1 ha.

Most abundant (a) and also with the greatest frequency (f) is *Topobea maurofernandeziana* (a: 0.2031; f: 0.1667). In terms of abundance then follows *Blakea litoralis* (0.1875). Concerning dominance, however, *B. litoralis* (0.2414) comes before *T. maurofernandeziana* (0.2241). *Schlegelia parviflora* follows in relative abundance (0.1094), and has the same value as *B. litoralis* in frequency (0.125), but is only forth in relative dominance (0.862), because *Ficus costaricana* has got a greater dominance (0.1379) but again a lower frequency value (0.625 equally as *Coussapoa glaberrima*), even below *Clusia amazonica*, *C. osaensis* and *Satyria panurensis* with a relative frequency of 0.833.

The species with the highest value of IVI are *T. maurofernandeziana* (59.39), *B. litoralis* (55.39), *S. parviflora* (32.06), *F. costaricana* (27.86) and *C. osaensis* (21.48). The remaining 9 species have a cumulated IVI of 103.83 (see TABLE 2).

Most abundant generas are *Blakea* and *Clusia* with a cumulative abundance of 0.2188 respectivley and *Topobea* with 0.2030. The most abundant family is therefore Melastomataceae with 0.4218. In relative diversity Clusiaceae (0.3571) is on top, followed by Melastomataceae and Moraceae (0.2143), Moraceae with a cumulated relative abundance of 0.1677.

The families with the highest value in FIV are Melastomataceae (115.34), Clusiaceae (71.38) and Moraceae (52.73). The remaining 3 families have a cumulated FIV of 0.6054 (see TABLE 3). Aquifoliaceae, Araliaceae, Asteraceae, Gesneriaceae, Rubiaceae and Solanaceae do not occur in this site.

Primary slope forest of LG (pl). In that plot we have found 56 individuals of pHEs in six species, four generas and families and no singletons. This is a density of 11.2 HEs per 0.1 ha.

Most abundant (a) and most dominant (d) are *Clusia amazonica* (a: 0.3393; d: 0.4624), *Schlegelia parviflora* (a: 0.2143; d: 0.2366) and *Satyria panurensis* (a: 0.1964; d: 0.1505). In terms of relative frequency *S. parviflora* and *S. panurensis* are equal with 0.2353 and *C. amazonica* is in third place with 0.2059.

The species with the highest value of IVI are also *C. amazonica* (100.75), *S. parviflora* (68.61) and *S. panurensis* (58.23), followd by *Topobea maurofernandeziana* (35.52) and *Clusia valerioi* (20.63). The remaining species *Clusia peninsulae* has an IVI of 16.25 (see TABLE 2).

The most abundant genera and family is *Clusia*/ Clusiaceae with a relative abundance of 0.4643. The family Clusiaceae has the highest value in relative diversity (0.50). All other three families have a relative diversity of 0.1667 with only one species each.

Therefore, the family with the highest value of FIV is Clusiaceae (152.34), followed by Schlegeliaceae (61.75), Ericaceae (51.36) and Melastomataceae (34.54) (see TABLE 3). There are only few families present, Aquifoliaceae, Araliaceae, Asteraceae, Cecropiaceae, Gesneriaceae, Moraceae, Rubiaceae and Solanaceae do not occur in this site.

Primary forest of SM (pl). There we have found 78 individuals of pHEs in 19 species, 10 generas and eight families, with eghit singletons. This is a density of 15.6 HEs per 0.1 ha.

Most abundant are *Drymonia alloplectoides* (0.2436), *Clusia amazonica* (0.1410) and *Satyria panurensis* (0.1282), all other species are below 0.10. The highest in relative dominance is *C. amazonica* (0.1905), followed by *Schlegelia parviflora* (0.1429) and *S. panurensis* (0.119). *D. alloplectoides* has a low relative dominance with 0.0476. Even lower than *Ficus costaricana*, *F. citrifolia* and *Lycianthes santaeclarae*. Concerning relative frequency *D. alloplectoides* (0.1818) has the highest value, followed again by *C. amazonica* and *S. panurensis* both with 0.1273.

The species with the highest IVI are therefore *D. alloplectoides* (47.30), *C. amazonica* (45.88) and *S. panurensis* (37.45), followed by *S. parviflora* (24.87) and *L. santaeclarae* (23.39). The 14 remaining species have a cumulated IVI of 121.11 (see TABLE 2).

Most abundant genera are *Drymonia* (0.2692) and *Cluisa* (0.1667), most abundant families are therefore Gesneriaceae (0.2692) and Clusiaceae and Ericaceae, both with 0.1667. The family with the highest relative diversity is Moraceae (0.2632), followed by Clusiaceae, Gesneriaceae and Melastmataceae with 0.1579 each.

The families with the highest FIV are Moraceae (64.04), Gesneriaceae (54.62) and Clusiaceae (51.5). The remaining five families have a cumulated FIV of 129.83 (see TABLE 3). Aquifoliaceae, Asteraceae, Cecropiaceae and Rubiaceae do not occur in this site.

Primary forest of Fila Costena (pm). In this plot we have found 303 individuals of pHEs in 16 species, 15 generas and nine families and seven singletons. This is a density of 60.6 HEs per 0.1 ha.

Most abundant species, with a relative abundance greater than 0.10, are *Topobea pittieri* (0.2145), *Schefflera brennesii* (0.1815) and *Cavendishia callista* (0.1188). *T. pittieri* is also highest in relative dominance with a value of 0.2167. *Psammisia ramiflora* follows with 0.1673 and *S. brennesii* with 0.1027. *C. callista* is only in fourth place with 0.0798 even behind *Clusia stenophylla* with 0.0989. In relative frequency, the order is again *T. pittieri* and *S. brennesii* both with 0.1026, followed by *C. callista* and *C. stenophylla* with 0.0855 each.

The species with the highest IVI are therefore *T. pittieri* (53.38), *S. brennesii*

(38.67), *P. ramiflora* (32.67), *C. callista* (28.41) and *C. stenophylla* (28.00). These species are followed by *S. warszewiczii, Topobea maurofernandeziana, Schlegelia parviflora, Clusia croatii* and *Drymonia macrantha* all with an IVI of between 10 and 15. The 16 remaining species have a cumulated IVI of 55.57 (see TABLE 2).

Most abundant genera are *Topobea* (0.2541) and *Schefflera* (0.2013) and most abundant families are, in colse intervals, Melastomataceae (0.2541), Ericaceae (0.2343) and Araliaceae (0.2211). The family with the highest relative diversity is Araliaceae (0.1923), followed by Ericaceae, Moraceae and Solanaceae with 0.1538 each.

The families with the highest FIV are Ericaceae (68.09), Melastomataceae (63.57) and Araliaceae (55.79). Clusiacae (34.39) and Moraceae (24.39) follow. The remaining 4 families have a cumulated FIV of 53.96 (see TABLE 3). Aquifoliaceae, Cecropiaceae and Rubiaceae do not occur in this site.

Primary forest of LS (al). There we have found 33 individuals of pHEs in 13 species, eight generas, six families and five singletons. This is a density of 6.6 HEs per 0.1 ha.

Most abundant is *Satyria panurensis* with 0.3939, second is *Topobea maurofernandeziana* with 0.0909, all other species' abundances are far lower than 0.10. *S. panurensis* is also most dominant and frequent, with a relative dominance of 0.5417 and a relative frequency of 0.3103. Second in relative dominance is *Clusia amazonica* (0.125), the individuals of *T. maurofernandeziana* have been only juvenile with no dominance value, but they have been frequent, so *T. maurofernandeziana* is second in relative frequency with 0.1034.

The by far highest IVI has therefore *S. panurensis* (124.6), followed by *C. amazonica* (25.46), *Cluisa valerioi* (21.29), *T. maurofernandeziana* (19.44) and *Clusia gracilis* (17.12). The 8 remaining species have a cumulated IVI of 92.1 (see TABLE 2).

Most abundant genera are *Satyria* with only one species, and *Clusia* with 5 species and a cumulative abundance of 0.2424. Most abundant families are Ericaceae with 0.30939 and Clusiceae with 0.2727. The family with the highest relative diversity is Clusiaceae (0.4615), followed by Melastomataceae and Moraceae with 0.1538 each.

The families with the highest FIV are therefore Clusiaceae (102.59) and

Ericaceae (101.25), followed by Melastomataceae (34.7). The remaining three families have a cumulated FIV of 61.45 (see TABLE 3). Aquifoliaceae, Araliaceae, Asteraceae, Cecropiaceae, Gesneriaceae, and Rubiaceae do not occur in this site.

Primary forest of LA (am) In this plot we have found 649 individuals of pHEs in 25 species, 15 generas, 11 families and four singletons. This is a density of 129.8 HEs per 0.1 ha.

Most abundant are *Blakea anomala* (0.1664) and *Clusia palmana* (0.1325). Concerning relative dominance *B. anomala* is also highest (0.1425) and *C. palmana* was equally high with *Cosmibuena valerii* (0.1145 each). Also a high value in realtive dominance has *Blakea* cf. *tuberculata* (0.0922). All species in LA are not very frequent. The highest relative frequency with each 0.0632 are reaching following species: *Oreopanax oerstedianum, C. palmana, Cavendishia bracteata* and *C. complectens, B. anomala* and *B.* cf. *tuberculata* and *C. valerii*.

The IVIs of these species are relatively low, the species with the highest values are *B. anomala* (37.2), *C. palmana* (31.02), *C. valerii* (25.47), *B.* cf. *tuberculata* (23.85) and *C. bracteata* (21.56). These species are followed by *Drymonia conchocalyx, Stayria panurensis/Psammisia ramiflora* (which are hard to distinguish in their vegetative state), *Oreopanax oerstedianum, O. capitatus* and *Schefflera rodriguesiana* all with an IVI between 10 and 20. The 16 remaining species have a cumulated IVI of 81.34 (see TABLE 2).

Most abundant genera are *Blakea* (0.2496) and *Clusia* (0.188). Most abundant families are Melastomataceae (0.2496), Clusiaceae (0.1895), Ericaceae (0.1818) and Araliaceae (0.1633). The families with the highest relative diversity are Ericaceae (0.2308), Clusiaceae (0.1923) and Araliaceae (0.1538).

The families with the highest FIV are Clusiaceae (57.18), Melastomataceae (56.12), followed by Ericaceae (56.06), Araliaceae (47.92) and Rubiaceae (23.00). The remaining 6 families have a cumulated FIV of 59.72 (see TABLE 3). In this forest only Aquifoliaceae could not be found. This family we have only found on LA's pasture.

Secondary forests

Secondary forest of LG (pl). There we have found 13 individuals of pHEs in eight species, four generas and families and four singletons. This is a density of 2.6 HEs per 0.1 ha.

All species are represented by a very low number of individuals, most abundant is *Schlegelia parviflora* (0.2308), being also the highest in relative dominance (0.375) and relative frequency (0.25).

Therefore *S. parviflora* has also the highest IVI with 85.58. It is followed by *Clusia valerioi* (48.72), *Ficus colubrinae* (41.03), *Satyria panurensis* and *Ficus pertusa* (32.05 each). The remaining 3 species have a cumulated IVI of 60.58 (see TABLE 2).

Most abundant genera and families are *Ficus*/Moraceae and *Clusia*/Clusiaceae, both with a relative abundance of 0.3077. The families with the highest relative diversity are also Clusiaceae and Moraceae (0.375 each).

The families with the highest FIV are therefore Clusiaceae (105.77) and Moraceae (93.27), followed by Schlegeliaceae (73.08). The remaining species Ericaceae has an FIV of 27.88 (see TABLE 3). There are only few families to be found. Aquifoliaceae, Araliaceae, Asteraceae, Cecropiaceae, Gesneriaceae, Melastomataceae, Rubiaceae and Solanaceae do not occur in this site.

Secondary forest of NG (al). In that plot have found 18 individuals of pHEs in six species, four generas and families and three singletons. Most abundant is *Clusia flava* (0.5), also very abundant are *Clusia uvitana* (0.2222) and *Lycianthes santaeclarae* in third place with 0.1111. Concerning relative dominance *L. santaeclarae* has the highest value (0.4545), *Ficus pertusa* followed (0.2727), *Clusia flava* is third (0.1818) and *C. uvitana* forth (0.0909). In terms of relative frequency it is again *Clusia flava* (0.3333) in first and *C. uvitana* (0.25) in second place. In third position *L. santaeclarae* (0.1667).

The highest IVI have *Clusia flava* (101.52), *Lycianthes santaeclarae* (73.23) and *Clusia uvitana* (56.31), followed by *Ficus pertusa* (41.16), *F.* aff. *colubrinae* and *Oreopanax* sp. (13.89 each) (see TABLE 2).

The most abundant genera and family is therefore *Clusia*/Clusiaceae with a relative abundance of 0.7222. The families with the highest relative diversity are Clusiaceae and Moraceae (0.3333 each).

The families with the highest FIV are Clusiaceae (132.83), Solanaceae (73.23) and Moraceae (71.72). The remaining species Araliaceae has an FIV of 22.22 (see TABLE 3). There are also only few families to be found. Aquifoliaceae, Asteraceae, Cecropiaceae, Ericaceae, Gesneriaceae, Melastomataceae, Rubiaceae and Schlegeliaceae do not occur in this site.

Pastures

On the pasture of LG (pl) we have found 22 individuals of pHEs in seven species, four generas and families and two singletons. Most abundant is *Ficus citrifolia* (0.4091), followed by *Clusia valerioi* (0.1818). The most abundant genera and family is therefore *Ficus*/Moraceae (0.5909).

On the pasture of SM (pl) we have found 25 individuals of pHEs in nine species, seven generas, six families and four singletons. Most abundant is *Drymonia alloplectoides* (0.36), followed by *Clusia valerioi* (0.16), both the only species in their families represented. Most abundant genera and families are *Drymonia*/Gesneriacea and *Clusia*/ Clusiacea.

