

Floristic composition and community structure of epiphytic angiosperms in a terra firme forest in central Amazonia

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ABSTRACT

This survey aimed to describe the floristic composition and structure of the epiphytic community occurring in a terra firme forest in the city of Coari, Brazil, in the Amazon region. Data collection was performed with a 1.5 ha plot method, with which upland, slope and lowland habitats were sampled. All angiosperm epiphytes and their host plants (diameter at breast height ≥ 10 cm) were sampled. We recorded 3,528 individuals in 13 families, 48 genera and 164 species. Araceae was the most prevalent family with regard to the importance value and stood out in all related parameters, followed by Bromeliaceae, Cyclanthaceae and Orchidaceae. The species with the highest epiphytic importance values were *Guzmania lingulata* (L.) Mez. and *Philodendron linnaei* Kunth. The predominant life form was hemiepiphytic. Estimated floristic diversity was 3.2 (H'). The studied epiphytic community was distributed among 727 host plants belonging to 40 families, 123 genera and 324 species. One individual of *Guarea convergens* T.D. Penn. was the host with the highest richness and abundance of epiphytes. Stems/trunks of host plants were the most colonized segments, and the most favorable habitat for epiphytism was the lowlands, where 84.1% of species and 48.2% of epiphytic specimens were observed.

Key words: Amazon rainforest, epiphytic groups, composition, diversity, distribution

Introduction

As support for their development, vascular epiphytes use other plants (phorophytes), where they spend their entire life cycle (typical epiphytes) or at least part of it (hemiepiphytes). Although the majority of vascular epiphytes are herbaceous, some hemiepiphytic species are woody. Epiphytes play a key role in the processes and maintenance of ecosystems, where they exert great influence on the cycling of water and nutrients within the forest due to their ability to produce suspended biomass (Benzing 1990). The retained water and organic matter are important resources for different organisms that inhabit the forest canopy (Odum & Pigeon 1970; Nadkarni 2000; Richards 1996). In addition, many species belonging to this group of plants have economic importance, be it for medical, dietary or ornamental use (Nadkarni 1992; Soares 2008).

In tropical and subtropical forests, vascular epiphytes represent an essential component (Benzing 1990; Richards 1996), and are usually very abundant and diverse (Nieder *et al.* 1999; 2000; Kelly *et al.* 1994; Barthlott *et al.* 2001; Burns & Dawson, 2005; Kersten 2010). There are approximately

29,000 epiphytic species distributed between 876 genera and 84 families, that is, approximately 10% of all vascular plants ever described (Gentry & Dodson 1987a, 1987b; Benzing 1990).

Despite the high epiphytic richness and complexity of this life form in ecosystems, the accumulated knowledge about the flora, ecology and distribution of epiphyte communities is still unsatisfactory given its importance. This has probably occurred due to methodological difficulties in sampling, the difficulty of accessing the forest canopy, the large size of the trees, difficulties in plant herborization (such as size, existence of spiny structures, myrmecophytic plants and the presence of invertebrates or poisonous animals), among other factors.

We performed approximately 120 floristic inventories with epiphytes in the Neotropics, including sampling areas of 1-1000 ha (Kuper *et al.* 2004). In Brazil, few studies have been performed involving vascular epiphytes—neither floristic reviews nor quantitative studies in different forest formations—and most of the work has been concentrated in the South and Southeast of Brazil (Waechter 1998; Gonçalves & Waechter 2003; Alves *et al.* 2008; Buzzato *et al.* 2008;

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Kersten *et al.* 2009a,b; Neto *et al.* 2009; Reis & Fontoura 2009; Geraldino *et al.* 2010; Kersten 2010; Blum *et al.* 2011; Pontes & Alves 2011). In the Amazon biome lack of information is even greater, although in the extra-Brazilian Amazon stand out studies by Baslev *et al.* (1998), Engwald *et al.* (2000), Nieder *et al.* (2000), Nieder *et al.* (2000), Schmit-Neuerburg (2002), Vasco (2002), Arévalo & Betáncur (2004), Kreft *et al.* (2004) and Benavides *et al.* (2005; 2006). In the Brazilian Amazon we can cite studies by Silva *et al.* (1995), Ribeiro *et al.* (1999), Sousa & Wanderley (2007), Pos & Slegers (2010), Medeiros & Jardim (2011) and Quaresma & Jardim (2012).

Given the above, the objective of this study was to describe the floristic composition and community structure of epiphytes occurring in a terra firme forest in Central Amazonia in order to evaluate the diversity of species there and contribute to the body of knowledge on this group of plants in support of future management and conservation projects.

Materials and methods

The study was conducted at the *Base Operacional Geólogo Pedro de Moura* (BOGPM, Pedro de Moura Base of Geological Operations), installed by the semi-public energy company Petrobras (Brazilian Petroleum) in the city of Coari, in the state of Amazonas, Brazil, 653 km from the city of Manaus (Fig. 1), located in the Urucu River basin (4°51'18"–4°52'16"S; 65°17'58"–65°20'01"W), an area with an average elevation of 60–70 m and a surface area of approximately 514.000 ha (PETROBRAS 1989).

The climate of the study area, according to the Köppen classification system, is type Af (humid year-round), corresponding to a tropical rainforest climate. The variation in temperature is small between the months of the year, ranging from 25.2°C to 26.2°C. The average annual rainfall is 2.300 mm and the average relative air humidity is 85%. The Urucu River basin has a very typical seasonal cycle of rainfall distribution, alternating between a rainy season from December to May and a drier season from June to November, with the rainy season representing 66.1% of total annual precipitation.

The BOGPM is located within the Central Amazonia physiographic region and its dominant physiognomic formation is the rainforest lowland (Veloso 1992). The vegetation is mostly characteristic of terra firme forests, with a closed canopy at heights from 25 to 35 m, where emergent trees can reach heights of 45 m. The soil consists of "Solimões formation" sediments. Most has a loamy texture, presenting an undulating pattern (Ribeiro *et al.* 2008). In terra firme forests, several types of environments occur, such as plateaus (terraces with flat topography and well-drained loamy soils), hillsides (steep slopes with accentuated drainage) and floodplains (periodically flooded areas along streams with sandy soil) (Ribeiro *et al.* 2008).

For data collection, a method was used in which a total

area of 1.5 ha was divided into plots. The plots were placed along 50 km of the BOGPM road. In each of the three environments (plateau, hillside and floodplain) eight plots of 25 × 25 m were defined, totaling 24 plots arranged at random distances from one another. The locations for the plots were selected for the ease of access they offered to the respective environments. In each plot, we recorded all trees with a diameter at breast height ≥ 10 cm hosting vascular epiphytes of the angiosperm group. We recorded all epiphytic individuals on phorophytes without distinguishing between youth and adults. Seedlings smaller than 5 cm were not sampled due to the difficulty of taxonomic identification.

All epiphytic specimens and their respective phorophytes were numbered and collected, being in either the fertile or sterile stage, for taxonomic identification. The collection and documentation were done through a combination of climbing the host tree and visual observation at a distance with the aid of binoculars. The specimens were deposited at the Herbarium in accordance with the usual procedures in floristic surveys (Vaz *et al.* 1992). The sterile material collected was filed as evidence and the fertile material was incorporated into the collection of the Herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil.

