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Physiological diversity and biogeography of vascular epiphytes at Río Changuinola, Panama

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ABSTRACT

The taxonomic composition of the vascular epiphyte flora at the Río Changuinola, Panama, was examined and complemented with an analysis of biogeographic affinities and physiological parameters related to plant water and nutrient relations. In an area of ca. 1000 ha, we found a total of 476 species of vascular epiphytes. This marks a new diversity record among lowland rainforest sites. Species composition was closely related to nearby lowland forest sites but not to montane sites. The floristic similarity with lowland sites decreased with distance and relative position towards the Andes. On basis of isotope discrimination, the proportion of species with Crassulacean Acid Metabolism (CAM) was found to be low compared to other studies, and many of these species showed a rather weak expression of this photosynthetic pathway. This observation and distributional shifts in 15% of the species in the study area towards lower elevations suggest that local water availability is high which in turn is arguably responsible for the high species richness.

Introduction

Vascular epiphytes are a conspicuous component of biological diversity in tropical forests. By definition, epiphytes grow non-parasitically on other plants, preferably trees. Any part from the stem base to the outer twigs of the tree crown can be used as support while the epiphytic flora changes from the inner tree crown to the outer branches (Johansson, 1974). In tropical lowland and premontane rainforests they constitute ca. 10–25% of the local flora (Nieder et al., 2001), whereas in montane rainforests their contribution to local plant diversity can reach 50% (Kelly et al., 1994). They also play a major ecological role for other trophic levels as they provide resources such as food, shelter and breeding sites for a great variety of organisms like amphibians, insects, and spiders (Kitching, 2000).

Given the extent of Neotropical rainforests, our knowledge about the local diversity of vascular epiphytes is still fragmentary. Since the publication of the classic comparison of vascular epiphyte diversity among different neotropical lowland forest sites by Gentry and Dodson (1987), only a few studies have investigated the diversity and composition of local epiphyte communities across different sites (Nieder et al., 1999; Kreft et al., 2004; Küper et al., 2004). This study is an attempt to broaden our understanding of vascular epiphyte community ecology by putting a detailed epiphyte census on the Atlantic side of the Central American Isthmus in a Neotropical context. To date, there are only some 15 thoroughly conducted studies in the primary literature that provide comparable information on the diversity of vascular epiphyte communities in tropical lowland rainforests. These include single censuses, e.g. at Río Caquetá (Benavides et al., 2005), Tiputini Biodiversity Station (Kreft et al., 2004), published local floras, e.g. the Flora of Barro Colorado Island (Croat, 1978), Kaieteur Falls National Park (Kelloff and Funk, 1998) and developing species databases related to important field sites, e.g. La Selva Biological Station (Taylor et al., 2008) and Jatun Sacha Biological Station (Missouri Botanical Garden, 2008). A similar paucity of basic information is true for montane rain forests with their high epiphyte diversity: eight studies that comprise complete local florulas are available to date (e.g. Catling and Lefkovitch, 1989; Bøgh, 1992; Kelly et al., 1994; Acebey and Krömer, 2001). This paucity contrasts sharply with the availability of information on tree communities of tropical lowland forests (e.g. Hubbell, 1979;

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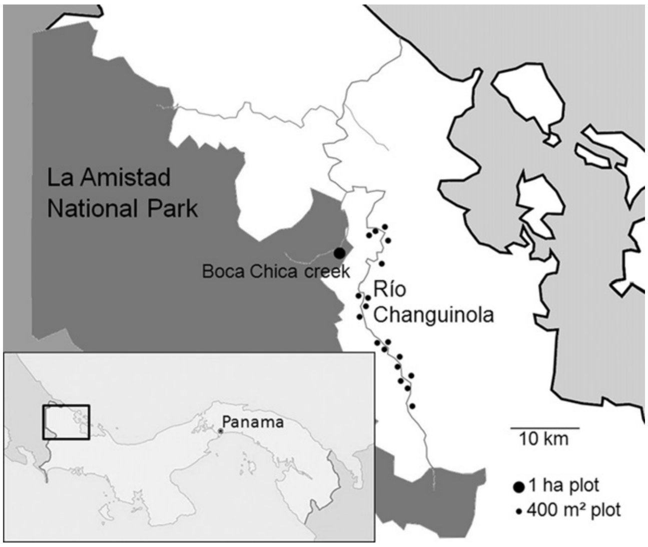

Fig. 1. Location of the study area and within study plots along the Río Changuinola in Western Panama.