On the pasture of FC (pm) we found 63 individuals of pHEs in 11 species, eight generas, six families and three singletons, there we have only observed 27 trees not 40 as on the other pastures. Most abundant is *Clusia stenophylla* (0.3810), followed by *Cavendishia callista* (0.2381). Most abundant genera and families are also *Clusia*/ Clusiaceae (0.4127) and *Cavendishia* (0.2381) of the family Ericaceae (0.3016).

On the pasture of NG (al) we have found 18 individuals of pHEs in five species, three gerneras and families and two singletons. Most abundant is *Clusia quadrangula* (0.3889), followed by *Clusia flava* (0.3333). The most abundant genera and family is therefore *Clusia*/Clusiaceae (0.7778).

On the pasture of LA (am) we have found 78 individuals of pHEs in 15 species, 11 generas, ten families and six singletons. Most abundant is *Cavendishia bracteata* (0.2564), followed by *Clusia palmana* (0.2308). *Cosmibuena valerii* has also a high relative abundance (0.1410). Most abundant genera and families are *Clusia*/Clusiaceae and *Cavendishia*/Ericaceae with a realtive abundance of 0.2949 each.

Multidimensional scaling

We have used the Expected Species Shared Index (NESS) for multidemensional scaling (MDS) for the genera and the families, based on their abundance date in the different sites. In three dimensions we see which family/genera is similar to ohter families and genera and wich ones are apart from the others in their reginal distribution.

Looking at the families (FIGURE 1) we see that in dimension 1 all families are clustered on the low edge, Moraceae has a distance to them and Cecropiaceae is even on the other edge. In dimension two most of the families are present in the middle, Rubiaceae has again the greatest distance in one edge. In the other edge, there are Solanaceae and Gesneriaceae apart from the other families. And finally in dimension three Schlegeliaceae is apart from the others, Clusiaceae is somewhere located in the middle, and also Ericaceae and Solanaceae show a tendency towards this side of the plot. The distance-D-hat plot shows that it fits well with scaling.

At the genera level (FIGURE 2) the scaling does not fit that well (distance-D-hat plot), but some genera also show more distance to the others in the plots. On dimension 1 it is *Coussapoa* being a little apart from the others, *Lycianthes* and *Topobea* also going in that direction. On dimension 2 there are *Coussapoa* and *Cosmibuena* on the one edge and *Lycianthes* on the other, all the other genera are cumulated in the middle. And in dimension three *Topobea* is on the one edge and *Lycianthes*, *Blakea* and *Drymonia* on the other, again a bulge of the other genera lying between them.

DISCUSSION

The most important family of HE is on all our sites Clusiaceae, which is in top position in FIV in all 8 forest sites and very abundant on 5 of our 6 pastures. Moraceae are on top FIVs in 5 forest sites and very abundant on one pasture (LG (pl)). These results confirm the importance of these two families of pHEs (Putz & Holbrook 1986). But also Melastomataceae and Ericaceae are high in FIV in 4 forests and Ericaceae is high in abundance on two of our pastures (FC (pm) and LA (am)). Schlegeliaceae is high in FIV is LG (pl) slope and secondary forests, Araliaceae in the forests of FC (pm) and LA (am). Rubiaceae is only of importance in LA (am) and Solanaceae in NG (al).

Inhomogeneous distribution of some hemiepiphytes may be determined by microhabitat variation and local distribution (Williams-Linera & Lawton 1995).

The eye catching family plotted in the MDS on dimension one is Cecropiaceae, which is only present in the LG (pl) gorge forest and on pastures in LG (pl), SM (pl), and NG (al) not on the montane pastures nor in the other forest plots, not even in the forest plot in LG (pl) with a low abundance and importance value. This family is therefore only abundant in lowland (up to 500 m) pastures. It may be that this family (especially *Coussapoa* sp.) needs more light to establish and finds these circumstances on freestanding trees. Moraceae also shows a relativly high value in this dimension. Looking at the FIVs we see that this family is higher in importance value in lowland sites up to 500m, especially in the less disturbed LG (pl) gorge forest and LG (pl) secondary forest and in SM (pl). Moraceae also shows a very high abundance on the pasture of LG (pl) and a realtively high abundance on the pastures of NG (al) and SM (pl). It is therefore similar in distribution to Cecropiacea, but not as specialized. On the other edge of dimension one is, among others, Araliaceae, which is high in FIV only in FC (pm) and LA (am) primary forests (1500 m asl) and is not present in any lowland forests except of one juvenile individual in NG (al). It does not occur on lowland pastures including the pasture of SM (pl), and on pastures of FC (pm) and LA (am) it is not as abundant as in their forests. Dimension 1 in MDS seems to be the distance of premontane forest to lowland pasture.

Families on the lower edge are more likely found in forests, families on the higher end on pastures. There are some HE families that etsablish only under certain light conditions. Cecropiaceae and also Moraceae need conditions they find on pastures more likly (light, solar radiation, froot dispersal and others) than most of the other families.

On dimension 2 Rubiaceae is on one edge. This familiy we only found in LA (am) in the forest and on the pasture, on both sites with minor but eye catching importance and abundance. On the other edge, beyond the family buldge in the middle, there are Gesneriaceae and Solanaceae. Solanaceae with the only mentionable FIV in NG (al), and Gesneriaceae in SM (pl), both families not very abundant nor important in the forest of LA (am), they have even lower values on its pasture. Moraceae has only a low value in dimension two and is also of low abundance in LA (am), especially on the pasture there. This dimension may therefore be the „dimension of Los Alpes“, plotting high importance there especially in the forest plots in relation to the other sites. LA (am) is our site which is not very similar to the others (Lenotti, unpublished) and has a high number of general abundance and is very rich in diversity. This may be a reason why importance in LA (am) is plotted on its own dimension.

On dimension 3 in MDS of famlies Schlegeliaceae is on the low value side, Clusiaceae and Solanaceae show a tendency towards it. All other families are on the other edge, on top of them, among others, Araliaceae, Asteraceae, Gesneriaceae and Rubiaceae. Schlegeliaceae has high FIVs in the disturbed forests of LG (pl). It is not present in the forest of NG (al), and in LA's (am) and LS's (al) forest it only has a low FIV. The FIV of Clusiaceae is on the lowland sites far greater with a higher distance to the other FIVs than in the premontane sites. In FC (pm) and SM (pl at 500 m asl) the FIV of Clusiaceae is only in fourth or third position, its value is not very high. In LA (am) it is in first, but the other FIVs are very similar to it. Solanaceae has the only top FIV in NG (al). On the other side Araliaceae has high FIVs in FC (pm) and LA (am), average FIVs in LG (pl) and LS (al) and has very low importance values in NG (al) and SM (pl). Rubiaceae only occurs in LA (am). Gesneriaceae is missing in the lowland sites as well as Asteraceae, and Melastomataceae has very high FIVs in LA (am) and FC (pm) and - beside the gorge forest in LG (pl) - low FIVs on all other lowland sites. Dimension three therefore shows the distance between lowland and premontane families.

MDS with the genera does not have these clear results. In dimension one *Coussapoa* as the genera of Cercropiacea, the lowland pasture family, is beyond the other genera on one edge. The other genera are more bulged toghether, on the very far other end is *Cosmibuena* of Rubiaceae which only occours in LA (am). *Oreopanax, Neomirandea.* and *Schefflera* are also on this edge, all are genera of Araliaceae, also a premontane abundant family. *Lycianthes* has a high IVI in NG (al) and only minor IVI in SM (pl at 500 m asl) and FC (pm), whereas *Meriontopodium* the other Solanaceae genera is in both FC (pm) and LA (am), as well as in LS (al) of minor importance. *Topobea* is of high importance in the lowland primary forests in LG (pl) and LS (al), and althogh it is of high importance in FC (pm), it does not occur in LA (am) and is of minor importance in SM (pl at 500 m asl). Dimension 1 here may be premontane – lowland sites.

The explenation for the differences in dimension 2 is unclear. This may be due to the not perfect MDS, on the genera level, or to a factor we could not see in our study. Here it is especially *Lycianthes* on the high value edge, and *Coussapoa* on the other. *Coussapoa* again as lowland pasture genera, and *Lycianthes* is also important in lowland but does only occur on the pasture of SM (pl at 500 m asl) and is even more not very abundant there. *Cosmibuena* as well as ist family Rubiaceae is typical for LA (am), abundant in both pasture and forest. *Blake* is also very imortand in the forest LA (am), but also in the gorge forest of LG (pl). It is not abundant at all on pastures.

On dimension 3 it is especially *Topobea,* which is considerably distant to all other genera. It is of high importance in the primary forest of LG (pl) and FC (pm), also in LS (al) but not at all in LA (am) or the secondary forests. *Lycianthes* on the other edge is of high importance in NG (al) and only of minor importance in the sites of FC (pm) and SM (pl), it does not occur in LG (pl) nor in LA (am). *Blakea* has the same direction as *Lycianthes*. This genera is important in LG's (pl) gorge forest but of real high importance with two species in LA (am). It shows abundance in SM (pl) and LS (al), but not in FC (pm) and NG (al). We may see a Carribean – Pacific influenced distance in this dimension, but as the sites are not that different in these pattern (Lenotti unpublished), it is not very clear.

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Table 1. Description of the study sites.

	Site	Location	Altitude (m)	Mean Precipitation (mm/year)	Mean Temperature (°C/year)	Inclination (%)	Coordinates
1	La Gamba gorge	Lowland/ Pacific slope	90	6000	25.2	15	8°42’16”N, 83°12’15”W
2	La Gamba slope	Lowland/ Pacific slope	90	6000	25.2	20-30	8°42’16”N, 83°12’15”W
3	La Gamba secondary	Lowland/ Pacific slope	115	6000	25.2	0-20	8°41’57”N, 83°12’09”W
4	San Miguel	Lowland/ Pacific slope	500	~6000	No data	30	8°44’59”N, 83°9’40”W
5	Fila Costeña	Premontane/ Pacific slope	1450	~6000	17-22.5	10	8°47’25”N, 83°8’21”W
6	Los Alpes	Premontane/ Pacific slope	1480	2500	18-21	7	10°8’N, 84°34’W
7	La Selva	Lowland/ Carribean slope	50	4000	25.8	0-3	10°25’27”N, 78°38’23”W
8	Nogal	Lowland/ Carribean slope	50	4000	25-26	0	10°27’86” N 83°57’02” W
9	La Gamba pasture	Lowland/ Pacific slope	90	6000	25.2	0-7	8°42’20”N, 83°11’41”W
10	San Miguel pasture	Lowland/ Pacific slope	500	~6000	No data	0-5	8°45’15”N, 83°8’42”W
11	Fila Costena pasture (27 trees)	Premontane/ Pacific slope	1310-1400	~6000	17-22.5	0	8°47’12” N 83°8’28” W
12	Los Alpes pasture	Premontane/ Pacific slope	1480	2500	18-21	10	10°8’N, 84°34’W
13	Nogal pasture	Lowland/ Carribean slope	50	4000	25.8	0	10°27’6” N 83°57’26” W

Table 2. Formulae applied.

Important Value Index	IVI = Dens. + Dom. + Freq.
Family Index Value	FIV = Dens. + Dom. + Div.

Dens. ....relative density	Dom.................... relative dominance
Frequ. .... relative frequency	Div. .... relative diversity

Table 3. IVI of the species with the top values in each site.

LG_Fp_g	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Topobea maurofernandeziana	20,31	22,41	16,67	59,39
Blakea litoralis	18,75	24,14	12,50	55,39
Schlegelia parviflora	10,94	8,62	12,50	32,06
Ficus costaricana	7,81	13,79	6,25	27,86
Clusia osaensis	6,25	6,90	8,33	21,48
Remaining species (9)	35,94	24,1	43,75	103,83

LG_Fs	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Schlegelia parviflora	23,08	37,50	25,00	85,58
Clusia valerioi	15,38	25,00	8,33	48,72
Ficus colubrinae	7,69	25,00	8,33	41,03
Satyria panurensis	15,38	0,00	16,67	32,05
Ficus pertusa	15,38	0,00	16,67	32,05
Remaining species (3)	32,08	12,50	25,00	60,58

LG_Fp_s	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Clusia amazonica	33,93	46,24	20,59	100,75
Schlegelia parviflora	21,43	23,66	23,53	68,61
Satyria panurensis	19,64	15,05	23,53	58,23
Topobea maurofernandeziana	12,50	5,38	17,65	35,52
Clusia valerioi	5,36	6,45	8,82	20,63
Remaining species (1)	7,14	3,23	5,88	16,25

NG_Fs	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Clusia flava	50,00	18,18	33,33	101,52
Lycianthes santaeclarae	11,11	45,45	16,67	73,23
Clusia uvitana	22,22	9,09	25,00	56,31
Ficus pertusa	5,56	27,27	8,33	41,16
Ficus aff. colubrinae	5,56	0,00	8,33	13,89
Remaining species (1)	5,56	0,00	8,33	13,89

SM_Fp	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Drymonia alloplectoides	24,36	4,76	18,18	47,30
Clusia amazonica	14,10	19,05	12,73	45,88
Satyria panurensis	12,82	11,90	12,73	37,45
Schlegelia parviflora	5,13	14,29	5,45	24,87
Lycianthes santaeclarae	8,97	7,14	7,27	23,39
Remaining species (14)	34,62	42,86	43,64	121,11

LS_Fp	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Satyria panurensis	39,39	54,17	31,03	124,60
Clusia amazonica	6,06	12,50	6,90	25,46
Clusia valerioi	6,06	8,33	6,90	21,29
Topobea maurofernandeziana	9,09	0,00	10,34	19,44
Clusia gracilis	6,06	4,17	6,90	17,12
Remaining species (8)	33,33	20,83	37,93	92,10

FC_Fp	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Topobea pittieri	21,45	21,67	10,26	53,38
Schefflera brennesii	18,15	10,27	10,26	38,67
Psammisia ramiflora	8,25	16,73	7,69	32,67
Cavendishia callista	11,88	7,98	8,55	28,41
Clusia stenophylla	9,57	9,89	8,55	28,00
Satyria warszewiczii	2,97	4,56	5,98	13,52
Topobea maurofernandeziana	3,30	4,56	5,13	12,99
Schlegelia parviflora	2,97	5,32	4,27	12,57
Clusia croatii	3,63	3,42	5,13	12,18
Drymonia macrantha	4,62	2,28	5,13	12,03
Remaining species (16)	13,2	13,3	29,06	55,57

LA_Fp	**Rel. Dens.**	**Rel. Dom.**	**Rel. Frequ.**	**IVI**
Blakea anomala	16,64	14,25	6,32	37,20
Clusia palmana	13,25	11,45	6,32	31,02
Cosmibuena valerii	7,70	11,45	6,32	25,47
Blakea cf. tuberculata	8,32	9,22	6,32	23,85
Cavendishia bracteata	7,70	7,54	6,32	21,56
Drymonia conchocalyx	6,01	8,10	5,79	19,90
Satyria/Psamisia pan./ram.	6,16	6,42	5,26	17,85
Oreopanax oerstedianum	4,16	5,31	6,32	15,78
Oreopanax capitatus	4,01	4,47	4,74	13,21
Schefflera rodriguesiana	4,16	3,91	4,74	12,81
Remaining species (16)	21,88	17,9	41,58	81,34

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal SM = San Miguel

Fp = primary forest, Fs = secundary forest, g = gorge, s = slope

Rel. Dens. = relative density, Rel. Dom. = relative dominance, Rel. Frequ. = relative frequency

IVI = Importance Value Index

Table 4. FIV of the families with the top values in each site.