The criteria used to quantify epiphytic specimens

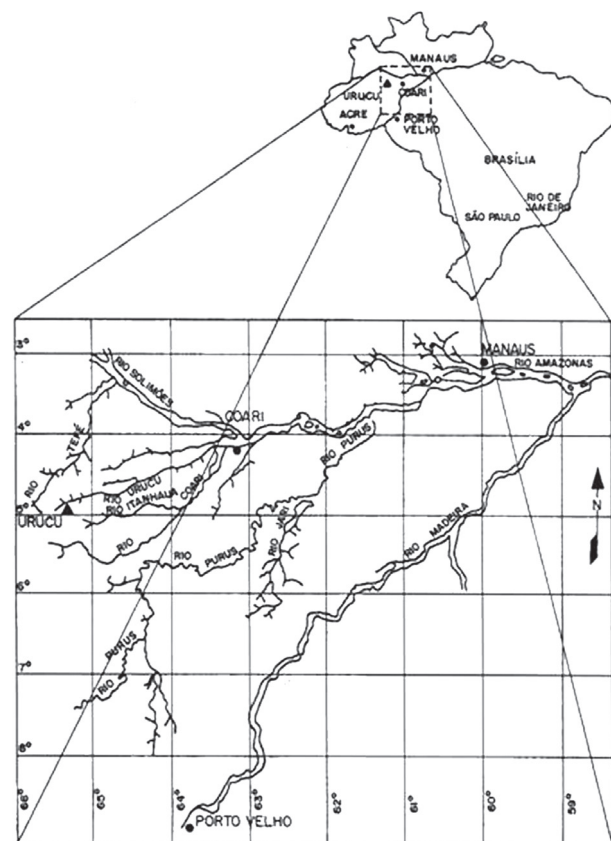


Figure 1. Location of the study area (Pedro de Moura Base of Geological Operations - Urucu River basin) in the municipality of Coari, central Amazônia, Brazil.

were the main stem (Araceae, Cyclanthaceae, Clusiaceae, Moraceae, etc.), the rosette or single reservoir (Bromeliaceae), or the set of stems/rhizomes/pseudobulbs (Orchidaceae), whether or not the specimens were genetically different. For species that occur in colonies (Gesneriaceae, Piperaceae), groupings were numbered that were distinctly separated from others on the host tree.

With regard to ecological categories, the epiphytes were classified into: holoeiphytes (or typical epiphytes), accidental or discretionary epiphytes and hemieiphytes (primary or secondary) (Benzing 1990).

Species identification was performed through a specific bibliography, comparison with the collection of the INPA Herbarium and consultation with parataxonomists and experts. The classification of species adhered to the classification system proposed in Angiosperm Phylogeny Group (APG) III (Angiosperm Phylogeny Group 2009). For nomenclatural correction of taxa, the site of the Missouri Botanical Garden and The Plant List site were consulted.

We recorded the occurrence of epiphytes on the two main segments of their phorophytes (1 = trunk, 2 = canopy). The height for the record of the region of occupation of the epiphytes was generalized to the maximum height at which the specimen had occurred, measuring even the highest leaf sprouts on the phorophyte.

To analyze the structure of the epiphytic community, host trees of epiphytes and the plots were considered sampling units. We used the parameters proposed by Waechter (1998), those being Absolute Frequency (FAi) and Relative Frequency (RFi) for individual phorophytes, Absolute Frequency (FAj) and Relative Frequency (RFj) for specific phorophytes and the epiphytic Importance Value Index (IVE), obtained through the following formulas:

$$\begin{aligned} FAi &= (Npi / Nfa) \times 100 \\ RFi &= (Npi / \sum Npi) \times 100 \\ FAj &= (Spi / Sfa) \times 100 \\ RFj &= (Spi / \sum Spi) \times 100 \\ IVE &= (RFi + RFj) / 2 \end{aligned}$$

where Npi is number of phorophytes occupied by the epiphytic species i ; Nfa is the total number of phorophytes sampled; Spi is the number of phorophytic species occupied by the epiphytic species i ; and Sfa is the total number of phorophytic species sampled.

The family importance value (FIV) of epiphytic species was calculated according to Mori *et al.* (1983), by the following formulas:

$$FIV = \sum DRel, DIVRel \text{ and } FRel$$

where DRel is the relative density (number of individuals in each family / total number of individuals \times 100); DIVRel is the relative diversity (number of species in each family / total number species \times 100); and FRel is the relative frequency (number of plots in which the family occurs / \sum

frequency of all families \times 100).

The distribution of the richness and abundance of epiphytic species on phorophytic species were estimated by calculations of ratios between epiphytes and phorophytes (Fontoura *et al.* 2009), and these ratios were considered high when ≥ 5.0 . The calculations were performed using the following phytosociological estimators:

$$Nepi/Nfor = \text{ratio of the abundance of epiphytes to the abundance of phorophytes}$$

$$Sepi/Nfor = \text{ratio of epiphyte richness to the abundance of phorophytes}$$

where $Nepi$ is the abundance of epiphytic on phorophytic species i ; $Nfor$ is the abundance of phorophytic species i ; and $Sepi$ is the richness of epiphytes on phorophytic species i .

The relative frequencies of species in phorophytic segments were calculated as follows:

$$\begin{aligned} \text{Trunks } (RFfi) &= Npi / \sum Npi \\ \text{Canopies } (RFci) &= Nci / \sum Nci \end{aligned}$$

where $RFfi$ is the relative frequency of species on the trunk (%); Npi is the number of trunks with epiphytic species i ; $RFci$ is the relative frequency of species in the canopy (%); and Nci is the number of canopies with epiphytic species i .

Epiphytic diversity was assessed using the Shannon index (H'), the logarithmic calculation basis of which is \log_e , and uniformity was calculated using Pielou's evenness index (J') (Krebs 1999). The analyses were performed using PAST software (Hammer *et al.* 2001).

Results and discussion

We recorded 3.528 epiphytic specimens distributed among 13 families, 48 genera and 164 species (Tab. 1). The monocot group, represented by four families, was the most diverse and contributed 113 species (68.9%), while eudicotyledons were represented by 49 species (29.8%) and magnoliids by 2 species (1.2 %).

The richness recorded in this study can be considered high. The number of epiphytic species recorded exceeds those cited in some studies in locations such as the Venezuelan Amazon (Engwald *et al.* 2000; Nieder *et al.* 2000; Schmit-Neuerburg 2002) and the Colombian Amazon (Vasco 2002; Benavides *et al.* 2006; 2011). However, the epiphytic richness of the Urucu area was lower than that recorded in other forests in the extra-Brazilian Amazon (Baslev *et al.* 1998; Arévalo & Betáncur 2004; Kreft *et al.* 2004; Benavides *et al.* 2005), as well as studies in the Brazilian Amazon (Ribeiro *et al.* 1999). The different methods used to quantify epiphytic flora, such as the size variation in the sample areas, the inclusion or exclusion of some epiphytic taxa, or differences in the criteria used to define

Table 1. Estimates of the abundance of epiphytic species sampled in the terra firme forest in the Urucu River basin, central Amazônia, Brazil.