Manokaran and LaFrankie, 1990; Sukumar et al., 1992; Condit et al., 2000; Pitman et al., 2001; Pyke et al., 2001), and is at least partly due to access problems: the epiphytic habitat is only accessible with difficulty and thus sampling is rather time-consuming. In addition, local epiphyte studies are rarely conducted using a standardized sampling scheme, which would allow broad-scale comparisons and meta-analyses.

The few quantitative inventories of epiphyte species composition published to date usually focus on aspects of biodiversity, e.g. species richness and taxonomic composition, eventually also phytogeography (e.g. Hsu and Wolf, 2009). Other, more functional aspects of biodiversity are normally not taken into account at the community level and beyond or are only addressed separately (e.g. Ingram and Nadkarni, 1993; Zotz, 2004). Here, we complement the taxonomic approach to the study of epiphyte communities with the analysis of physiological parameters related to plant water and nutrient relations. Thus, the results of our study will be not only a valuable basis for the analysis of biogeographical patterns of species richness and floristic similarity and for conservation purposes, but simultaneously have a bearing on our understanding of the functional importance of diversity for, e.g. nutrient relationships in the entire ecosystem.

Materials and methods

Study area

We sampled the vascular epiphyte flora of the Río Changuinola valley, which is situated in the Province of Bocas del Toro, Republic of Panama. The Río Changuinola originates in the highlands close to Volcan Baru and discharges after ca. 100 km into the Caribbean Sea. Close by is the National Park “La Amistad”, a UNESCO World heritage site consisting of ca. 568,000 ha of montane and lowland rainforest, which is shared with Costa Rica. Fieldwork was carried out in the central section of the Río Changuinola valley. The surveyed area in the valley ranged from 9°13′N; 82°29′W to 9°03′N; 82°28′W comprising an area of about 1,000 ha (Fig. 1). The topography of the study region is hilly with peaks of 500 to 1000 m a.s.l. surrounding the valley.

The Río Changuinola region is characterized by heterogeneous climatic conditions. The lowland part of the river valley close to the Caribbean coast is characterized by annual rainfall of about 3000 mm with a short dry season from February to April with an average monthly precipitation of only about 150 mm and <10 days with rainfall (pers. com. with Empresa de Transmisión Eléctrica S.A. – ETESA). In the southern, pre-montane part of the valley the dry season is less pronounced. Here, annual precipitation reaches 4500 mm, the lowest monthly precipitation being on average 240 mm, with a minimum number of rainy days of 16 per month during the drier season. Mean temperature in the valley is 26.1 °C (range: 22.7–29.1) while the pre-montane area’s mean temperature is 24.3 °C with slight seasonality (range: 20.1–27.3 °C; ETESA, unpubl. data). According to Holdridge’s (1967) life zone classification, the forest at the Río Changuinola is a “tropical moist forest”. Most of the region is covered with primary forest although some areas in direct vicinity of the Río Changuinola are populated by small indigenous communities. There, much of the original forest has been converted to small pastures, plantain or cocoa plantations, which are partly in succession to secondary forests. Along the Río Changuinola’s banks frequently inundated riparian forest is found.

Field survey

Eighteen sampling plots of 400 m^2 (20 m × 20 m) each were established at elevations ranging from 140 to 300 m a.s.l. in the Río Changuinola valley from May through October 2007, covering primary forest, secondary forest, riparian forest, and plantations. These plots were sampled for occurrence of epiphyte species. Abundance of species was documented in a single 1-ha plot situated at 550 m a.s.l. in primary rainforest on a hill slope close to the Río Changuinola’s “Boca Chica” tributary, 5.8 km southwest of the indigenous community of Charco La Pava (Fig. 1). All trees and shrubs (dbh >1 cm) within these plots were surveyed for the occurrence of vascular epiphytes. For trees with trunks located inside the plot, the whole crown was considered for epiphyte occurrences even when projecting outside the plot. On the other hand, tree crowns that were projecting inside a sampled plot were excluded from the census when the tree trunk was outside the boundaries of the observed plot. Epiphytes were examined by means of binoculars. Ground-based observation is a fast and safe way to assess a local epiphyte flora, however, with this method total species richness is underestimated by ca. 20% (Flores-Palacios and García-Franco, 2001). To reduce the degree of underestimation of species numbers, crowns of one to two selected trees in each plot were accessed using alpine climbing techniques (Perry, 1978). We cut off tree branches and twigs with gardening pruners or telescope saws and lowered them down to facilitate the collection of specimens. This allowed us to make collections and observations of epiphytes directly in the canopy. Additionally, we gathered fallen plant material and sampled from recently fallen trees and branches. We also made collections of epiphytes in the vicinity of our field camps and during hikes to the plots.