LG_Fp_g

Family	FIV
Melastomataceae	115,34
Clusiaceae	71,38
Moraceae	52,73
Remaining families (3) (Schlegeliaceae, Cecropiaceae, Ericaceae*)	60,54

LG_Fs

Family	FIV
Clusiaceae	105,77
Moraceae	93,27
Schlegeliaceae	73,08
Remaining families (1) (Ericaceae)	27,88

LG_Fp_s

Family	FIV
Clusiaceae	152,34
Schlegeliaceae	61,75
Ericaceae	51,36
Remaining families (1) (Melastomataceae)	34,54

NG_Fs

Family	FIV
Clusiaceae	132,83
Solanaceae	73,23
Moraceae	71,72
Remaining families (1) (Araliaceae)	22,22

SM_Fp

Family	FIV
Moraceae	64,04
Gesneriaceae	54,62
Clusiaceae	51,50
Remaining families (5) (Ericaceae, Melastomataceae, Schlegeliaceae, Solanaceae, Araliaceae*)	129,83

LS_Fp

Family	FIV
Clusiaceae	102,59
Ericaceae	101,25
Melastomataceae	34,70
Remaining families (3) (Moraceae, Solanaceae, Schlegeliaceae*)	61,45

FC_Fp

Family	FIV
Ericaceae	68,09
Melastomataceae	63,57
Araliaceae	55,79
Clusiaceae	34,20
Moraceae	24,39
Remaining families (4) (Solanaceae, Gesneriaceae, Schlegeliaceae, Asteraceae*)	53,96

LA_Fp

Family	FIV
Clusiaceae	57,18
Melastomataceae	56,12
Ericaceae	56,06
Araliaceae	47,92
Rubiaceae	23,00
Remaining families (6) (Gesneriaceae, Moraceae, Asteraceae, Schlegeliaceae, Solanaceae, Cecropiaceae*)	59,72

FC = Fila Costena, LA = Los Alpes, LG = La Gamba, LS = La Selva, NG = Nogal, SM = San Miguel
Fp = primary forest, Fs = secundary forest, g = gorge, s = slope
FIV = Family Importance Value
* in order of their FIV

Figure 1: MDS of families

Multidimensional Scaling

Families:

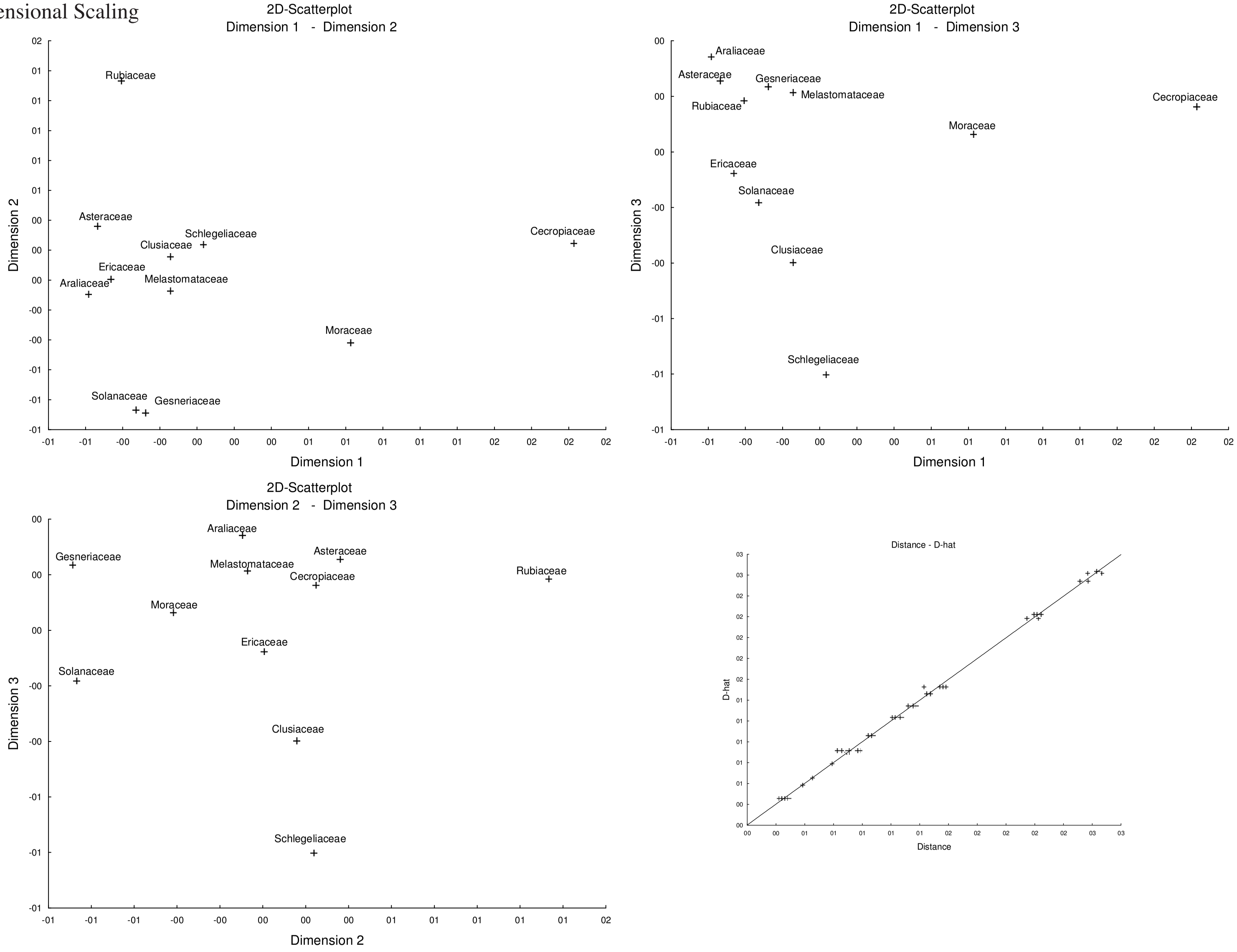
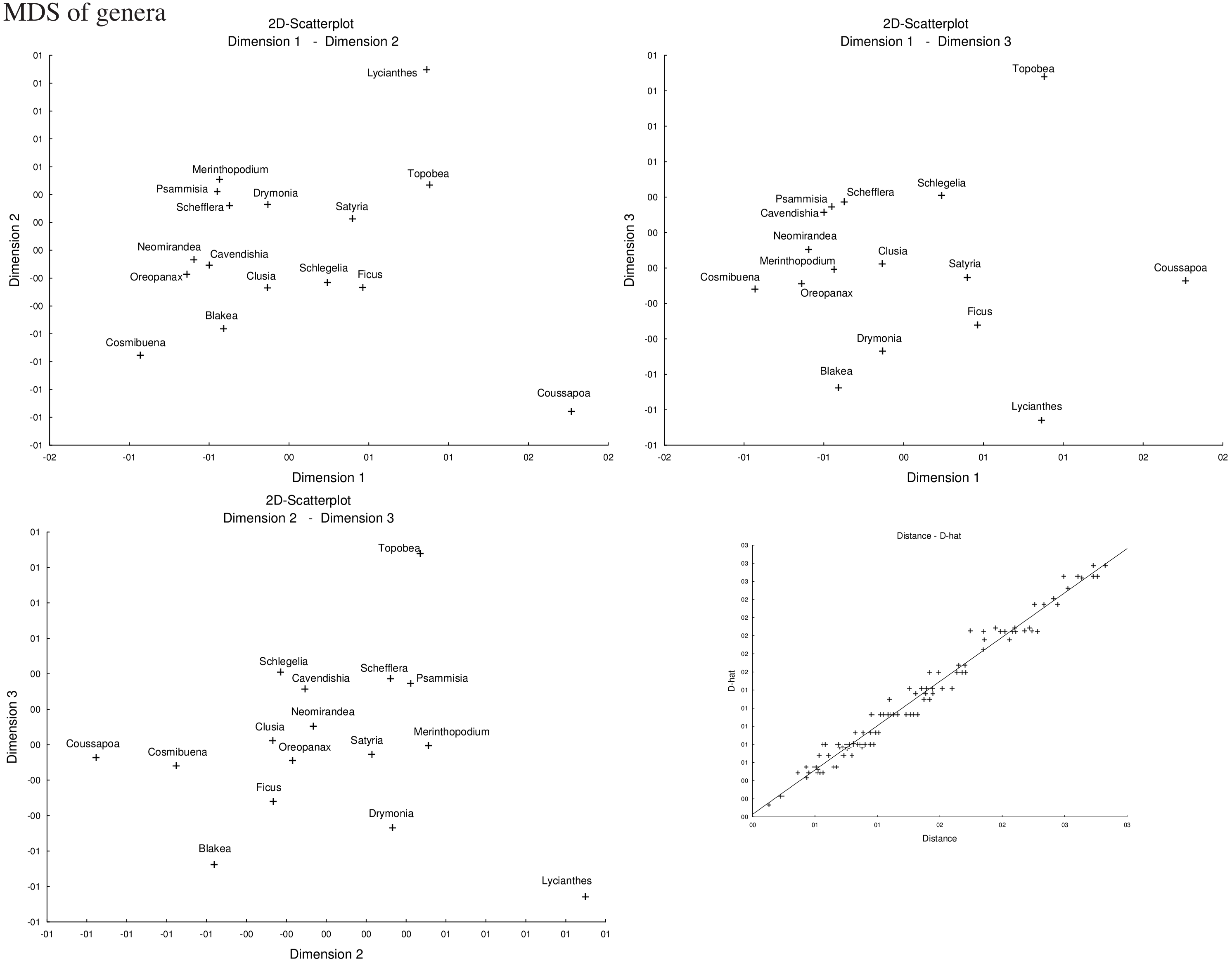


Figure 2: MDS of genera

Genera:



APPENDIX: Appendix table 5. FIV and IVI of all species and families in the different sites

La Gamba primary forest gorge

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Cecropiaceae	*Coussapoa glaberrima*	0,60	4,69	3,00	5,17	25,00	6,25	1,00	7,14	16,11	17,00
Clusiaceae	*Clusia amazonica*	0,80	6,25	1,00	1,72	33,33	8,33			16,31	
Clusiaceae	*Clusia cf. peninsulae*	0,80	6,25	1,00	1,72	16,67	4,17			12,14	
Clusiaceae	*Clusia cylindrica*	0,20	1,56	0,00	0,00	8,33	2,08			3,65	
Clusiaceae	*Clusia osaensis*	0,80	6,25	4,00	6,90	33,33	8,33			21,48	
Clusiaceae	*Clusia valerioi*	0,20	1,56	2,00	3,45	8,33	2,08	5,00	35,71	7,09	71,38
Ericaceae	*Satyria panurensis*	0,80	6,25	2,00	3,45	33,33	8,33	1,00	7,14	18,03	16,84
Melastomataceae	*Blakea cf. subpeltata*	0,40	3,13	3,00	5,17	16,67	4,17			12,46	
Melastomataceae	*Blakea litoralis*	2,40	18,75	14,00	24,14	50,00	12,50			55,39	
Melastomataceae	*Topobea maurofernandeziana*	2,60	20,31	13,00	22,41	66,67	16,67	3,00	21,43	59,39	115,34
Moraceae	*Ficus citrifolia*	0,60	4,69	2,00	3,45	25,00	6,25			14,39	
Moraceae	*Ficus colubrinae*	0,20	1,56	0,00	0,00	8,33	2,08			3,65	
Moraceae	*Ficus costaricana*	1,00	7,81	8,00	13,79	25,00	6,25	3,00	21,43	27,86	52,73
Schlegeliaceae	*Schlegelia parviflora*	1,40	10,94	5,00	8,62	50,00	12,50	1,00	7,14	32,06	26,70
total		12,80	100,00	58,00	100,00	400,00	100,00	14,00	100,00		

La Gamba primary forest slope

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Clusiaceae	*Clusia amazonica*	3,80	33,93	43,00	46,24	58,33	20,59			100,75	
Clusiaceae	*Clusia peninsulae*	0,80	7,14	3,00	3,23	16,67	5,88			16,25	
Clusiaceae	*Clusia valerioi*	0,60	5,36	6,00	6,45	25,00	8,82	3,00	50,00	20,63	152,34
Ericaceae	*Satyria panurensis*	2,20	19,64	14,00	15,05	66,67	23,53	1,00	16,67	58,23	51,36
Melastomataceae	*Topobea maurofernandeziana*	1,40	12,50	5,00	5,38	50,00	17,65	1,00	16,67	35,52	34,54
Schlegeliaceae	*Schlegelia parviflora*	2,40	21,43	22,00	23,66	66,67	23,53	1,00	16,67	68,61	61,75
total		11,20	100,00	93,00	100,00	283,33	100,00	6,00	100,00		