Family	AD	Npi	Spi	RFi	RFj	IVe
Epiphytic species						
Araceae						
<i>Alloschemone inopinata</i> Bogner & P.C. Boyce	20	15	12	0.75	0.77	0.76
<i>Alloschemone occidentalis</i> (Poepp.) Engl. & K. Krause	92	79	61	3.97	3.91	3.94
<i>Anthurium bonplandii</i> G.S. Bunting	52	46	36	2.31	2.31	2.31
<i>Anthurium clavigerum</i> Poepp.	1	1	1	0.05	0.06	0.06
<i>Anthurium eminens</i> Schott	44	41	35	2.06	2.24	2.15
<i>Anthurium gracile</i> Croat	17	14	14	0.70	0.90	0.80
<i>Anthurium moonenii</i> Croat	3	3	3	0.15	0.19	0.17
<i>Anthurium trinervium</i> Kunth.	1	1	1	0.05	0.06	0.06
<i>Anthurium trisectum</i> Sodino	2	1	1	0.05	0.06	0.06
<i>Heteropsis croatii</i> M.L. Soares & Mayo	1	1	1	0.05	0.06	0.06
<i>Heteropsis flexuosa</i> (Kunth) G.S. Bunting	36	34	32	1.71	2.05	1.88
<i>Heteropsis macrophylla</i> A.C. Sm.	1	1	1	0.05	0.06	0.06
<i>Heteropsis oblongifolia</i> Kunth	17	16	15	0.80	0.96	0.88
<i>Heteropsis peruviana</i> K. Krause	13	13	12	0.65	0.77	0.71
<i>Heteropsis robusta</i> (Bunting) M.L. Soares	2	2	2	0.10	0.13	0.11
<i>Heteropsis spruceana</i> Schott	1	1	1	0.05	0.06	0.06
<i>Heteropsis steyermarkii</i> G.S. Bunting	9	8	7	0.40	0.45	0.43
<i>Heteropsis tenuispadix</i> G.S. Bunting	13	13	13	0.65	0.83	0.74
<i>Monstera adansonii</i> var. <i>klotzschiana</i> (Schott) Madison	1	1	1	0.05	0.06	0.06
<i>Monstera adansonii</i> Schott	6	6	6	0.30	0.38	0.34
<i>Monstera dubia</i> (Kunth) Engl. & K. Krause	2	2	2	0.10	0.13	0.11
<i>Monstera obliqua</i> Miq.	6	4	4	0.20	0.26	0.23
<i>Monstera spruceana</i> (Schott) Engl.	2	2	1	0.10	0.06	0.08
<i>Monstera</i> sp. 1	1	1	1	0.05	0.06	0.06
<i>Monstera</i> sp. 2	1	1	1	0.05	0.06	0.06
<i>Philodendron applanatum</i> G.M. Barroso	8	7	7	0.35	0.45	0.40
<i>Philodendron asplundii</i> Croat & M.L. Soares	58	42	35	2.11	2.24	2.18
<i>Philodendron barrosoanum</i> Bunting	4	4	4	0.20	0.26	0.23
<i>Philodendron billietiae</i> Croat	2	2	2	0.10	0.13	0.11
<i>Philodendron brevispathum</i> Schott	1	1	1	0.05	0.06	0.06
<i>Philodendron burle-marxii</i> G.M. Barroso	6	6	6	0.30	0.38	0.34
<i>Philodendron callosum</i> K. Krause	3	3	3	0.15	0.19	0.17
<i>Philodendron campii</i> Croat.	20	18	18	0.90	1.15	1.03
<i>Philodendron cataniapoense</i> G.S. Bunting	2	2	2	0.10	0.13	0.11
<i>Philodendron elaphoglossoides</i> Schott	8	7	7	0.35	0.45	0.40
<i>Philodendron fragrantissimum</i> (Hook.) G. Don.	58	51	43	2.56	2.76	2.66
<i>Philodendron heterophyllum</i> Poeppig	8	7	5	0.35	0.32	0.34

Continues

Table 1. Continuation.

Family	AD	Npi	Spi	RFi	RFj	IVe
Epiphytic species						
<i>Philodendron hopkinsianum</i> M. L. Soares & S. Mayo	105	74	51	3.71	3.27	3.49
<i>Philodendron hylaeae</i> Bunting	33	32	25	1.61	1.60	1.60
<i>Philodendron insigne</i> Schott	14	13	11	0.65	0.71	0.68
<i>Philodendron linnaei</i> Kunth	794	291	173	14.61	11.09	12.85
<i>Philodendron maximum</i> K.Krause	7	5	5	0.25	0.32	0.29
<i>Philodendron megalophyllum</i> Schott	6	6	6	0.30	0.38	0.34
<i>Philodendron ornatum</i> Schott	1	1	1	0.05	0.06	0.06
<i>Philodendron pedatum</i> (W. J. Hooker) Kunth	10	10	10	0.50	0.64	0.57
<i>Philodendron placidum</i> Schott.	1	1	1	0.05	0.06	0.06
<i>Philodendron platypodum</i> Gleason	4	4	4	0.20	0.26	0.23
<i>Philodendron pulchrum</i> G.M. Barroso	14	9	9	0.45	0.58	0.51
<i>Philodendron rudgeanum</i> Schott	9	8	8	0.40	0.51	0.46
<i>Philodendron solimoesense</i> A. C. Smith	2	2	2	0.10	0.13	0.11
<i>Philodendron sphalerum</i> Schott	2	2	2	0.10	0.13	0.11
<i>Philodendron surinamense</i> (Miq.) Engl.	7	6	6	0.30	0.38	0.34
<i>Philodendron tortum</i> M.L. Soares & Mayo	50	40	38	2.01	2.44	2.22
<i>Philodendron toshibai</i> M.L. Soares & Mayo	71	59	43	2.96	2.76	2.86
<i>Philodendron venezuelense</i> G.S. Bunting	4	3	2	0.15	0.13	0.14
<i>Philodendron wittianum</i> Engler	65	51	41	2.56	2.63	2.59
<i>Philodendron</i> sp. 1	12	10	10	0.50	0.64	0.57
<i>Philodendron</i> sp. 2	2	2	2	0.10	0.13	0.11
<i>Philodendron</i> sp. 3	1	1	1	0.05	0.06	0.06
<i>Philodendron</i> sp. 4	18	17	15	0.85	0.96	0.91
<i>Philodendron</i> sp. 5	2	2	2	0.10	0.13	0.11
<i>Philodendron</i> sp. 6	20	14	14	0.70	0.90	0.80
<i>Philodendron</i> sp. 7	1	1	1	0.05	0.06	0.06
<i>Philodendron</i> sp. 8 (sub-gênero <i>Pteromischum</i>)	3	2	2	0.10	0.13	0.11
<i>Rhodospatha oblongata</i> Poepp.	10	10	10	0.50	0.64	0.57
<i>Rhodospatha venosa</i> Gleason	6	5	4	0.25	0.26	0.25
<i>Rhodospatha</i> sp.	2	1	1	0.05	0.06	0.06
<i>Stenospermation multiovulatum</i> (Engl.) N.E. Br.	3	2	2	0.10	0.13	0.11
<i>Stenospermation spruceanum</i> Schott	31	27	24	1.36	1.54	1.45
<i>Syngonium podophyllum</i> Schott	2	2	2	0.10	0.13	0.11
Bromeliaceae						
<i>Aechmea bromeliifolia</i> (Rudge) Baker	1	1	1	0.05	0.06	0.06
<i>Aechmea contracta</i> (Mart. ex Schult.f.)	15	14	13	0.70	0.83	0.77
<i>Aechmea corymbosa</i> (Mart. ex Schult. & Schult. f.) Mez	15	11	11	0.55	0.71	0.63
<i>Aechmea mertensii</i> (G. Mey.) Schult. & Schult. f.	5	5	5	0.25	0.32	0.29

Continues

Table 1. Continuation.