Whenever possible, specimens were identified in the field and pressed and dried on the day of collection. When necessary, we transferred non-flowering living plants to the headquarters of the Smithsonian Tropical Research Institute (STRI) in Panama City, and cultivated them until flowering. Plants were compared with herbarium material at the University of Panama Herbarium (PMA). Sometimes vouchers of observed species could not be taken due to access problems. In these cases, we took photographs of the plants *in situ*. Field guides to the most common species were prepared (Laube et al., 2008). Identifications were kindly reviewed by T.B. Croat (MO, Araceae), R.C. Moran (NYBG, ferns in part), E. Hágsater (AMO, *Epidendrum*), H.E. Luther (Selby, Bromeliaceae), C. Luer (Orchidaceae in part) and S. Dalstrøm (Selby, Genus *Gongora*). Voucher specimens are deposited at the PMA and the STRI herbarium at Tupper Center (SCZ).

To determine vascular epiphyte abundance, we conducted a census within the 1-ha plot. After dividing the plot into 100, 10 m × 10 m subplots, 8 subplots, totalling 800 m^2, were randomly chosen. All trees and shrubs within these subplots were sampled for the occurrence of vascular epiphytes of all sizes. As detailed above, the location of the trunk, and not the crown, was used to determine whether the tree was included or excluded from the census. In this study we use the term "epiphyte" in a broad sense including vascular holoepiphytes, i.e. plants that spend their entire life on a host plant, and hemi-epiphytes which are epiphytic only during part of their life cycle. Hemi-parasitic plants (e.g. Loranthaceae) found in the canopy were excluded as they can rely upon continuous supply of water and nutrients and therefore differ ecologically from epiphytes.

$\delta^{13}C$ values and leaf nitrogen contents

Small subsamples from vouchers and from additional collections were used to obtain dried plant tissue for the determination of $\delta^{13}C$ values and leaf nitrogen contents. This was not possible in species with missing vouchers or in those cases in which voucher material was insufficient to allow sampling because it would have destroyed the entire specimen (e.g. *Platystele* sp., *Utricularia* sp.). Hence, our collection is lacking data on $\delta^{13}C$ and nitrogen content for some species. Leaf material was dried at 80 °C for 24 h and ground to powder in a ball mill. Aliquots (2 mg) were transferred into tin capsules and analyzed for $\delta^{13}C$ and N concentration by continuous-flow isotope ratio mass spectrometry (IRMS). The instrument consisted of an elemental analyzer (EA 1110, CE Instruments, Milano, Italy) coupled via a ConFlo III interface (Finnigan MAT, Bremen, Germany) to the IRMS (DeltaPLUS, Finnigan MAT). The natural abundance of the heavy carbon isotope ^{13}C is given in δ units, calculated as follows:

$$\delta^{13}\mathrm{C}\ \ [‰\ \ \mathrm{vs.}\ \ \mathrm{V\text{-}PDB}] = (R_{\mathrm{sample}} : R_{\mathrm{standard}} - 1) \times 1000,$$

where R is the ratio ^{13}C:^{12}C of the sample or standard (Vienna PeeDee Belemnite, V-PDB), respectively. Repeated measurements of laboratory standards indicate a long-term variability of 0.15‰ (S.D.).