La Gamba secondary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Clusiaceae	*Clusia amazonica*	0,20	7,69	1,00	12,50	8,33	8,33			28,53	
Clusiaceae	*Clusia peninsulae*	0,20	7,69	0,00	0,00	8,33	8,33			16,03	
Clusiaceae	*Clusia valerioi*	0,40	15,38	2,00	25,00	8,33	8,33	3,00	37,50	48,72	105,77
Ericaceae	*Satyria panurensis*	0,40	15,38	0,00	0,00	16,67	16,67	1,00	12,50	32,05	27,88
Moraceae	*Ficus citrifolia*	0,20	7,69	0,00	0,00	8,33	8,33			16,03	
Moraceae	*Ficus colubrinae*	0,20	7,69	2,00	25,00	8,33	8,33			41,03	
Moraceae	*Ficus pertusa*	0,40	15,38	0,00	0,00	16,67	16,67	3,00	37,50	32,05	93,27
Schlegeliaceae	*Schlegelia parviflora*	0,60	23,08	3,00	37,50	25,00	25,00	1,00	12,50	85,58	73,08
	total	2,60	100,00	8,00	100,00	100,00	100,00	8,00	100,00		

San Miguel primary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Araliaceae	*Schefflera brennesii*	0,40	2,56	1,00	2,38	16,67	3,64	1,00	5,26	8,58	10,21
Clusiaceae	*Clusia amazonica*	2,20	14,10	8,00	19,05	58,33	12,73			45,88	
Clusiaceae	*Clusia cf. stenophylla*	0,20	1,28	0,00	0,00	8,33	1,82			3,10	
Clusiaceae	*Clusia sp.*	0,20	1,28	0,00	0,00	8,33	1,82	3,00	15,79	3,10	51,50
Ericaceae	*Cavendishia callista*	0,60	3,85	2,00	4,76	16,67	3,64			12,24	
Ericaceae	*Satyria panurensis*	2,00	12,82	5,00	11,90	58,33	12,73	2,00	10,53	37,45	43,86
Gesneriaceae	*Drymonia alloplectoides*	3,80	24,36	2,00	4,76	83,33	18,18			47,30	
Gesneriaceae	*Drymonia macrantha*	0,20	1,28	1,00	2,38	8,33	1,82			5,48	
Gesneriaceae	*Drymonia warscewicziana*	0,20	1,28	2,00	4,76	8,33	1,82	3,00	15,79	7,86	54,62
Melastomataceae	*Blakea litoralis*	1,40	8,97	1,00	2,38	41,67	9,09			20,45	
Melastomataceae	*Blakea subpeltata*	0,20	1,28	0,00	0,00	8,33	1,82			3,10	
Melastomataceae	*Topobea maurofernandeziana*	0,20	1,28	0,00	0,00	8,33	1,82	3,00	15,79	3,10	29,71
Moraceae	*Ficus cf. osensis*	0,20	1,28	1,00	2,38	8,33	1,82			5,48	
Moraceae	*Ficus citrifolia*	0,60	3,85	3,00	7,14	25,00	5,45			16,44	
Moraceae	*Ficus colubrinae*	0,20	1,28	1,00	2,38	8,33	1,82			5,48	
Moraceae	*Ficus costaricana*	0,40	2,56	4,00	9,52	16,67	3,64			15,72	
Moraceae	*Ficus pertusa*	0,40	2,56	2,00	4,76	16,67	3,64	5,00	26,32	10,96	64,04
Schlegeliaceae	*Schlegelia parviflora*	0,80	5,13	6,00	14,29	25,00	5,45	1,00	5,26	24,87	24,68
Solanaceae	*Lycianthes santaeclarae*	1,40	8,97	3,00	7,14	33,33	7,27	1,00	5,26	23,39	21,38
total		15,60	100,00	42,00	100,00	458,33	100,00	19,00	100,00		

Fila Costena primary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Araliaceae	*Oreopanax aff. striatus*	0,60	0,99	2,00	0,76	25,00	2,56			4,31	
Araliaceae	*Oreopanax capitatus*	0,20	0,33	2,00	0,76	8,33	0,85			1,95	
Araliaceae	*Oreopanax oerstedianum*	0,40	0,66	3,00	1,14	16,67	1,71			3,51	
Araliaceae	*Schefflera brennesii*	11,00	18,15	27,00	10,27	100,00	10,26			38,67	
Araliaceae	*Schefflera robusta*	1,20	1,98	4,00	1,52	33,33	3,42	5,00	19,23	6,92	55,79
Asteraceae	*Neomirandea standleyi*	0,60	0,99	4,00	1,52	25,00	2,56	1,00	3,85	5,08	6,36
Clusiaceae	*Clusia croatii*	2,20	3,63	9,00	3,42	50,00	5,13			12,18	
Clusiaceae	*Clusia stenophylla*	5,80	9,57	26,00	9,89	83,33	8,55	2,00	7,69	28,00	34,20
Ericaceae	*Cavendishia callista*	7,20	11,88	21,00	7,98	83,33	8,55			28,41	
Ericaceae	*Psammisia ramiflora*	5,00	8,25	44,00	16,73	75,00	7,69			32,67	
Ericaceae	*cf. Satyria panurensis*	0,20	0,33	0,00	0,00	8,33	0,85			1,18	
Ericaceae	*Satyria warszewiczii*	1,80	2,97	12,00	4,56	58,33	5,98	4,00	15,38	13,52	68,09
Gesneriaceae	*Drymonia macrantha*	2,80	4,62	6,00	2,28	50,00	5,13			12,03	
Gesneriaceae	*Drymonia macrophylla*	1,00	1,65	2,00	0,76	25,00	2,56	2,00	7,69	4,97	17,00
Melastomataceae	*Topobea maurofernandeziana*	2,00	3,30	12,00	4,56	50,00	5,13			12,99	
Melastomataceae	*Topobea multiflora*	0,40	0,66	1,00	0,38	16,67	1,71			2,75	
Melastomataceae	*Topobea pittieri*	13,00	21,45	57,00	21,67	100,00	10,26	3,00	11,54	53,38	63,57
Moraceae	*Ficus sp0*	1,40	2,31	14,00	5,32	41,67	4,27			11,91	
Moraceae	*Ficus sp1*	0,20	0,33	0,00	0,00	8,33	0,85			1,18	
Moraceae	*Ficus sp2*	0,20	0,33	0,00	0,00	8,33	0,85			1,18	
Moraceae	*Ficus sp4*	0,20	0,33	1,00	0,38	8,33	0,85	4,00	15,38	1,56	24,39
Schlegeliaceae	*Schlegelia parviflora*	1,80	2,97	14,00	5,32	41,67	4,27	1,00	3,85	12,57	12,14
Solanaceae	*Cestrum sp.*	0,20	0,33	1,00	0,38	8,33	0,85			1,56	
Solanaceae	*cf. Cuatresia riparia*	0,40	0,66	1,00	0,38	16,67	1,71			2,75	
Solanaceae	*Lycianthes synanthera*	0,20	0,33	0,00	0,00	8,33	0,85			1,18	
Solanaceae	*Merinthopodium neuranthum*	0,60	0,99	0,00	0,00	25,00	2,56	4,00	15,38	3,55	18,46
total		60,60	100,00	263,00	100,00	975,00	100,00	26,00	100,00		

La Selva primary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Clusiaceae	*Clusia amazonica*	0,4	6,060606	3	12,5	16,66667	6,8965517			25,4572	
Clusiaceae	*Clusia cf. cylindrica*	0,2	3,030303	1	4,1666667	8,333333	3,4482759			10,6452	
Clusiaceae	*Clusia gracilis*	0,4	6,060606	1	4,1666667	16,66667	6,8965517			17,1238	
Clusiaceae	*Clusia uvitana*	0,2	3,030303	0	0	8,333333	3,4482759			6,47858	
Clusiaceae	*Clusia valerioi*	0,4	6,060606	2	8,3333333	16,66667	6,8965517			21,2905	
Clusiaceae	*Clusiella isthmensis*	0,2	3,030303	0	0	8,333333	3,4482759	6	46,15385	6,47858	102,593
Ericaceae	*Satyria panurensis*	2,6	39,39394	13	54,166667	75	31,034483	1	7,692308	124,595	101,253
Melastomataceae	*Blakea scarletina*	0,4	6,060606	1	4,1666667	16,66667	6,8965517			17,1238	
Melastomataceae	*Topobea maurofernandeziana*	0,6	9,090909	0	0	25	10,344828	2	15,38462	19,4357	34,7028
Moraceae	*Ficus cahuitensis*	0,2	3,030303	1	4,1666667	8,333333	3,4482759			10,6452	
Moraceae	*Ficus cf. pertusa*	0,2	3,030303	1	4,1666667	8,333333	3,4482759	2	15,38462	10,6452	29,7786
Schlegeliaceae	*Schlegelia parviflora*	0,4	6,060606	0	0	16,66667	6,8965517	1	7,692308	12,9572	13,7529
Solanaceae	*Merinthopodium neuranthum*	0,4	6,060606	1	4,1666667	16,66667	6,8965517	1	7,692308	17,1238	17,9196
total		6,6	100	24	100	241,6667	100	13	100		

Nogal secondary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Araliaceae	Oreopanax sp.	0,20	5,56	0,00	0,00	8,33	8,33	1,00	16,67	13,89	22,22
Clusiaceae	Clusia flava	1,80	50,00	2,00	18,18	33,33	33,33			101,52	
Clusiaceae	Clusia uvitana	0,80	22,22	1,00	9,09	25,00	25,00	2,00	33,33	56,31	132,83
Moraceae	Ficus aff. colubrinae	0,20	5,56	0,00	0,00	8,33	8,33			13,89	
Moraceae	Ficus pertusa	0,20	5,56	3,00	27,27	8,33	8,33	2,00	33,33	41,16	71,72
Solanaceae	Lycianthes santaeclarae	0,40	11,11	5,00	45,45	16,67	16,67	1,00	16,67	73,23	73,23
total		3,60	100,00	11,00	100,00	100,00	100,00	6,00	100,00		

Los Alpes primary forest

Family	Hemiepiphyte	dens.	rel. dens.	dom.	rel. dom.	freq.	rel. freq.	div.	rel. div.	IVI	FIV
Araliaceae	*Oreopanax capitatus*	5,20	4,01	16,00	4,47	75,00	4,74			13,21	
Araliaceae	*Oreopanax oerstedianum*	5,40	4,16	19,00	5,31	100,00	6,32			15,78	
Araliaceae	*Schefflera robusta*	5,20	4,01	9,00	2,51	91,67	5,79			12,31	
Araliaceae	*Schefflera rodriguesiana*	5,40	4,16	14,00	3,91	75,00	4,74	4,00	15,38	12,81	47,92
Asteraceae	*Neomirandea parasitica*	1,60	1,23	0,00	0,00	33,33	2,11			3,34	
Asteraceae	*Neomirandea psoralea*	0,40	0,31	1,00	0,28	16,67	1,05	2,00	7,69	1,64	9,51
Cecropiaceae	*Cecropia peltata*	0,20	0,15	0,00	0,00	8,33	0,53	1,00	3,85	0,68	4,00
Clusiaceae	*Chrysochlamis allenii*	0,20	0,15	0,00	0,00	8,33	0,53			0,68	
Clusiaceae	*Clusia minor*	0,40	0,31	1,00	0,28	16,67	1,05			1,64	
Clusiaceae	*Clusia multiflora*	4,20	3,24	19,00	5,31	66,67	4,21			12,75	
Clusiaceae	*Clusia palmana*	17,20	13,25	41,00	11,45	100,00	6,32			31,02	
Clusiaceae	*Clusia torresii*	2,60	2,00	7,00	1,96	66,67	4,21	5,00	19,23	8,17	57,18
Ericaceae	*Cavendishia bracteata*	10,00	7,70	27,00	7,54	100,00	6,32			21,56	
Ericaceae	*Cavendishia complectens*	4,40	3,39	1,00	0,28	100,00	6,32			9,98	
Ericaceae	*Psammisia ramiflora*	0,60	0,46	1,00	0,28	16,67	1,05			1,79	
Ericaceae	*Psammisia williamsii*	0,20	0,15	0,00	0,00	8,33	0,53			0,68	
Ericaceae	*Satyria panurensis*	0,40	0,31	1,00	0,28	16,67	1,05			1,64	
Ericaceae	*Sat/Psa panurensis/ramiflora*	8,00	6,16	23,00	6,42	83,33	5,26	6,00	23,08	17,85	56,06
Gesneriaceae	*Drymonia conchocalyx*	7,80	6,01	29,00	8,10	91,67	5,79	1,00	3,85	19,90	17,96
Melastomataceae	*Blakea anomala*	21,60	16,64	51,00	14,25	100,00	6,32			37,20	
Melastomataceae	*Blakea cf. tuberculata*	10,80	8,32	33,00	9,22	100,00	6,32	2,00	7,69	23,85	56,12
Moraceae	*Ficus crassiuscula*	3,60	2,77	3,00	0,84	83,33	5,26			8,87	
Moraceae	*Ficus sp6*	0,20	0,15	1,00	0,28	8,33	0,53	2,00	7,69	0,96	11,74
Rubiaceae	*Cosmibuena valerii*	10,00	7,70	41,00	11,45	100,00	6,32	1,00	3,85	25,47	23,00
Schlegeliaceae	*Schlegelia parviflora*	2,60	2,00	12,00	3,35	58,33	3,68	1,00	3,85	9,04	9,20
Solanaceae	*Merinthopodium neuranthum*	1,60	1,23	8,00	2,23	58,33	3,68	1,00	3,85	7,15	7,31
total		129,80	100,00	358,00	100,00	1583,33	100,00	26,00	100,00		