Family	AD	Npi	Spi	RFi	RFj	IVe
Epiphytic species						
<i>Aechmea</i> sp. 1	1	1	1	0.05	0.06	0.06
<i>Aechmea</i> sp. 2	5	4	4	0.20	0.26	0.23
<i>Aechmea</i> sp. 3	1	1	1	0.05	0.06	0.06
<i>Araecococus micranthus</i> Brongn.	5	4	4	0.20	0.26	0.23
<i>Araecococus parviflorus</i> (Mart. ex Schult. f.) Lindm.	3	3	3	0.15	0.19	0.17
<i>Billbergia venezuelana</i> (Mez)	2	2	2	0.10	0.13	0.11
<i>Billbergia</i> sp. 1	2	2	2	0.10	0.13	0.11
<i>Billbergia</i> sp. 2	1	1	1	0.05	0.06	0.06
<i>Guzmania lingulata</i> (L.) Mez	1083	337	201	16.92	12.88	14.90
<i>Guzmania vittata</i> (Mart. ex Schult.f.) Mez	9	1	7	0.05	0.45	0.25
<i>Neoregelia eleutheropetala</i> (Ule) L.B.Sm. var. <i>eleutheropetala</i>	3	3	3	0.15	0.19	0.17
<i>Vriesea splitgerberi</i> (Mez) L.B.Sm & Pittendr.	1	1	1	0.05	0.06	0.06
Clusiaceae						
<i>Clusia amazonica</i> Planch. & Triana	4	4	4	0.20	0.26	0.23
<i>Clusia insignis</i> Mart.	2	2	2	0.10	0.13	0.11
<i>Clusia panapanari</i> (Aubl.) Choisy	3	3	3	0.15	0.19	0.17
<i>Clusia penduliflora</i> Engl.	38	35	29	1.76	1.86	1.81
<i>Clusia renggerioides</i> Planch. & Triana	2	2	2	0.10	0.13	0.11
<i>Clusia scrobiculata</i> Mart.	4	4	4	0.20	0.26	0.23
<i>Clusia spathulaefolia</i> Engl.	7	7	7	0.35	0.45	0.40
<i>Clusia</i> sp. 1	9	9	8	0.45	0.51	0.48
<i>Clusia</i> sp. 2	1	1	1	0.05	0.06	0.06
<i>Clusia</i> sp. 3	1	1	1	0.05	0.06	0.06
<i>Clusia</i> sp. 4	1	1	1	0.05	0.06	0.06
<i>Clusia</i> sp. 5	4	4	4	0.20	0.26	0.23
<i>Clusia</i> sp. 6	1	1	1	0.05	0.06	0.06
<i>Oedematopus obovatus</i> Spruce ex Planch.	4	4	4	0.20	0.26	0.23
<i>Oedematopus octandrus</i> (Poepp. & Endl.) Planch & Triana	4	4	4	0.20	0.26	0.23
Cyclanthaceae						
<i>Asplundia vaupesiana</i> Harl.	87	67	54	3.36	3.46	3.41
<i>Asplundia xiphophylla</i> Harling	41	30	25	1.51	1.60	1.55
<i>Asplundia</i> sp. 1	2	2	2	0.10	0.13	0.11
<i>Asplundia</i> sp. 2	1	1	1	0.05	0.06	0.06
<i>Evodianthus funifer</i> (Point) Lindm.	38	30	23	1.51	1.47	1.49
<i>Ludovia lancifolia</i> Brong	44	38	33	1.91	2.12	2.01
<i>Thoracocarpus bissectus</i> (Vell.) Harl.	1	1	1	0.05	0.06	0.06
Gesneriaceae						
<i>Codonanthe calcarata</i> (Miq.) Hanst.	12	8	7	0.40	0.45	0.43

Continues

Table 1. Continuation.

Family	AD	Npi	Spi	RFi	RFj	IVe
Epiphytic species						
<i>Codonanthe crassifolia</i> (H. Focke) C.V. Morton	56	22	22	1.10	1.41	1.26
<i>Codonanthe</i> sp.	5	4	4	0.20	0.26	0.23
<i>Codonanthopsis hubneri</i> Mansf.	11	6	6	0.30	0.38	0.34
<i>Codonanthopsis ulei</i> Mansfeld	12	11	11	0.55	0.71	0.63
<i>Codonanthopsis</i> sp.	1	1	1	0.05	0.06	0.06
<i>Gesneriaceae</i> 1	1	1	1	0.05	0.06	0.06
Marcgraviaceae						
<i>Norantea guianensis</i> Aubl.	1	1	1	0.05	0.06	0.06
Melastomataceae						
<i>Adelobotrys marginata</i> Brade	1	1	1	0.05	0.06	0.06
<i>Bellucia grossularioides</i> (L.) Triana	2	2	2	0.10	0.13	0.11
<i>Clidemia epibaterium</i> DC.	13	11	10	0.55	0.64	0.60
<i>Clidemia</i> sp. 1	2	2	1	0.10	0.06	0.08
<i>Clidemia</i> sp. 2	5	3	2	0.15	0.13	0.14
<i>Henriettella caudata</i> Gleason	1	1	1	0.05	0.06	0.06
<i>Leandra candelabrum</i> (J.F.Macbr.) Wurdack	9	8	8	0.40	0.51	0.46
<i>Loreya spruceana</i> Benth. ex Triana	1	1	1	0.05	0.06	0.06
<i>Miconia argyrophylla</i> DC.	3	2	2	0.10	0.13	0.11
<i>Miconia biglandulosa</i> Gleason	3	2	2	0.10	0.13	0.11
<i>Miconia duckei</i> Gleason	1	1	1	0.05	0.06	0.06
<i>Miconia regelii</i> Cogn.	1	1	1	0.05	0.06	0.06
<i>Miconia splendens</i> (Sw.) Griseb.	3	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 1	1	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 2	3	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 3	1	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 4	1	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 5	1	1	1	0.05	0.06	0.06
<i>Miconia</i> sp. 6	1	1	1	0.05	0.06	0.06
<i>Melastomataceae</i> 1	1	1	1	0.05	0.06	0.06
Moraceae						
<i>Ficus gomelleira</i> Kunth & Bouché	2	2	2	0.10	0.13	0.11
<i>Ficus krukovii</i> Standl.	1	1	1	0.05	0.06	0.06
<i>Ficus paraensis</i> (Miq.) Miq.	1	1	1	0.05	0.06	0.06
Orchidaceae						
<i>Acacallis fimbriata</i> (Rchb.f.) Schltr.	5	5	5	0.25	0.32	0.29
<i>Batemannia colleyi</i> Lindl.	19	17	15	0.85	0.96	0.91
<i>Catasetum cristatum</i> Lindl.	3	2	2	0.10	0.13	0.11
<i>Catasetum</i> sp.	1	1	1	0.05	0.06	0.06

Continues

Table 1. Continuation.