Statistics

Information on species geographic and altitudinal distributions were derived from the Tropicos (2008) database. We defined four broad groups according to their center of geographic distibution: (1) Central American species, i.e. species found mostly from Mexico through Panama and with a southernmost occurrence in Colombia, (2) South American species, i.e. species found mainly in South American countries with a northernmost occurrence in Costa Rica, (3) Neotropically distributed species, i.e. species found in Central and South American countries, and (4) endemic species, i.e. species that are found only in Panama and Costa Rica.

Species accumulation curves, bootstrap, analysis of correlation, Unweighted Pair Group Method with Arithmetic mean (UPGMA) cluster analysis, and a Principal Correspondence Analysis (PCoA) to determine floristic relationships between different lowland rain forest sites was performed using the "vegan" and "cluster" package of R Version 2.8.0.Windows (R Development Core Team, 2008). Chao species richness estimators (Chao, 1984) were calculated with EstimateS 8.0 for Windows (Colwell, 2008). For UPGMA and PCoA, we chose the β_{sim}-Diversity Index (No. 22, in Koleff et al., 2003) based on Simpson's (1943) diversity Index as a measure of floristic dissimilarity with our presence–absence data. β_{sim} is calculated as $\min(b,c)/(\min(b,c)+a)$, where a is the number of shared species and b and c the number of unique species to site 1 and 2, respectively. β_{sim} is thus little affected by difference in species richness among sites (Simpson, 1943; Lennon et al., 2001; Baselga et al., 2007).

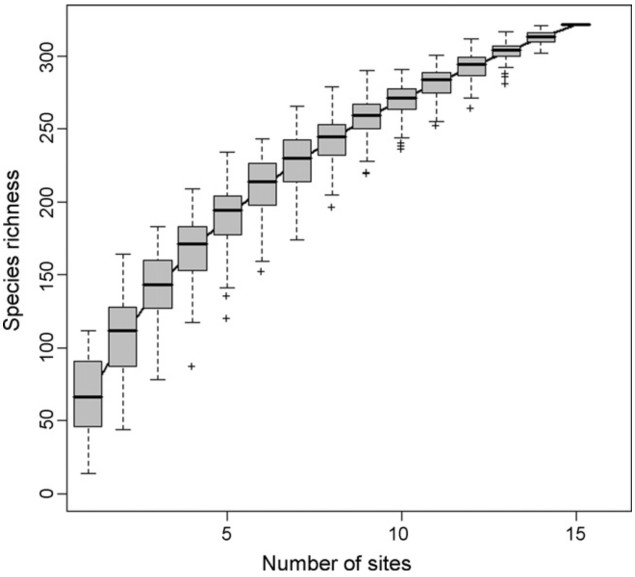

Fig. 2. Species accumulation curve for the 15 standardized 0.04-ha plots within the study area. The curve was generated by random selection of sites with 100 iterations. Boxplots depict median species number, interquartile range (IQR), 1.5 × IQR (whiskers), and outliers estimated from permutations.

Results

In total, we found 476 species of vascular epiphytes of which we identified 350 to species level (a complete species list is given in Appendix A). These species belong to 31 families and to at least 122 genera. The Orchidaceae were by far the most diverse family in the area with 183 species (38%) followed by the Araceae (85 spp., 17.7%), Bromeliaceae (34 spp., 7.1%), Polypodiaceae (26 spp., 5.5%), Hymenophyllaceae (23 spp., 4.8%), and Piperaceae (17 spp., 3.5%, Table 1). These five families constituted more than 75% of the local epiphyte flora while the majority of families were represented by only one to five species. Ferns and lycopods were represented by 93 species. A species accumulation curve generated with all 15 standardized 0.04-ha plots that comprised a total of 322 species showed no saturation (Fig. 2) suggesting that the observed species number within these plots is far from the total species number in the area. Indeed, all used species richness estimators that account for unseen species predicted higher total numbers of epiphyte species for this subset of observation sites ranging from 379 ± 20 species (Bootstrap; Smith and Belle, 1984) to 478 ± 35 species (Chao Estimator; Chao, 1984) and were close to the number of species actually observed in the entire study area.

Frequency and abundance

The distribution of species incidences is typical for a tropical rainforest species assemblage with a few abundant species and a long tail of rare species. The most common species were *Peperomia rotundifolia* (occurrence in 78% of all sampled plots; Appendix A), the fern *Asplenium auritum* (70%) and the bromeliad *Guzmania subcorymbosa* (65%). A total of 301 species (63% of the total) were encountered only once.