Appendix table 6. Abundances of all species and families in the different sites

La Gamba

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Cecropiaceae	*Coussapoa glaberrima*	6	3,87		
Clusiaceae	*Clusia amazonica*	24	15,48		
Clusiaceae	*Clusia peninsulae*	9	5,81		
Clusiaceae	*Clusia cylindrica*	1	0,65		
Clusiaceae	*Clusia osaensis*	4	2,58		
Clusiaceae	*Clusia valerioi*	10	6,45	30,97	
Ericaceae	*Satyria panurensis*	17	10,97		
Melastomataceae	*Blakea cf. subpeltata*	2	1,29		
Melastomataceae	*Blakea litoralis*	12	7,74	9,03	
Melastomataceae	*Topobea maurofernandeziana*	20	12,90	12,90	21,93
Moraceae	*Ficus citrifolia*	13	8,39		
Moraceae	*Ficus colubrinae*	2	1,29		
Moraceae	*Ficus costaricana*	7	4,52		
Moraceae	*Ficus nympheifolia*	1	0,65		
Moraceae	*Ficus pertusa*	2	1,29		
Moraceae	*Ficus sp.*	1	0,65	16,77	
Schlegeliaceae	*Schlegelia parviflora*	24	15,48		
total		155	100		

La Gamba primary forest gorge

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Cecropiaceae	*Coussapoa glaberrima*	3	4,69	4,69	
Clusiaceae	*Clusia amazonica*	4	6,25		
Clusiaceae	*Clusia cf. peninsulae*	4	6,25		
Clusiaceae	*Clusia cylindrica*	1	1,56		
Clusiaceae	*Clusia osaensis*	4	6,25		
Clusiaceae	*Clusia valerioi*	1	1,56	21,88	
Ericaceae	*Satyria panurensis*	4	6,25	6,30	
Melastomataceae	*Blakea cf. subpeltata*	2	3,13		
Melastomataceae	*Blakea litoralis*	12	18,75	21,88	
Melastomataceae	*Topobea maurofernandeziana*	13	20,31	20,30	42,18
Moraceae	*Ficus citrifolia*	3	4,69		
Moraceae	*Ficus colubrinae*	1	1,56		
Moraceae	*Ficus costaricana*	5	7,81	14,06	
Schlegeliaceae	*Schlegelia parviflora*	7	10,94	10,90	
total		64	100,00		

La Gamba primary forest slope

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Clusiaceae	*Clusia amazonica*	19	33,93		
Clusiaceae	*Clusia peninsulae*	4	7,14		
Clusiaceae	*Clusia valerioi*	3	5,36	46,43	
Ericaceae	*Satyria panurensis*	11	19,64	19,60	
Melastomataceae	*Topobea maurofernandeziana*	7	12,50	12,50	
Schlegeliaceae	*Schlegelia parviflora*	12	21,43	21,40	
total		56	100,00		

La Gamba secondary forest

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Clusiaceae	*Clusia amazonica*	1	50,00		
Clusiaceae	*Clusia peninsulae*	1	50,00		
Clusiaceae	*Clusia valerioi*	2	100,00	200,00	
Ericaceae	*Satyria panurensis*	2	100,00	15,40	
Moraceae	*Ficus citrifolia*	1	50,00		
Moraceae	*Ficus colubrinae*	1	50,00		
Moraceae	*Ficus pertusa*	2	100,00	200,00	
Schlegeliaceae	*Schlegelia parviflora*	3	150,00	23,10	
total		13	650,00		

La Gamba pasture

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Clusiaceae	*Clusia valerioi*	4	18,18		
Cecropiaceae	*Coussapoa glaberrima*	3	13,64		
Moraceae	*Ficus citrifolia*	9	40,91		
Moraceae	*Ficus costaricana*	2	9,09		
Moraceae	*Ficus nympheifolia*	1	4,55		
Moraceae	*Ficus sp.*	1	4,55	59,09	
Schlegeliaceae	*Schlegelia parviflora*	2	9,09		
total		22	100		

San Miguel

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Schefflera brennesii*	2	1,94		
Cecropiaceae	*Coussapoa villosa*	3	2,91		
Clusiaceae	*Clusia amazonica*	11	10,68		
Clusiaceae	*Clusia cf. stenophylla*	1	0,97		
Clusiaceae	*Clusia sp.*	1	0,97		
Clusiaceae	*Clusia valerioi*	4	3,88	16,50	
Ericaceae	*Cavendishia callista*	5	4,85		
Ericaceae	*Satyria panurensis*	13	12,62	17,48	
Gesneriaceae	*Drymonia alloplectoides*	28	27,18		
Gesneriaceae	*Drymonia macrantha*	1	0,97		
Gesneriaceae	*Drymonia warscewicziana*	1	0,97	29,13	
Melastomataceae	*Blakea litoralis*	7	6,80		
Melastomataceae	*Blakea subpeltata*	1	0,97	7,77	
Melastomataceae	*Topobea maurofernandeziana*	2	1,94	1,90	9,67
Moraceae	*Ficus cf. osensis*	1	0,97		
Moraceae	*Ficus citrifolia*	3	2,91		
Moraceae	*Ficus colubrinae*	2	1,94		
Moraceae	*Ficus costaricana*	2	1,94		
Moraceae	*Ficus nympheifolia*	1	0,97		
Moraceae	*Ficus pertusa*	3	2,91	11,65	
Schlegeliaceae	*Schlegelia parviflora*	4	3,88		
Solanaceae	*Lycianthes santaeclarae*	7	6,80		
total		103	100,00		

San Miguel primary forest

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Schefflera brennesii*	2	2,56	2,60	
Clusiaceae	*Clusia amazonica*	11	14,10		
Clusiaceae	*Clusia cf. stenophylla*	1	1,28		
Clusiaceae	*Clusia sp.*	1	1,28	16,67	
Ericaceae	*Cavendishia callista*	3	3,85		
Ericaceae	*Satyria panurensis*	10	12,82		16,67
Gesneriaceae	*Drymonia alloplectoides*	19	24,36		
Gesneriaceae	*Drymonia macrantha*	1	1,28		
Gesneriaceae	*Drymonia warscewicziana*	1	1,28	26,92	
Melastomataceae	*Blakea litoralis*	7	8,97		
Melastomataceae	*Blakea subpeltata*	1	1,28	10,26	
Melastomataceae	*Topobea maurofernandeziana*	1	1,28	1,30	11,6
Moraceae	*Ficus cf. osensis*	1	1,28		
Moraceae	*Ficus citrifolia*	3	3,85		
Moraceae	*Ficus colubrinae*	1	1,28		
Moraceae	*Ficus costaricana*	2	2,56		
Moraceae	*Ficus pertusa*	2	2,56	11,54	
Schlegeliaceae	*Schlegelia parviflora*	4	5,13	5,10	
Solanaceae	*Lycianthes santaeclarae*	7	8,97	9,00	
total		78	100,00		

San Miguel pasture

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Ericaceae	*Cavendishia callista*	2	8,00		
Clusiaceae	*Clusia valerioi*	4	16,00		
Cecropiaceae	*Coussapoa villosa*	3	12,00		
Gesneriaceae	*Drymonia alloplectoides*	9	36,00		
Moraceae	*Ficus colubrinae*	1	4,00		
Moraceae	*Ficus nympheifolia*	1	4,00		
Moraceae	*Ficus pertusa*	1	4,00	12,00	
Ericaceae	*Satyria panurensis*	3	12,00		
Melastomataceae	*Topobea maurofernandeziana*	1	4,00		
total		25	100,00		

Fila Costena

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Oreopanax aff. striatus*	7	1,91		
Araliaceae	*Oreopanax capitatus*	1	0,27		
Araliaceae	*Oreopanax oerstedianum*	2	0,55	2,73	
Araliaceae	*Schefflera brennesii*	56	15,30		
Araliaceae	*Schefflera robusta*	9	2,46	17,76	20,49
Asteraceae	*Neomirandea standleyi*	3	0,82		
Clusiaceae	*Clusia croatii*	13	3,55		
Clusiaceae	*Clusia stenophylla*	53	14,48	18,03	
Ericaceae	*Cavendishia callista*	51	13,93		
Ericaceae	*Psammisia ramiflora*	25	6,83		
Ericaceae	*cf. Satyria panurensis*	1	0,27		
Ericaceae	*Satyria warszewiczii*	13	3,55	3,83	24,59
Gesneriaceae	*Drymonia macrantha*	14	3,83		
Gesneriaceae	*Drymonia macrophylla*	5	1,37	5,19	
Melastomataceae	*Topobea maurofernandeziana*	14	3,83		
Melastomataceae	*Topobea multiflora*	2	0,55		
Melastomataceae	*Topobea pittieri*	66	18,03	22,40	
Moraceae	*Ficus sp0*	7	1,91		
Moraceae	*Ficus sp1*	1	0,27		
Moraceae	*Ficus sp2*	1	0,27		
Moraceae	*Ficus sp4*	1	0,27	2,73	
Schlegeliaceae	*Schlegelia parviflora*	13	3,55		
Solanaceae	*Cestrum sp.*	1	0,27		
Solanaceae	*cf. Cuatresia riparia*	2	0,55		
Solanaceae	*Lycianthes synanthera*	2	0,55		
Solanaceae	*Merinthopodium neuranthum*	3	0,82	2,19	
total		366	100,00		

Fila Costena pasture

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Oreopanax aff. striatus*	4	6,35		
Araliaceae	*Schefflera brennesii*	1	1,59		
Araliaceae	*Schefflera robusta*	3	4,76	12,70	
Clusiaceae	*Clusia croatii*	2	3,17		
Clusiaceae	*Clusia stenophylla*	24	38,10	41,27	
Ericaceae	*Cavendishia callista*	15	23,81		
Ericaceae	*Satyria warszewiczii*	4	6,35	30,16	
Melastomataceae	*Topobea maurofernandeziana*	4	6,35		
Melastomataceae	*Topobea pittieri*	1	1,59	7,94	
Schlegeliaceae	*Schlegelia parviflora*	4	6,35		
Solanaceae	*Lycianthes synanthera*	1	1,59		
total		63	100,00		

Fila Costena primary forest

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Oreopanax aff. striatus*	3	0,99		
Araliaceae	*Oreopanax capitatus*	1	0,33		
Araliaceae	*Oreopanax oerstedianum*	2	0,66	1,98	
Araliaceae	*Schefflera brennesii*	55	18,15		
Araliaceae	*Schefflera robusta*	6	1,98	20,13	22,11
Asteraceae	*Neomirandea standleyi*	3	0,99	1,00	
Clusiaceae	*Clusia croatii*	11	3,63		
Clusiaceae	*Clusia stenophylla*	29	9,57	13,20	
Ericaceae	*Cavendishia callista*	36	11,88		
Ericaceae	*Psammisia ramiflora*	25	8,25		
Ericaceae	*cf. Satyria panurensis*	1	0,33		
Ericaceae	*Satyria warszewiczii*	9	2,97	3,30	23,43
Gesneriaceae	*Drymonia macrantha*	14	4,62		
Gesneriaceae	*Drymonia macrophylla*	5	1,65	6,27	
Melastomataceae	*Topobea maurofernandeziana*	10	3,30		
Melastomataceae	*Topobea multiflora*	2	0,66		
Melastomataceae	*Topobea pittieri*	65	21,45	25,41	
Moraceae	*Ficus sp0*	7	2,31		
Moraceae	*Ficus sp1*	1	0,33		
Moraceae	*Ficus sp2*	1	0,33		
Moraceae	*Ficus sp4*	1	0,33	3,30	
Schlegeliaceae	*Schlegelia parviflora*	9	2,97	3,00	
Solanaceae	*Cestrum sp.*	1	0,33		
Solanaceae	*cf. Cuatresia riparia*	2	0,66		
Solanaceae	*Lycianthes synanthera*	1	0,33		
Solanaceae	*Merinthopodium neuranthum*	3	0,99	2,31	
total		303	100,00		

Nogal secondary forest

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	Oreopanax sp.	1	5,56	5,60	
Clusiaceae	Clusia flava	9	50,00		
Clusiaceae	Clusia uvitana	4	22,22	72,22	
Moraceae	Ficus aff. colubrinae	1	5,56		
Moraceae	Ficus pertusa	1	5,56	11,11	
Solanaceae	Lycianthes santaeclarae	2	11,11		
total		18	100,00		

Nogal pasture

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Clusiaceae	*Clusia flava*	6	33,33		
Clusiaceae	*Clusia quadrangula*	7	38,89		
Clusiaceae	*Clusia uvitana*	1	5,56	77,78	
Cecropiaceae	*Coussapoa villosa*	1	5,56		
Moraceae	*Ficus colubrinae*	3	16,67		
total		18	100,00		

La Selva and Nogal

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Araliaceae	*Oreopanax sp.*	1	1,45		
Cecropiaceae	*Coussapoa villosa*	1	1,45		
Clusiaceae	*Clusia amazonica*	2	2,90		
Clusiaceae	*Clusia cf. cylindrica*	1	1,45		
Clusiaceae	*Clusia flava*	15	21,74		
Clusiaceae	*Clusia gracilis*	2	2,90		
Clusiaceae	*Clusia quadrangula*	7	10,14		
Clusiaceae	*Clusia uvitana*	6	8,70		
Clusiaceae	*Clusia valerioi*	2	2,90	50,72	
Clusiaceae	*Clusiella isthmensis*	1	1,45		52,17
Ericaceae	*Satyria panurensis*	13	18,84	18,84	
Melastomataceae	*Blakea scarletina*	2	2,90		
Melastomataceae	*Topobea maurofernandeziana*	3	4,35	7,25	
Moraceae	*Ficus colubrinae*	4	5,80		
Moraceae	*Ficus cahuitensis*	1	1,45		
Moraceae	*Ficus pertusa*	2	2,90	10,14	
Schlegeliaceae	*Schlegelia parviflora*	2	2,90		
Solanaceae	*Lycianthes santaeclarae*	2	2,90		
Solanaceae	*Merinthopodium neuranthum*	2	2,90	5,80	
total		69	100,00		