Family	AD	Npi	Spi	RFi	RFj	IVe
Epiphytic species						
<i>Maxillaria amazonica</i> Schltr.	6	5	5	0.25	0.32	0.29
<i>Maxillaria parkeri</i> Hook	2	2	2	0.10	0.13	0.11
<i>Maxillaria perparva</i> Garay & Dunsterv	6	3	3	0.15	0.19	0.17
<i>Maxillaria tenuis</i> Schweinf	1	1	1	0.05	0.06	0.06
<i>Octomeria brevifolia</i> Cogn.	4	3	3	0.15	0.19	0.17
<i>Octomeria grandiflora</i> Lindl.	1	1	1	0.05	0.06	0.06
<i>Ornithidium parviflorum</i> (Poepp. & Endl.) Rchb.f.	1	1	1	0.05	0.06	0.06
<i>Paphinia grandiflora</i> Barb. Rodr.	2	1	1	0.05	0.06	0.06
<i>Polycycnis vittata</i> (Lindl.) Rchb.f.	11	5	3	0.25	0.19	0.22
<i>Polystachya estrellensis</i> Rchb.f.	1	1	1	0.05	0.06	0.06
<i>Rudolfiella aurantiaca</i> (Lindl.) Hoehne	7	5	5	0.25	0.32	0.29
<i>Sobralia fimbriata</i> Poepp. & Endl.	1	1	1	0.05	0.06	0.06
<i>Sobralia macrophylla</i> Rchb. f.	2	2	2	0.10	0.13	0.11
<i>Stanhopea grandiflora</i> (Lodd.) Lindl.	1	1	1	0.05	0.06	0.06
<i>Vanilla palmarum</i> Lindl.	1	11	1	0.55	0.06	0.31
Piperaceae						
<i>Piper dactylostigmum</i> Yuncker	1	1	1	0.05	0.06	0.06
<i>Piper paraense</i> (Miq.) C.DC.	1	1	1	0.05	0.06	0.06
Rubiaceae						
<i>Hillia ulei</i> K.Krause	1	1	1	0.05	0.06	0.06
Solanaceae						
<i>Markea camponoti</i> Ducke	2	2	2	0.10	0.13	0.11
<i>Markea ulei</i> (Dammer) Cuatrec.	3	3	3	0.15	0.19	0.17
Urticaceae						
<i>Coussapoa latifolia</i> Aubl.	1	1	1	0.05	0.06	0.06
Undetermined	2	2	1	0.10	0.06	0.08
Total	3528	1992	1560	100	100	100

AD – absolute density; Npi – Number of phorophytic individuals occupied by epiphytic species i; Spi – number of phorophytic species occupied by epiphytic species i; RFi – relative frequency on phorophytic individuals; RFj – relative frequency of specific phorophytes; IVe – epiphytic importance value.

the epiphytic appearance may be related to the differences observed.

The families with highest species richness were Araceae, with 70 species (42.6%), followed by Melastomataceae, Orchidaceae, Bromeliaceae and Clusiaceae, which together contain 85.4% of all species sampled (Fig. 2). The most abundant families were Araceae, Bromeliaceae and Cyclanthaceae, which contained 90.7% of all specimens sampled (Tab. 2).

The most prominent families in the epiphytic community were Araceae and Bromeliaceae, which contributed 55.9% of the total familial importance (Tab. 2). Araceae

stood out in the three phytosociological estimators, which demonstrates the capacity of the family to adapt to the conditions in the study area and denotes its importance to the phytophysiognomic formation of the forest. In a study in the Colombian Amazon, Arévalo and Betáncur (2004) also reported higher FIV for this family. However, the authors obtained a less expressive value (74.21). According Ibish *et al.* (1996), the high richness and abundance of Araceae is typical in lowland forests.

The relevance of Araceae to the epiphytic community recorded in the present study confirms the results obtained by other authors in different regions of the extra-Brazilian

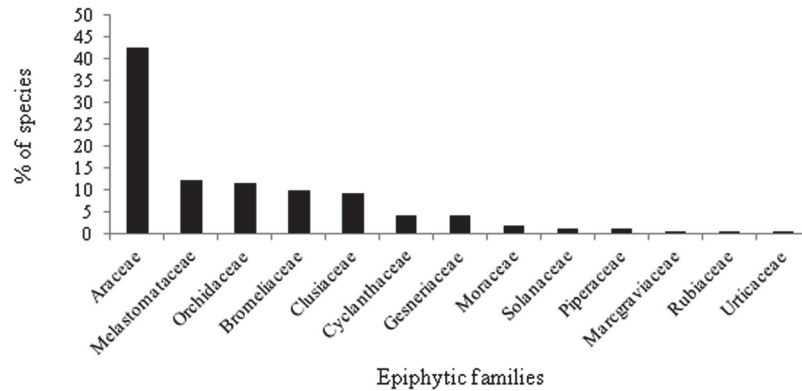


Figure 2. Overall percentage of the number of epiphytic species recorded per family in the terra firme forest of the Urucu River basin, central Amazônia, Brazil.

Table 2. Representativeness of epiphytic families registered in a terra firme forest in the Urucu River basin, central Amazônia, Brazil.

Family	Genera	Species	Individuals	DRel	DIVRel	FRel	FIV
	n	n	n	(%)	(%)	(%)	
Araceae	8	70	1834	52.01	42.68	16.44	111.13
Bromeliaceae	6	16	1152	32.67	9.76	14.38	56.81
Cyclanthaceae	4	7	214	6.07	4.27	15.07	25.41
Orchidaceae	13	19	75	2.13	11.59	11.64	25.36
Clusiaceae	2	15	85	2.41	9.15	12.33	23.89
Melastomataceae	7	20	54	1.53	12.2	8.22	21.95
Gesneriaceae	2	7	98	2.78	4.27	13.7	20.75
Solanaceae	1	2	5	0.14	1.22	2.74	4.10
Moraceae	1	3	4	0.11	1.83	2.05	4.10
Piperaceae	1	2	2	0.06	1.22	1.37	2.65
Marcgraviaceae	1	1	1	0.03	0.61	0.68	1.32
Rubiaceae	1	1	1	0.03	0.61	0.68	1.32
Urticaceae	1	1	1	0.03	0.61	0.68	1.32
Undetermined	-	-	2	-	-	-	-
Total	48	164	3528	100	100	100	300

FIV – family importance value; DRel – relative density; DIVRel – relative diversity; FRel – relative frequency.

Amazon, where this family contributed the greatest diversity of species (Balslev *et al.* 1998; Rudas & Pietro 1998; Vasco 2002; Arévalo & Betancur 2004; Benavides *et al.* 2005; 2006; 2011), as well as a study in the Brazilian Amazon (Pos & Slegers 2010). The high abundance of Araceae recorded in the present survey is also similar to results found in studies in the Venezuelan Amazon, where this family contributed 47% of specimens sampled (Nieder *et al.* 2000), which represented 43.3% of total abundance (Engwald *et al.* 2000) and in the Colombian Amazon, where Araceae contributed 58.8% of specimens and 76% of the epiphytic biomass of the sampled site (Benavides *et al.* 2006).