La Selva primary forest

Family	Hemiepiphyte	Abun.	%	Cum. %	Cum. %
Clusiaceae	*Clusia amazonica*	2	6,06		
Clusiaceae	*Clusia cf. cylindrica*	1	3,03		
Clusiaceae	*Clusia gracilis*	2	6,06		
Clusiaceae	*Clusia uvitana*	1	3,03		
Clusiaceae	*Clusia valerioi*	2	6,06	24,24	
Clusiaceae	*Clusiella isthmensis*	1	3,03		27,27
Ericaceae	*Satyria panurensis*	13	39,39	39,40	
Melastomataceae	*Blakea scarletina*	2	6,06		
Melastomataceae	*Topobea maurofernandeziana*	3	9,09	15,15	
Moraceae	*Ficus cahuitensis*	1	3,03		
Moraceae	*Ficus cf. pertusa*	1	3,03	6,00	
Schlegeliaceae	*Schlegelia parviflora*	2	6,06		
Solanaceae	*Merinthopodium neuranthum*	2	6,06		
total		33	100,00		

Los Alpes

Family	**Hemiepiphyte**	**Abun.**	**%**	**Cum. %**	**Cum. %**
Aquifoliaceae	*Ilex hemiepiphytica*	1	0,14		
Araliaceae	*Oreopanax capitatus*	27	3,71		
Araliaceae	*Oreopanax oerstedianum*	31	4,26	7,98	
Araliaceae	*Schefflera robusta*	27	3,71		
Araliaceae	*Schefflera rodriguesiana*	28	3,85	7,57	15,54
Asteraceae	*Neomirandea parasitica*	10	1,38		
Asteraceae	*Neomirandea psoralea*	2	0,28	1,65	
Cecropiaceae	*Cecropia peltata*	1	0,14		
Clusiaceae	*Chrysochlamis allenii*	1	0,14		
Clusiaceae	*Clusia minor*	2	0,28		
Clusiaceae	*Clusia multiflora*	26	3,58		
Clusiaceae	*Clusia palmana*	104	14,31		
Clusiaceae	*Clusia torresii*	13	1,79	19,94	20,08
Ericaceae	*Cavendishia bracteata*	70	9,63		
Ericaceae	*Cavendishia complectens*	25	3,44	13,07	
Ericaceae	*Psammisia ramiflora*	3	0,41		
Ericaceae	*Psammisia williamsii*	1	0,14		
Ericaceae	*Satyria panurensis*	2	0,28		
Ericaceae	*Sat/Psa panurensis/ramiflora*	40	5,50	6,33	19,39
Gesneriaceae	*Drymonia conchocalyx*	41	5,64		
Melastomataceae	*Blakea anomala*	108	14,86		
Melastomataceae	*Blakea cf. tuberculata*	55	7,57	22,42	
Moraceae	*Ficus crassiuscula*	19	2,61		
Moraceae	*Ficus sp6*	1	0,14	2,75	
Rubiaceae	*Cosmibuena valerii*	61	8,39		
Schlegeliaceae	*Schlegelia parviflora*	20	2,75		
Solanaceae	*Merinthopodium neuranthum*	8	1,10		
total		727	100,00		

Los Alpes primary forest

Family	**Hemiepiphyte**	**Abun.**	**%**	**Cum. %**	**Cum. %**
Araliaceae	*Oreopanax capitatus*	26	4,01		
Araliaceae	*Oreopanax oerstedianum*	27	4,16	8,17	
Araliaceae	*Schefflera robusta*	26	4,01		
Araliaceae	*Schefflera rodriguesiana*	27	4,16	8,17	16,33
Asteraceae	*Neomirandea parasitica*	8	1,23		
Asteraceae	*Neomirandea psoralea*	2	0,31	1,54	
Cecropiaceae	*Cecropia peltata*	1	0,15		
Clusiaceae	*Chrysochlamis allenii*	1	0,15		
Clusiaceae	*Clusia minor*	2	0,31		
Clusiaceae	*Clusia multiflora*	21	3,24		
Clusiaceae	*Clusia palmana*	86	13,25		
Clusiaceae	*Clusia torresii*	13	2,00	18,80	18,95
Ericaceae	*Cavendishia bracteata*	50	7,70		
Ericaceae	*Cavendishia complectens*	22	3,39	11,09	
Ericaceae	*Psammisia ramiflora*	3	0,46		
Ericaceae	*Psammisia williamsii*	1	0,15		
Ericaceae	*Satyria panurensis*	2	0,31		
Ericaceae	*Sat/Psa panurensis/ramiflora*	40	6,16	7,09	18,18
Gesneriaceae	*Drymonia conchocalyx*	39	6,01		
Melastomataceae	*Blakea anomala*	108	16,64		
Melastomataceae	*Blakea cf. tuberculata*	54	8,32	24,96	
Moraceae	*Ficus crassiuscula*	18	2,77		
Moraceae	*Ficus sp6*	1	0,15	2,93	
Rubiaceae	*Cosmibuena valerii*	50	7,70		
Schlegeliaceae	*Schlegelia parviflora*	13	2,00		
Solanaceae	*Merinthopodium neuranthum*	8	1,23		
total		649	100,00		

Los Alpes pasture

Family	**Hemiepiphyte**	**Abun.**	**%**	**Cum. %**	**Cum. %**
Aquifoliaceae	*Ilex hemiepiphytica*	1	1,28		
Araliaceae	*Oreopanax capitatus*	1	1,28		
Araliaceae	*Oreopanax oerstedianum*	4	5,13		
Araliaceae	*Schefflera robusta*	1	1,28		
Araliaceae	*Schefflera rodriguesiana*	1	1,28	8,97	
Asteraceae	*Neomirandea parasitica*	2	2,56		
Clusiaceae	*Clusia multiflora*	5	6,41		
Clusiaceae	*Clusia palmana*	18	23,08	29,49	
Ericaceae	*Cavendishia bracteata*	20	25,64		
Ericaceae	*Cavendishia complectens*	3	3,85	29,49	
Gesneriaceae	*Drymonia conchocalyx*	2	2,56		
Melastomataceae	*Blakea cf. tuberculata*	1	1,28		
Moraceae	*Ficus crassiuscula*	1	1,28		
Rubiaceae	*Cosmibuena valerii*	11	14,10		
Schlegeliaceae	*Schlegelia parviflora*	7	8,97		
total		78	100,00		

4 Foto Field Guide:

PHOTO FIELD GUIDE OF PRIMARY HEMIEPIPHYTES IN COSTA RICA

LENOTTI CARINA

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Photo Field Guide of Primary Hemiepiphytes in Costa Rica

This guide is part of a study concerning diversity and abundance of primary hemiepiphytes in Costa Rica. It is meant as help for identification or classifiication of primary hemiepiphytes in the field. For exact species determination systematic keys and work in herbariums should be done. Most of the hemiepiphytes we have found in our plots are pictured here, and some (to us) usefull notes to their appearance were made below the pictures. Plants are sorted by family and genus, a list with other hemiepiphytes in the respective genus is listed below the description. There may are some other genera with hemiepiphytic species, or at least species that coud be facultative hemiepiphytic.

Additionally to general distribution data, we also list the description in our different plots:
Pacific-influenced premontane sites: Fila Costena (FC) and San Miguel (SM)
Pacific-influenced lowland sites: La Gamba (LG) and Baru (BA)
Carribean-influenced premontane site: Los Alpes (LA)
Carribean-influenced lowland sites: La Selva (LS) and Nogal (NG)

Picture references: first note references the voucher, second note references the foto:
For Example: ***Clusia stenophylla*** (c: B. Hammel, 8803, 25.5.80, CR; *):
voucher of Hammel, foto of Carina Lenotti
* ... foto is from Carina Lenotti/voucher is from David Bröderbauer and Carina Lenotti
LI ... foto/voucher is from Biologiezentrum Linz/Werner Huber & Anton Weißenhofer
only one sign... there is only a foto reference

For more information on our plots, and research results see the studies of David Bröderbauer 2008 and my own 2010.

Primary Hemiepiphytes: a brief introduction

Primary hemiepiphytes are an important element of tropical rainforests. The highest abundance they are reaching in wet lowland and montane forests (Gentry 1986; Williams-Linera & Lawton 1995). They start their life cycle as epiphytes on trees and send roots to the ground later on (Putz & Holbrook 1986). Most species are woody plants, belonging to more than 20 dicotyledonous families. (Williams-Linera & Lawton 1995; Prosperi et al. 2001).

Whereas holo-epiphytes, are well-studied objects, reasearch on hemiepiphytes is often only included in these studies (Kelly 1985; Ingram et al. 1996). More over, data and analyses are often limited on a single genus or species of primary woody hemiepiphytes such as *Clusia* and *Ficus* (Putz & Holbrook 1989) and on small sample sizes within commensurate areas (Nieder et al 2001). Information on hemiepiphyte abundance and diversitiy is very rare, and there is a need for further investigations (cf. Bröderbauer 2008).

a

b

c

d

e

Aquifoliaceae:

Ilex hemiepiphytica (a: **): Leaves alternate, obovate, stiples, fruits: dark
Distribution: LA pasture; Costa Rica

primary hemiepiphytes of that genus in Costa Rica: *I. costaricensis, I. vulcanicola* (Hahn, 1996, Ingram 1996)

Araliaceae:

Oreopanax* aff. *striatus (b: *)
fruits: unripe green
Distribution: FC primary forest and pasture; Costa Rica and Panama

Oreopanax capitatus (c: **)
petiols disproporionate; glabrous
Distribution: FC primary forest, LA primary forest and pasture; Peru and French Guiana to Mexico, incl. Dominican Republic

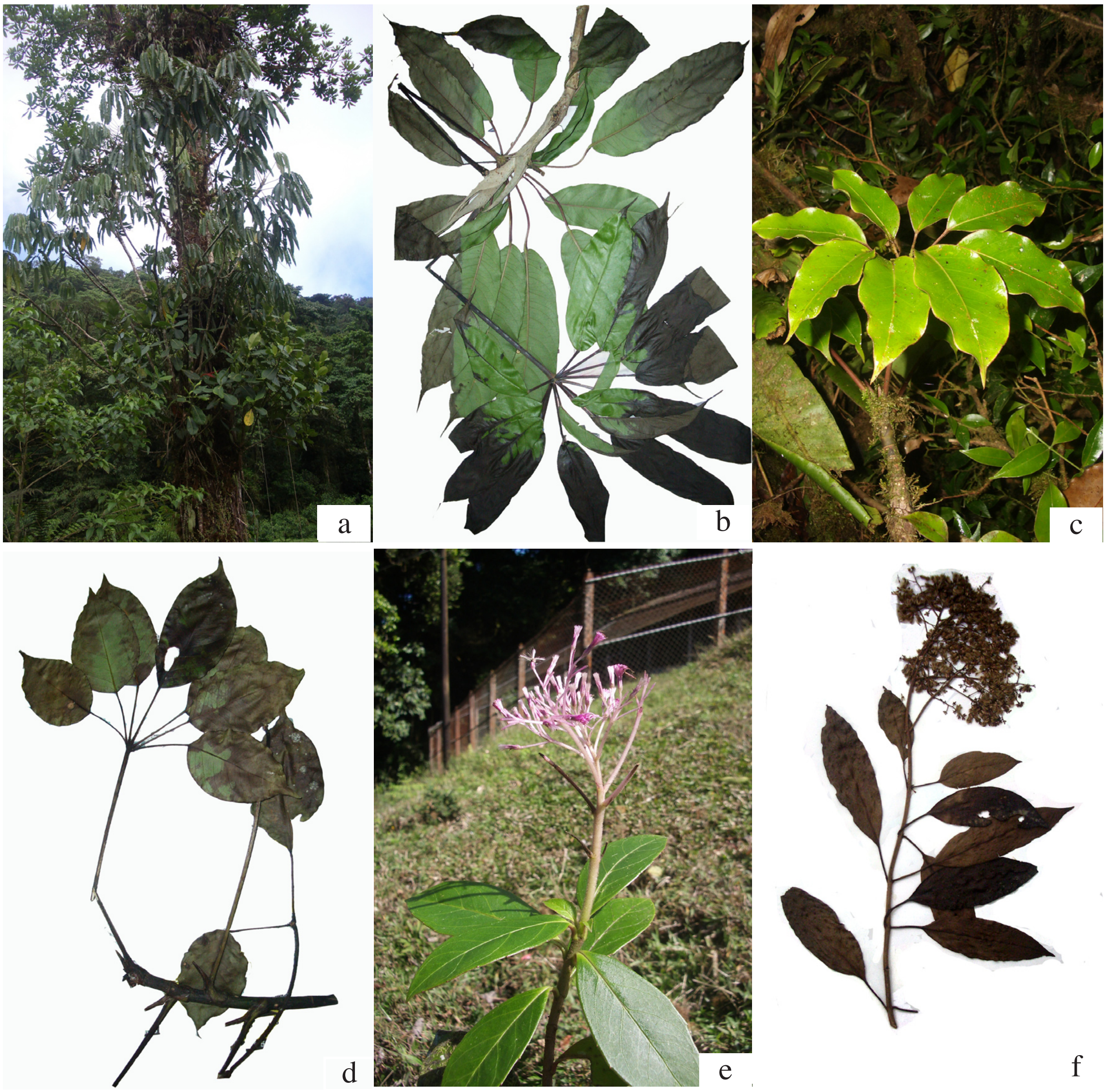
Oreopanax oerstedianum (d: **)
pubescent; flowers: white, scent
Distribution: FC primary forest, LA primary forest and pasture

primary hemiepiphytes of that genus in Costa Rica: ***O. nicaraguensis, O. nubigenus, O. obtusifolius, O. standleyi, O. vestitus*** (Monteverde Epidata, 2000)

Schefflera brennesii (e: A.C. Smith, 758, 4.9.97, LI; LI)

a single leaf-whorl; fruit: whitish-greenish, apicals are red

Distribution: SM primary forest, FC primary forest and pasture; Costa Rica



Araliaceae:

Schefflera robusta (a-b: **)
two leaf-whorls; flowers: green to red; fruits: pink
Distribution: FC and LA primary forest and pasture; Costa Rica and Panama

Schefflera rodriguesiana (c-d: **)
a single leaf-whorl; petiols red
Distribution: LA primary forest and pasture; Costa Rica and Panama

primary hemiepiphytes of that genus in Costa Rica: ***S. systyla*** (La Selva, 1994)

Asteraceae:

Neomirandea parasitica (e: *)
flowers: purple, inflorescence, leaves elliptic, alternate
Distribution: LA primary forest and pasture; Costa Rica and Panama

Neomirandea psoralea (f: W. D. Stevens, 14134, 10.9.79, CR; *)
inflorescence many branched, leaves elliptic, apex acute
Distribution: LA primary forest; Costa Rica and Panama

primary hemiepiphytes of that genus in Costa Rica: ***N. standleyi*** (FC primary forest), ***N. araliifolia*** (Monteverde Epidata, 2000) and other species as potential hemiepiphtes

a

b

c

d

e

Cecropiaceae:

Cecropia peltata (a: L. Landrum, 10408, 21.5.02, CR; *): Lamina peltate, radially incisted, venetion radial, inflorescence digitate clusters of spikes (Berg et al., 1990)
Distribution: LA primary forest; Ecuador and Guyana to Mexico incl. Dom. Republic

primary hemiepiphytes of that genus in Costa Rica: ***C. obtusifolia*** (Monteverde Epidata, 2000, La Selva, 1994)

Coussapoa glaberrima (b: W. Burger, 1292, 28.8.98, WU; LI): glabrous (leaves, twigs, inflorescence, petiole, stipules), leaves obovate to elliptic, apex acute, flowers: greenish (Berg et al 1990)
Distribution: LG primary forest and pasture; Panama to Nicaragua

Coussapoa villosa (c: **): apex acuminated; nearly no auricles; flowers: green, Latex: clear, leaves broadly ovate to subovate (Berg et al 1990)
Distribution: SM and NG pasture; Bolivia to Honduras

primary hemiepiphytes of that genus in Costa Rica: ***C. nymphaeifolia, C. parviceps*** (Monteverde Epidata, 2000, La Selva, 1994)

Clusiaceae:

Chrysochlamis allenii (d: **): leaves elliptic to slightly obovate, apex rounded, base acuminate, Latex: white
Distribution: LA primary forest; Costa Rica and Panama

Clusia amazonica (e: **): lianescent; leaves acumilated, petiolate; dioecious; flowers creme-coloured, stamina free; latex: white to clear
Distribution: LG primary and secondary forest, SM and FC primary forest; Bolivia and Brazil to Nicaragua

Clusiaceae:

Clusia croatii (a: **), ***C.* cf. *croatii*** (b: **): leaves small, acuminated, petiolate; dioecious; flowers small, pink, sometimes white apex, sweet scent, resin; latex: internal yellow, external white to creamy
Distribution: FC primary forest and psture; Panama to Nicaragua

Clusia cylindrica (c: **): leaves slender, acuminated, short petiols; flowers: pink to yellow-green, stamina free; fruits: green; latex: milky
Distribution: LG primary forest; Columbia to Nicaragua

Clusia flava (d-f; **): leaves round, short petiols, diocious; flowers yellow to creamy, succulent, stamina free, arranged in a square; fruits green; latex yellow-creamy
Distribution: Nogal secondary forest and pasture; Costa Rica to Mexico

Clusia gracilis (g: B. Hammel, 8803, 25.5.80, CR; *): leaf & leaf base acuminated; diocious; flowers yellow/red, stamina free; fruits unripe green, red basis; latex white
Distribution: La Selva primary forest; Panama to Nicaragua

Clusia minor (h: B. Hammel, 14245, 20.7.85, CR; *): leaves small, acuminated, petiolate, young red; monoecious; flowers pink, small, resin; fruit geen-red; latex yellow
Distribution: LA primary forest; Bolivia and Suriname to Mexico incl. Dominican Republic

Clusiaceae:

Clusia multiflora (a: B. Hammel, 19067, 1.10.93, CR; *): leaves obovat to round, peripterous, sessile; latex: white to creamy
Distribution: LA primary forest and pasture; Bolivia to Mexico

Clusia osaensis (b-c: **): leaves broadly obovate elliptic, base acute, flowers: petals creamy, yellow, medical scent, stamina free; latex: clear
Distribution: LG primary forest; Costa Rica

Clusia palmana (d-g: **): leaves elongate to roundish, peripterous; petals yellow to green, sweet scent, stamina free, creamy; latex: clear
Distribution: LA primary forest and pasture; Ecuador to Costa Rica

Clusia peninsulae (h: **): leaves elliptic, apex and base acute, petals pink to white, latex: yellow to white
Distribution: LG primary and secondary forst; Csta Rica and Panama (Darien)

Clusiaceae:

Clusia quadrangula (a-b: **): leaves elongate, acuminate, petiolate; dioecious; flowers white to creamy, stamina free; fruits green; latex: white
Distribution: NG pasture; Panama to Mexico

Clusia stenophylla (c: B. Hammel, 8932, 4.6.80, CR; *): leaves big without apex, slightly peripterous; flowers white, resin; latex: yellow
Distribution: FC and SM primary forest, FC pasture; Ecuador to Mexico

Clusia torresii (d: **): leaves rather slender, apex rounded, petiolate; latex: clear; bracts red
Distribution: LA primary forest; Panama to Nicaragua

Clusia uvitana (e-h: **): leaves round, lightly acuminate, petiolate; dioecious; flowers white to red, resin; fruits green; latx: white
Distribution: LS and Nogal forest and pasture; Panama to Nicaragua

Clusiaceae:

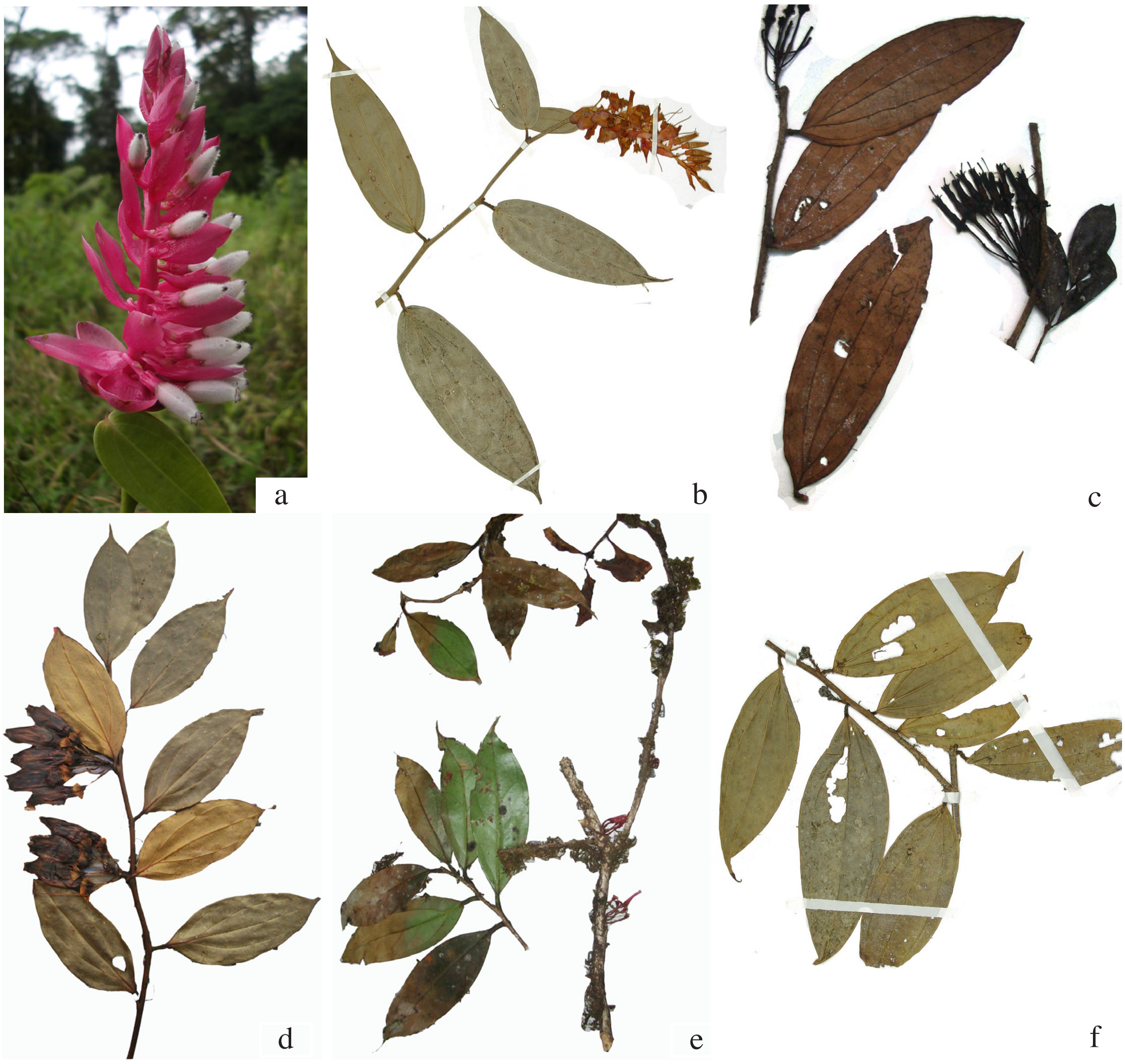
Clusia valerioi (a-d: **): leaves obovat elliptic, broad acuminate; dioecious; flowers big, pink, resin; fruits green; latex: yellow to white
Distribution: LG, LS, BA forestsa and LG, SM pasture; Columbia to Nicaragua

primary hemiepiphytes of that genus in Costa Rica: ***C. heterosavia, C. oedematopodia, C. rosea, C. rotundata, C. modesta*** (Monteverde Epidata, 2000, Hammel, 1986)

Clusiella isthmensis (e: D. Smith, 457, 29.10.81, CR; *): leaves elliptic, apex long-acuminate, base acute, petals white to yellow, Latex clear
Distribution: LS primary forest; Costa Rica and Panama

Ericaceae:

Cavendishia bracteata (f-h: **): leaves rather elongate, base round, apex abrupt acumilate, short petiols, nerves cut in
Distribution: LA primary forest and pasture; Bolivia to Mexico



Ericaceae:

Cavendishia callista (a: *; b: W.Huber&A. Weissenhofer, 671, 15.5.97, LI; LI): leave base slightly cordate, drip-tip long drawn-out; inflorescence terminal, Flower white, bracts pink
Distribution: SM, FC primary forest, pasture; Ecuador and french Guiana to Guatemala

primary hemiepiphytes of that genus in Costa Rica: **_C. complectens_** (LA primary forest and pasture; leaves rotund), **_C. axillaris, C. capitulata, C. chiriquiensis, C. endresii, C. lactiviscida, C. linearifolia, C. melastomoides, C. quercina, C. quereme, C. osaensis_** (Monteverde Epidata 2000, Luteyn 1983, LG Filed Guide, 2001)

Psammisia ramiflora (c: F. C. Rodriguez, 4961, 23.2.93, CR; *): leaves: 3 to 5 nerves, ovate, base acuminate, drip-tip tapered; flowers and fruits clearly ramiflor
Distribution: FC and LA primary forest; Columbia to Costa Rica

Psammisia williamsii (d: **): leaves: base acumunate, petiols thin, drip-tip abrupt; flowers and fruits closer to axil, flowers relatively big
Distribution: LA primary forest; Costa Rica and Panama

Satyria panurensis (e: **): leaves: base acuminate; drip-tip taperd, petiols thick; flowers small - Distribution: LG forests, SM primary forest and pasture, LS and LA primary forest; Peru and french Guiana to Mexico

Satyria warszewiczii (f: W.Huber&A. Weissenhofer, 503, 24.494, LI; LI): leave: base acuminate, 5 nerves, petiols thick
Distribution: FC primary forest and pasture; peru and Veenzuela to Mexico

Gesneriaceae:

Drymonia alloplectoides (a: **): strong pilous, looks often like climber, leaves subequle, ovate, flowers solitary and white calyx purple,

Distribution: SM primary forest and pasture; Peru to Nicaragua

Drymonia conchocalyx (b-c: **):

pink-purple and white flowers, pinkish calyx

Distribution: LA primary forest and pasture; Ecuador to Nicaragua

Drymonia macrantha (d-e: *): flowers yellow, calyx orange, densely packed in inflorescence; big leaves, broadly ovate

Distribution: SM and FC primary forest; from Mxico to Costa Rica and Panama

Drymonia macrophylla (f: Hammel&Chacon, 13351, 8.8.83, CR; *): leaves bigger and elongate

Distribution: FC primary forest; Peru to Nicaragua

Drymonia warscewicziana (g: *)

big leaves, flowers yellw to green

Distribution: SM primary forest; Costa Rica, Ecuador

primary hemiepiphytes of that genus in Costa Rica: ***D. multiflora, D. serrulata*** (Monteverde Epidata, 2000, LS online) and other species as potential hemiepiphtes


a


b


c


d


e


f


g

Melastomataceae:

Blakea anomala (a: *):
small leaves, flowers white, stamina yellow, filaments pink
Distribution: LA primary forest; Cota Rica

Blakea litoralis (b: Huber&Weisseinhofer, 686, 20.5.97, CR; *)
leaves small, ovate, apex acute, petals white with pink apex
Distribution: LG and SM primary forest; Costa Rica and Panama

Blakea scarletina (c: **)
unripe fruits: sepals green to yellow
Distribution: LS primary forest; Costa Rica Nicaragua

Blakea subpeltata (d: Huber & Weisseinhofer, 2459, 16.3.01; *)
leaves bigger, ovate, abrupt acumilate, base round
Distribution: SM primary forest; Costa Rica

primary hemiepiphytes of that genus in Costa Rica: ***B. litoralis, B. tuberculata*** (Monteverde Epidata, 2000, LG, Ingram 1996)

Topobea maurofernandeziana (e: **): big leaves, round to acuminate; flowers pink and white
Distribution: LG and LA primary forest, SM and LS primary forest and pasture; Panama to Nicaragua