Araceae is reported as one of the most important families of neotropical epiphytic flora, considering that its wealth is

concentrated in the tropics (Gentry & Dodson 1987b; Mayo *et al.* 1997). For Brazil, approximately 460 Araceae species are recognized in 35 genera (Coelho *et al.* 2010). On the other hand, in the Atlantic Forest region in southern and southeastern Brazil, Araceae occupies the sixth position among the most diverse families and on average represents only 4% of the richness in the 62 surveys of epiphytic flora analyzed by Kersten (2010). This family demonstrates incredibly high phenotypic plasticity and ability to grow under adverse conditions (Leimbeck & Balslev 2001; Soares & Jardim-Lima 2005; Coelho *et al.* 2009). Therefore, a variety of morphological and physiological adaptations used as survival strategies, as well as the ability to colonize different strata in the forest and propagate vegetatively may be some

of the factors responsible for the high diversity of species recorded for this family in the present study.

Bromeliaceae showed the second greatest FIV and stood out for its high density, which confirms results found by Alzate *et al.* (2001) in a study in Colombia, where it was the most abundant family. The richness of Bromeliaceae in the study area was high compared to other studies of epiphytic flora in the South and Southeast of Brazil (Giongo & Waechter 2004; Alves *et al.* 2008; Buzzato *et al.* 2008; Kersten & Kuniyoshi 2009; Geraldino *et al.* 2010). However, higher values were cited in Brazil by Neto *et al.* (2009), Reis & Fontoura (2009), Fontoura & Santos (2010) and by Blum *et al.* (2011).

The richness of bromeliads was also higher than previously reported for the Brazilian Amazon in studies of terra firme forests (Ribeiro *et al.* 1999) and floodplain forests (Quaresma & Jardim 2012). On the other hand, the family was not even recorded in studies in a terra firme forest in the Brazilian state of Pará (Pos & Slegers 2010), nor in a savanna in Humaitá, Brazil (Gottsberger & Morawetz 1993). The high occurrence of Bromeliaceae in surveys of the epiphytic community is expected for the Atlantic forest, as this is one of the main centers of diversity of this family (Wanderley *et al.* 2007), where Bromeliaceae is often cited as the second most diverse (Kersten 2010). In the Brazilian Amazon, the bromeliads are found more frequently in floodplains (baixios), low whitesand forests (campinas), high whitesand forests (campinaranas) and seasonally blackwater-flooded Amazon forests (igapó) (Sousa & Wanderley 2007). Nonetheless, in the present study the family was well represented in number of species and individuals in all environments studied.

Melastomataceae, surprisingly, was the second most diverse family, although classified in sixth position with regard to FIV, as it was represented by only a few individual specimens. Despite the presence of common accidental epiphytes belonging to various families in the inventories of epiphytic flora, there are few studies that quantify and report the occurrence of species in this taxon (Barthlott *et al.* 2001; Arévalo & Betancur 2004; Kelly *et al.* 2004; Zotz & Schultz 2008), be those specimens behaving as epiphytes, hemiepiphytes, accidental epiphytes or facultative epiphytes. Furthermore, in many regions, it is uncommon for members of this family to present epiphytism. Nonetheless, the diversity of the family recorded in the present study is similar to results found by Benavides *et al.* (2005) in the Colombian Amazon, where the authors recorded 16 species and 418 individuals, classifying them as holoepiphytes or hemiepiphytes. However, in the present study specimens from Melastomataceae were classified as accidental or facultative epiphytes, as these occurrences can be dispersive accidents with successful germination, and thus, merely examples of colonization of an epiphytic habitat, as these plants are usually terrestrial (trees, shrubs and lianas).

Orchidaceae was recorded as the third most diverse fam-

ily and ranked in fourth position in terms of FIV, a result that contradicts expectations and contrasts with the standard of most of the epiphytic flora inventories in Neotropical regions, since it is often cited in the first position (Kreft *et al.* 2004; Kelly *et al.* 2004; Kuper *et al.* 2004; Kromer *et al.* 2005; Zotz & Schultz 2008). In the subtropical forests of Brazil, Orchidaceae is also cited as the most diverse family (Alves *et al.* 2008; Neto *et al.* 2009; Kersten 2010; Blum *et al.* 2011). However, despite not having the highest species richness in the present study, Orchidaceae showed the most generic diversity. This low species richness may be related to the fact that, in the Amazon, orchids are more common along river banks, in seasonally flooded whitewater forests (várzea), in the seasonally blackwater-flooded forests (igapó) and, mainly, in low whitesand forests (campinas) (Silva *et al.* 1995), whereas in terra firme forests the lowest number of Orchidaceae species occur.

The Cyclanthaceae species stood out in this study for their abundance and frequency. The family was ranked third with regard to FIV and was also reported in lowland forests in the Neotropics (Kreft *et al.* 2004) and in the Colombian Amazon, where it was the second most abundant (Benavides *et al.* 2006). The species with the highest density and widest distribution in the area was *Asplundia vaupesiana* Harling (87 ind.), a hemiepiphyte whose distribution is restricted to the state of Amazonas (Leal 2012).

The most diverse genera were *Philodendron*, *Clusia*, *Miconia* and *Heteropsis*, which together accounted for 43.9% of total species (Fig. 3). The most abundant genera were *Philodendron*, *Guzmania*, *Asplundia*, *Anthurium* and *Alloschemone*, which contained 81.3% of all epiphytes sampled.

Philodendron had the highest generic diversity and abundance in the present study, a result that is consistent with those obtained by Nieder *et al.* (2000) and Benavides *et al.* (2005; 2006; 2011). The representativeness of *Philodendron* is also cited in other Brazilian forest formations. In the survey by Neto *et al.* (2009), which included 24 studies carried out in the Brazilian Southeast, *Philodendron* was among the five most diverse genus. It is an exclusively Neotropical genus and approximately 500 species have been described (Mayo 1989). According to Sakuragui (2001), there are approximately 70 species in Brazil and the regions with the highest diversity are within the states of Rio de Janeiro, Espírito Santo and Amazonas.

The general pattern of distribution of epiphytic species in tropical forests is one of many individuals of a few species and a few individuals of many species (Richards 1996). According to Rudolph *et al.* (1998), Smith-Neuerburg (2002), Kuper *et al.* (2004) and Benavides *et al.* (2011), the epiphytic population is small and well distributed, since the majority of species has a low abundance and contributes less than 1% of individuals sampled. Often, more than 25% of species in a given area are represented by fewer than five individuals. This pattern was confirmed in the present study: although some species showed high abundance, 59.1% were repre-

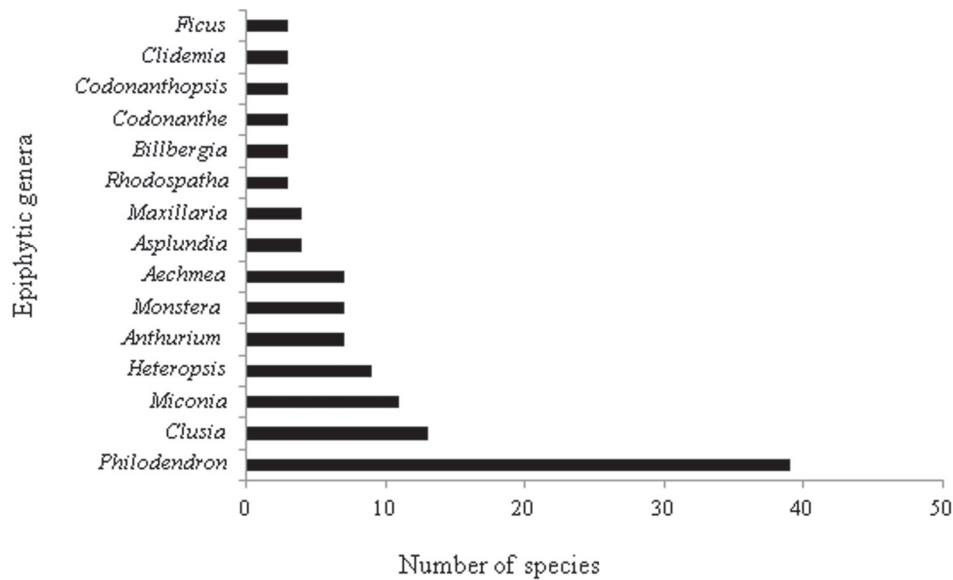


Figure 3. Number of species from the 15 most diverse epiphytic genera recorded in the terra firme forest of the Urucu basin, central Amazônia, Brazil.

sented by fewer than five individuals (97 species) and 32.9% were represented by only one individual (54 species).

Considering the 15 species presenting the greatest sociological importance according to the IVE calculation, 11 belong to Araceae (Tab 1.), which demonstrates their substantial contribution in the diversity of epiphytic flora in the region. The species that most stood out with regard to IVE, which together make up 27.7% of the total index, were *Guzmania lingulata* (L.) Mez. (Bromeliaceae) with 14.9% and *Philodendron linnaei* Kunth. (Araceae) with 12.8%. These figures show that the two species are well distributed in the area, possibly due to their efficiency in reproduction and dispersion as well as survival strategies specific to each. This indicates a high colonization capacity in the various environments, strata and species of phorophytes available in the forest.

The representativeness of *G. lingulata* was also observed with the bromeliads of Combu-Pará Island (Quaresma & Jardim 2012), where it was also the most abundant, representing 51.3% of specimens. In Brazil, its geographical distribution is restricted to the states of the North and Northeast (Forzza *et al.* 2012). The high abundance of *P. linnaei* corroborates the findings from a study by Arévalo & Betancur (2004), who reported it as the second most abundant species, and the study of Benavides *et al.* (2005), where it appears among the five highest densities.

The predominant ecological category in the study area was the hemiepiphytic growth habit. This was represented by 93 species belonging mainly to families Araceae, Cyclanthaceae and Clusiaceae, which make up 56.7% of all individuals recorded here. The holoepiphytes were represented by 50 species (30.5%), mainly occurring in families Orchi-

daceae, Bromeliaceae and Gesneriaceae. A similar result was reported by Benavides *et al.* (2006), where hemiepiphytes accounted for 52.4%. However, this result differs from the standard cited by most studies that address epiphytism both in the extra-Brazilian Amazon (Engwald *et al.* 2000; Nieder *et al.* 2000; Benavides *et al.* 2011) and in different forest types in Brazil (Kersten & Kuniyoshi 2009; Kersten *et al.* 2009b, Neto *et al.* 2009; Blum *et al.* 2011), where these authors reported the predominance of characteristic holoepiphytes. In addition to these growth habits, there also occurred accidental and facultative holoepiphytes. This habit represented 12.8% of total species and was recorded in the family Melastomataceae and in a species of Moraceae (*Ficus gomelleira* Kunth & C.D. Bouché).

The distribution of the epiphytic community occurred over 727 phorophytic individuals from 40 families, 123 genera and 324 species. The greatest diversity of species used as phorophytes was recorded in the families Fabaceae (14.8%), Sapotaceae (14.5%), Chrysobalanaceae (9.8%) and Lecythidaceae (8.0%), which comprised 47.2% of total species. Furthermore, these were the most abundant and contained 55.1% of the total phorophytic individuals recorded (Tab. 3).

The representativeness of these families as hosts is understandable, since these are the most diverse and abundant families according to various floristic surveys in the Amazon, although these studies do not associate them with the epiphytic community (Amaral *et al.* 2000; Duque *et al.* 2003; Oliveira *et al.* 2008; Silva *et al.* 2008). This result may indicate that epiphytes occurred more frequently on these phorophytes because these species possess a wide distribution, as well as high density in terra firme forests

in the Amazon and, therefore, the majority of available species and individuals in this forest may be conducive to epiphytic colonization.

The most diverse phorophytic genera were *Pouteria* (Sapotaceae), *Licania* (Chrysobalanaceae) and *Eschweilera* (Lecythidaceae) with 27, 26 and 19 species, respectively. These genera were also the most abundant, albeit in reverse order (Tab. 3).

As expected, the most abundant phorophytic species in this study accumulated the highest absolute richness of epiphytes, among which stood out *Eschweilera wachenheimii* (Benoiist) Sandwith (Lecythidaceae), registered 57 times as support, which hosted 38 species and 189 epiphytic individuals. A similar result was obtained by Hernández-Rosas (2001) when studying the occupation of phorophytes by epiphytes in Venezuela, where a species of the same genus was also the most used as a phorophyte. In this classification sequence, species that stood out were *Oenocarpus bataua* Mart. (Arecaceae) with 18 repetitions and host of 35 epiphytic species and *Heterostemon ellipticus* Mart. ex Benth. (Fabaceae), with 17 and 31 species, respectively.

Generally, the epiphytic species and individuals uniformly colonized host trees. Of the total phorophytic species sampled, 91.3% presented a ratio of richness of epiphytes to abundance of phorophytes ≤ 5.0 (296 species) and, also regarding the calculation of epiphytic and phorophytic abundance, 58.6% of phorophytes (190 species) presented a ratio ≤ 5.0 . This indicates that these phorophytes were used as substrates by a maximum of five species and by up to five epiphytic individuals. Furthermore, 22.2% of host species (72 species) were substrates for only one epiphytic

species (ratio = 1.0). However, 8.6% of phorophytic species presented a ratio ≥ 5.0 (28 species) and represented the main concentration of epiphytic richness, namely: *Guarea convergens* T.D. Penn. (Meliaceae), *Vantanea parviflora* Lam. (Humiriaceae) and *Brosimum* sp. (Moraceae). Finally, 9.2% of phorophytic species (30 species) were abundantly colonized and showed epiphytic abundance ratios ≥ 10.0 .

An individual of species *G. convergens* hosted the highest species richness (18 species) and abundance of epiphytes (73 ind.). However, higher values have been reported for the Neotropics (Kreft *et al.* 2004; Kromer *et al.*, 2005; Zotz & Schultz 2008), the record being set by Schuettelpelz & Trapnell (2006) in Costa Rica, who recorded 126 species occurring on a *Pseudolmedia mollis* Standl. (Moraceae).

The epiphytic concentration on some host species may be linked to certain specific individual characteristics not evaluated in this study (type of shell, architecture, inclination, etc.) and that may facilitate or hinder epiphytic establishment. More detailed studies on the influence of these variables on epiphytic colonization are necessary to better understand the relationship between epiphytes and their phorophytes.