Topobea pittieri (f: **, g: F. Almeda, 3846, 1978, CR; *): leaveas round but acumulate, domatias
Distribution: FC primary forest and pasture; Ecuador to Costa Rica

primary hemiepiphytes of that genus in Costa Rica: ***T. multiflora*** (FC primary forest : leaves roundish, flowers pink), ***T. brennesii*** (Monteverde Epidata, 2000) and other species as potential hemiepiphtes

Moraceae:

Ficus americana (a: W.Huber&A.Weissenhofer, 2035, 28.8.00, LI; LI)
latex white, small leaves, elliptic
Distribution: BA forests and pasture; brazil to Mexico incl. Dominican Republic

Ficus cahuitensis (b:**)
latex white, leaves bundled, ovate, apex round
Distribution: LS primary forest; Panama to Honduras

Ficus citrifolia (c: J. González, 1995, CR; *): leaves oblong-ovate to oblong-elliptic, latex thik milky to clear, figs pedunculate, ripe red, unripe yellow with red spots
Distribution: LG forests and pasture, SM primary forest, BA pasture; Brazil to Mexico incl. Dominican Republic and Cuba

Ficus cf. colubrinae (d:**)leaves elliptic to obovate, stipuls glabrous or densly pubescent, latex white, figs sessile, yellow to pink
Distribution: LG forests; SM primary forest & pasture; NG pasture; Panama to Mexico

Ficus costaricana (e: Hammel, 13030, 28.6.82, CR; *): leaves ovate oblong or elliptic, stipuls usually galbrous, latex white, figs sessile in pairs in leaf axils
Distribution: LG primary forest and pasture, SM primary forest; Ecuador to Mexico

Ficus crassiuscula (f: L.R: Holdrige, 6676, 12.3.1972, CR; *):
leaves loong obovate, apex acumulate, latex clear
Distribution: LA primary forest and pasture; Bolivia and Venezuela to Guatemala

a

b

c

d

e

Moraceae:

Ficus nympheifolia (a: W.Huber&A.Weissenhofer, 1477, 20.2.99, LI; LI): leaves big obovate, base cordate, stipules galbrous, latex white, figs sessile in pairs in leaf axils
Distribution: LG and SM pasture; Brazil to Honduras

Ficus obtusifolia (b: W.Huber, 3047, 30.1.02, LI; LI)
leaves bundled, ovate, apex round, base acumulate, stipules, latex white
Distribution: BA pasture; Brazil to Mexico

Ficus* cf. *osensis (c: **)
leaves slender elliptic, acumulate, stipules
Distribution: SM primary forest; Columbia to Costa Rica

Ficus pertusa (d: W.Huber, H 16, 13.6.97, LI; LI)
small leaves, acumulate, figs red, sessile, latex clear to white
Distribution: LG & NG secondary forest, SM primary forest & past.; Brazil to Mexico

primary hemiepiphytes of that genus in Costa Rica: ***F. bullenii, F. brevibracteata, F. cotinifolia, F. crassivenosa, F. donnell-smithii, F. goldmannii, F. laterisyce, F. lasiosyce, F. macbridei, F. moraziniana, F. popenoei, F. schippii, F. tonduzii, F. trachelosyce, F. tuerckheimii, F. velutina*** (LG, Hammel, 1986, Putz, 1989, Velerio, 2004, Monteverde Epidata, 2000) and other species as potential hemiepiphtes

Rubiaceae:

Cosmibuena valerii (e: *): Sipules forming a cap over the shoot apex in early stages, stipules red, flower white, capsula brown, pith has aromatic scent
Distribution: LA primary forest and pasture; Costa Rica and Panama

primary hemiepiphytes of that genus in Costa Rica: ***C. grandiflora, C. macrocarpa*** (Burger, 1993, Todzia, 1986, Monteverde Epidata, 2000)


a


b


c


d


e


f

Schlegeliaceae:

Schlegelia parviflora (a: Khan, Tebbs&Vickery, 671, 30.1.84, CR; *): leaves dark green, acumilate, opposite, petiols thick; lianescent, fruits white to purple
Distribution: LG forests and pasture, SM primary forest, FC and LA primary forest and pasture; Peru and French guiana to Mexico

primary hemiepiphytes of that genus in Costa Rica: ***S. fuscata*** (Ingram, 1996, Monteverde Epidata, 2000)

Solanaceae:

Cuatresia riparia (b: J.L.Gentry&W.Burger, 2842, 30.5.73, CR; *): anisophylly (reduced "oposite"), fruit yellow, smaller leaf roun, only few flowers/fruits per node
Distribution: FC primary forest; Ecuador and venezuela to Guatemala

Lycianthes santaeclarae (c-d: **): anisophylly, leaves pubescent, ovate to oblong-ovate; flowers purple, fruits orange
Distribution: SM primary forest and BG secondary forest

Lycianthes synanthera (e: J. Quesada, 1635, 1.6.86, CR; *): flowers pink, stamina yellow, buds violacious, citrus-scent; fruits green to brown; pith scents
Distribution: FC primary forest and pasture; Peru to Guatemala

Merinthopodium neuranthum (f:**): flowers green to yellow, faint scent, flower hanging on long stem; leaves obovate-elliptic
Distribution: FC, NG and LA primary forest; Panama to Belize

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5 Zusammenfassung

Diese Diplomarbeit ist Teil einer Studie über primäre Hemiepiphyten in verschiedenen Regionen Costa Ricas, ihre Einnischung, Verbreitung und Diversität. An der Studie arbeiteten David Bröderbauer und ich gemeinsam, betrachteten allerdings unterschiedliche Aspekte und verfassten jeweils eigene Diplomarbeiten zu unseren jeweiligen Themen. Während David sich in seiner Diplomarbeit (2008) mit „Spatial Distribution of Primary Hemiepiphytes in Different Costa Rican Rainforests“, also der Einnischung von primären Hemiepiphyten im Regenwald auseinandersetzte, wird in dieser - meiner - Arbeit die Diversität und Abundanz betrachtet.

In sieben Regionen wurden sieben Aufnahmeflächen in Primärwäldern, zwei in Sekundärwäldern und sechs Weiden untersucht. Wir unterscheiden dabei Tieflandflächen von prämontanen Flächen, sowie Flächen, die von pazifischem bzw. atlantischem Klima beeinflusst sind. Die Feldarbeit fand von Januar bis Mai 2007 gemeinsam mit David Bröderbauer statt. Die Auswertung der Daten erfolgte nach unterschiedlichen Schwerpunkten getrennt.

Zur Lage der Untersuchungsflächen: Zwei Primärwaldflächen, eine Sekundärwaldfläche und eine Weide lagen nahe der Tropenstation La Gamba, in der Nähe des Piedras Blancas Nationalpark, an der südlichen Pazifikküste. Eine Weide lag etwas nördlich davon, in der Nähe von Dominical an der Hacienda Baru. Östlich von La Gamba, auf dem Gebirgszug Fila Costeña lagen je eine Primärwaldfläche und eine Weide in der Nähe des Dorfes San Miguel (auf 500 m Seehöhe) und unterhalb des Gebirgsrücken auf 1500 m Seehöhe. Auch diese Gebiete sind von pazifischem Klima beeinflusst. Ebenso an der Pazifikküste lag die 0,2 ha große Primärwaldfläche eines Trockenwaldes im Nationalpark Santa Rosa, der im Norden von Costa Rica liegt. Eine weitere Primärwaldfläche und eine Weide befand sich auf der Cordillera de Tilaran im nördlichen Teil des Landes im privaten Reservat „Los Alpes“ auf 1500 m Seehöhe. Im Tiefland untersuchten wir zusätzlich eine Primärwaldfläche im Wald der Tropenstation La Selva, sowie, nicht weit davon, eine Sekundärwaldfläche und eine Weide im Reservat der Compañía Bananera del Atlántico Ltda. in Nogal. Die letzten Regionen (Los Alpes und La Selva und Nogal) stehen unter dem Einfluss des Atlantischen Klimas.

Unsere Waldflächen waren je 0,5 ha groß (eine war 0,2 ha groß) und in Subflächen von 20 x 20 m unterteilt. Auf den Weiden wurden je 40 Bäume, bzw. einmal 20 und einmal 27 Bäume, untersucht. In jeder Fläche wurden alle Bäume mit mehr als 10 cm Durchmesser auf Brusthöhe nach Hemiepiphyten abgesucht, deren Höhe geschätzt und ihr Durchmesser mit einem Maßband ermittelt. Die Hemiepiphyten wurden mithilfe von Ferngläsern bestimmt, exemplarische Belege wurden gesammelt und im Nationalmusem in San José

/CR, sowie auf der Universität Wien hinterlegt. Die Größe der Hemiepiphyten wurde in fünf Größenklassen, abhängig von der Abdeckung der Krone des Wirtsbaumes, eingeteilt: 0) < 5 %, 1) 5-25 &, 2) 26-50 %, 3) 51-75 %, 4) 75-100 %. Neben deskriptiver Statistik (Verbreitung, Artenreichtum – absolut und prozentual) wurden Familiy Important Value und Important Value Index der Arten, Gattungen und Familien berechnet. Außerdem wurden verschiedene Diversitätsindizes (Shannon-Wiener, Hs - und Simpson-Yule, Ds), Indizes zur Errechnung des Artenreichtums (ACE und MM) und Ähnlichkeitsindizes (Jacard, Soerenson, Bray-Crtis und Ness) bezogen auf die Untersuchungsflächen berechnet. Nonumerische Multidimensionale Skalierungen für die Arten und Familien wurde auf der Basis des Ähnlichkeitsmaßes NESS erstellt. Für die Berechnungen wurden SPSS, EstimateS und Excel genutzt.

Wir haben eine hohe Verbreitung von primären Hemiepiphyten in allen unseren Primärwaldflächen gefunden. Im Tiefland waren das 6,6 bis zu 12,8 Individuen pro 0,1 ha, im Hochland sogar bis zu 129,8 Individuen pro 0,1 ha. Die Diversitätsindize gaben eine höhere Diversität in Primärwäldern (Hs bis zu 2,74) als in Sekundärwäldern (Hs bis zu 1,23) an. Auf Weiden maß der Hs 1,01 bis 2,16. Die Schätzung des Artenreichtums mit ACE ergab bis zu über 38 Arten in prämontanen Primärwäldern und um die 17 Arten in Primärwäldern im Tiefland, sowie knapp über 8 Arten in Sekundärwäldern des Tieflandes. Die Ergebnisse zeigen, dass die Verbreitung und Diversität mit der Höhenlage zunimmt, die verschiedenen Klimaeinflüsse spielen keine bedeutende Rolle. Außerdem wird klar, dass die Diversität in gestörten Wäldern und mit zunehemender Trockenheit deutlich abnimmt. Die Verbreitung pro Baum nimmt auf freistehenden Bäumen auf Weiden zu, die Diversität allerdings nicht. Die Wälder zeigen Ähnlichkeit in ihrer Hemiepiphyten Zusammensetzung, wenn der Waldtyp sich ähnelt. Regionale Einflüsse spielen hingegen eine untergeordnete Rolle.

Es zeigt sich weiters, dass unterschiedliche Familien und Arten in unterschiedlichen Gebieten eine Rolle spielen. Neben Clusiaceae und Moraceae sind einige andere Familien von größerer Bedeutung, wie Melastomataceae und Ericaceae. Für die unterschiedliche Verbreitung von einzelnen Familien sind regionale und/oder ökologische Parameter eher von Bedeutung, als z.B. mehr Licht auf freistehenden Bäumen. So zeigt sich, dass Arten der Familie Cecropiaceae, aber auch jene der Moraceaeen, vorwiegend auf Weiden im Tiefland vorkommen. Araliaceaeen und Rubiaceaeen hingegen kommen eher in den prämontanen Primärwäldern vor. Ebenso zeigt sich, dass Arten der Familien Schlegeliaceae und Clusiaceae von größerer Bedeutung im Tiefland sind, während neben den schon erwähnten Araliaceaeen, auch die Familien Asteraceae und Gesneriaceae in den prämontanen Regionen die höhere Bedeutung haben.

6 Curriculum Vitae

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Persönliche Daten

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Bildung

seit WS 2008	Lehramtsstudium der Biologie und Umweltkunde sowie der Informatik und des Informatikmanagements
2002 - 2008	Studium der Publizistik und Kommunikationswissenschaft in Wien: Abschluss mit Bakk. phil.
seit SS 2004	Studium der Ökologie, Vegetationsökologie und Naturschutz (Stzw.)
2002 - 2004	Studium der Biologie in Wien
14. 6. 2002	Reifeprüfung mit Gutem Erfolg bestanden
1994 - 2002	Bundesgymnasium und Bundesrealgymnasium Gänserndorf
1990 - 1994	Volksschule Bockfließ

Berufliche Tätigkeit

seit 9. 2010	AHS Lehrerin für Informatik am BG & BRG Keimgasse Mödling
10. 2002 - 9. 2010	Lernhilfe im KTH Vorgartenstraße 91
Winter 2007	Postergestaltung für die Tropenstation La Gamba, Costa Rica
Herbst 2007	Literaturrecherche im Rahmen des OMV-Korridorprojekts der Tropenstation La Gamba, Costa Rica
7. - 8. 2007	Internship beim Magazin Nature in München
2005 - 2007	Besucherbetreuung beim Kindernationalparkcamp Lobau
8. 2002 & 7. 2004	Direktmarketing für Wesser - Öffentlichkeitsarbeit für den B.U.N.D. in Deutschland
7. 2003	Praktikum im Tiergarten Schönbrunn (Tierhilfspflege & Tierbetreuung)

Fremdsprachen

Englisch in Wort und Schrift
Grundkenntnisse in Französisch und Spanisch (in Wort und Schrift)

Auslandsaufenthalte

1. - 5. 2007	Datenerhebung für meine Diplomarbeit der Biologie in Costa Rica
7 - 8. 2007	Internship beim Magazin Nature in München
2006 (3 Wochen)	Zoologisch Botanische Exkursion und Praktikum in Costa Rica
2002 & 2004	je einmonatige Tätigkeit im Direktmarketing in Deutschland

Schul-Sprachwochen in Irland und Frankreich, sowie Intensivsprachkurs in Malta