Many studies conducted in the Neotropics mention that the canopy is the area of greatest epiphytic richness and abundance (Rudolph *et al.* 1998; Kelly *et al.* 2004; Schuettelpelz & Trapnell 2006; Pos & Slegers 2010). According to these authors, the high species richness in the canopy can be attributed to the greater diversity of substrates for attachment (bifurcations and different lighting conditions in the branches). However, the results obtained in the current study suggest greater epiphytic richness and abundance on

Table 3. Representativeness of the main phorophytic families recorded in the terra firme forest in the Urucu River basin, central Amazônia, Brazil.

Family	Totals		Genera by diversity		Genera by abundance	
	n of species	n of individuals	Genus	n of species	Genus	n of individuals
Fabaceae	48	85	Pouteria	27	Eschweilera	121
Sapotaceae	47	99	Licania	26	Licania	73
Chrysobalanaceae	32	86	Eschweilera	19	Pouteria	55
Lecythidaceae	26	131	Iryanthera	13	Iryanthera	30
Lauraceae	19	26	Micropholis	10	Micropholis	25
Myristicaceae	17	40	Inga	9	Oenocarpus	19
Moraceae	16	33	Protium	8	Brosimum	18
Burseraceae	13	20	Ocotea	8	Heterostemon	17
Annonaceae	8	15	Sloanea	7	Sclerolobium	14
Myrtaceae	8	8	Sclerolobium	7	Protium	13
Arecaceae	7	29	Swartzia	6	Ocotea	13
Elaeocarpaceae	7	9	Brosimum	6	Chrysophyllum	13
Malvaceae	7	13	Eugenia	6	Senefeldera	12
Euphorbiaceae	6	31	Chrysophyllum	5	Swartzia	11

phorophytic trunks (148 species, 3.152 ind.) than in their canopies (85 species, 376 ind.). Furthermore, in the analysis of the relative frequency of the species in the two segments, 57.9% were recorded on trunks and 42.1% in the canopy.

Most epiphytic species proved to be specialists regarding occurrence in the two main phorophytic segments. Of the total species recorded, 59.1% (97 species) were unique to one of these segments, while 40.8% were generalists and colonized both segments (67 species). Most exclusive species are restricted to the trunk, representing 83.5% (81 species). Among these, the ones with the highest number of exclusive individuals in this segment were: *Alloschemone occidentalis* (Poepp.) Engl. & K. Krause (Araceae), *Evodianthus funifer* (Poir.) Lindl. (Cyclanthaceae), *Alloschemone inopinata* Bogner & P.C. Boyce (Araceae) and *Philodendron* sp.6 (Araceae). The species that had the highest frequency on trunks were *Guzmania lingulata* (L.) Mez. (Bromeliaceae) and *Philodendron insigne* (Araceae). Among the unique species of the canopy, the most abundant were *Codonanthe* sp. 1 (Gesneriaceae) and *Clusia amazonica* Planch. & Triana (Clusiaceae).

According to Benzing (1990), the epiphytic preference for certain regions of phorophyte is related to factors such as the search for moisture, light and substrate conditions. The preferential distribution of most epiphytes (95 species) on the trunks of their phorophytes, regardless of their growth habit, showed a possible preference of these species for the forest understory, where climatic conditions are stable and the humidity is higher when compared to the canopy at the upper ranges of height.

The floodplain environment proved most favorable to epiphytism, where 84.1% of species and 48.2% of individuals sampled were found. This was also the environment most colonized by those species for which only one individual was recorded in the study area (64.8%) and was the environment where there was the greatest occurrence of unique species (57 species). Water availability is a limiting factor for the establishment and survival of epiphytes (Padmawathe *et al.* 2004), and during periods of low rainfall the floodplains accumulate more moisture compared to plateaus and hillsides—a fact that may favor epiphytic colonization of these environments.

For the epiphytic community, the floristic diversity (H') was 3.2 and the evenness (J') was 0.64. The H' value can be considered moderate since it reached more than 50% of the maximum predicted variation (zero to 5.0) and was higher than those reported in some studies in Brazil (Waechter 1998; Kersten & Silva 2002; Reis & Fontoura 2009; Kersten & Kuniyoshi 2009; Kersten *et al.* 2009b; Quaresma & Jardim 2012), Colombia (Alzate *et al.* 2001) and Venezuela (Barthlott *et al.* 2001). However, some Brazilian studies have shown higher values (Giongo & Waechter 2004; Kersten *et al.* 2009a; Geraldino *et al.* 2010). In the Urucu River basin, the diversity analysis showed that the epiphytic community contributed significantly to

the abundance and floristic richness of the forest, which supports several authors who have cited epiphytes as an important component for floristic diversity in the Neotropics (Kelly *et al.* 1994; Clarke *et al.* 2001).

Many studies report that the factors that most influence epiphytic diversity are precipitation, the distribution of rainfall throughout the year (Gentry & Dodson 1987a,b; Benzing 1990) and elevation (Kuper *et al.* 2004; Kromer *et al.* 2005). Epiphytic richness reaches its maximum value in Neotropical montane forests at medium elevations (between 1000-1500 m) with average annual rainfall of 4000 mm and little seasonality, where the highest rates of endemism, biomass and epiphytic diversity are concentrated (Kreft *et al.* 2004).

In a study by Nieder *et al.* (2001), the authors state that the centers of diversity for vascular plants in the Neotropics are the Andes, the northwestern Amazon and the Atlantic Forest in Brazil, where epiphytes in abundance and diversity are concentrated. Nieder *et al.* (1999) point out that in the Amazon, epiphytic diversity is concentrated in the “Sub-andean belt”, at elevations of 400-600 m. In a comparative study of 16 inventories of epiphytic flora in the Neotropics, Kreft *et al.* (2004) state that in the northern and central regions of the Amazon the largest percentage of epiphytic flora occurs at elevations of 0-500 m. These authors state that there are significant differences in epiphytic diversity between regions of the Amazon and that these differences are associated with average annual rainfall and its distribution throughout the year. The same authors also postulate that in the Amazon, the number of epiphytic species is strongly influenced by the moisture gradient (the diminished dry season) and by the higher elevation and soil fertility in the western Andes.

The Urucu river basin varies in elevation from 60 m to 70 m and has a very characteristic seasonality. Although the temperature range and annual variation in rainfall are small, the period of least rainfall (June to November) represents 33.9% of the total annual rainfall. The low elevation and the annual cycle of rainfall in this forest may be the factors responsible for the epiphytic richness recorded there. Araceae was the most diverse and abundant family, and the hemiepiphytic growth habit was dominant. This result confirms the expectation stated by Nieder *et al.* (1999), who claim that in the central Amazon, the greatest epiphytic richness of aroids occurs. According to Ibish *et al.* (1996), the peak richness of this family occurs at elevations of 0-500 m. Kreft *et al.* (2004) and Kromer *et al.* (2005) agree with this hypothesis and claim that, unlike other taxa, such as Orchidaceae, whose maximum richness is found between 1500-2000 m, the richness of Araceae decreases at elevations above 1000 m. As for the prevalence of the hemiepiphytic growth habit, this may be related to the fact that Araceae species benefit not only from sexual reproduction, but also vegetative propagation, which leads to greater success in the establishment and colonization of the species.

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