Sampling eight 100 m^2 subplots within a 1-ha plot, we encountered 8819 epiphyte individuals comprising 147 species from 19 families. The most abundant species was the small orchid *Platystele compacta* that accounted for ca. 8% of all individuals. Again, orchids in this plot represented the dominant plant family (30%

Table 1
Summary table of vascular epiphyte communities in Neotropical lowland forest sites. Relative contributions of different families to species pools are given as percentages. Orch – Orchidaceae, Pter – Pteridophytes, Arac. – Araceae, Brom – Bromeliaceae, Eric – Ericaceae, Gesn – Gesneriaceae, Pipe – Piperaceae.

Country	Site	Elevation (m a.s.l.)	Size (ha)	Precip. (mm/a)	No. spp.	No. gen.	No. fam.	Orch.%	Pterid.%	Arac.%	Brom.%	Erica.%	Gesn.%	Piper. %	Others%
Panama	Río Changuinola[1]	110–550	400	4000	480	124	32	38	19.8	17.7	7.1	1.7	2.5	3.5	9.7
Costa Rica	La Selva[2]	35–135	1500	3950	425	123	29	29.5	19.5	19	7.1	0.5	4.6	4.4	15.4
Ecuador	Jatun Sacha[3]	450	2000	3900	393	118	25	35.4	17.3	17.6	4.6	1	4.8	3.1	16.2
Ecuador	Tiputini Biodiversity Station[4]	220	650	3200	313	100	25	29.8	21.9	22.2	6.7	0	2.5	3.5	13.4
Ecuador	Río Palenque[5]	220		2650	297	129	29	34	12	15	7.5	1	5	2.4	23.1
Brazil	Reserva Ducke; Manaus[6]	80		2100	248	100	29	33.9	14.9	17.8	6.2	0.4	2.5	0.4	23.9
Colombia	Río Caquetá[8]	120		3060	210	79	27	17.1	21.0	26.7	7.6	1	2.9	1.9	21.8
Guayana	Kaieteur[8]	750		3000	202	84	33	31.1	26	10.7	15.3	1.7	1.7	2.6	10.9
Guayana	Iwokrama[9]	120		2000	178	84	29	34.2	26.7	17.4	3.1	0	2.5	3.5	12.6
Panama	Barro Colorado Island[10]	25–165	1500	1500	162	78	13	50.6	24.7	14.8	11.1	0	0.6	6.2	4.9
Bolivia	Madidi[11]	250–500		2000	152	72	19	35.5	28.3	15.8	6.6	0	0.7	8.6	4.5
Venezuela	Surumoni Crane Project[12]	100	1.5	3000	148	62	23	45.9	11.5	20.9	7.4	0	2.7	5.4	6.2
Panama	San Lorenzo[13]	50	1	3500	125	72	17	40.8	740.8	12.8	6.4	0	2.4	4	8.8

Data sources: [1]This study; [2]Taylor et al. (2008); [3]Missouri Botanical Garden (2008); [4]Kreft et al. (2004); [5]Gentry and Dodson (1987); [6]Ribeiro et al. (1999); [7]Benavides et al. (2005); [8]Kelloff and Funk (1998); [9]Clarke et al. (2001); [10]Croat (1978); [11]Acebey and Krömer (2001); [12]Schmit-Neuerburg (2002); [13]Zotz and Schultz (2008).

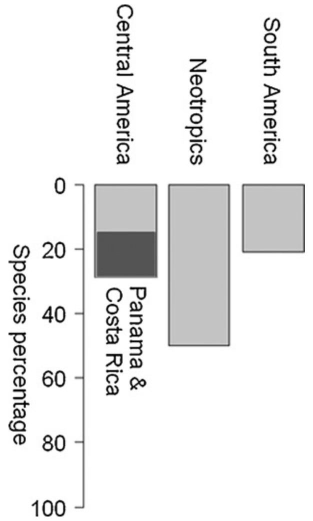

Fig. 3. Geographical distribution of the vascular epiphyte species found at Río Changuinola. Neotropical species have the widest distribution that ranges from Central to South America. South American species have a wide distribution within South America, but reach their northermost limit in Panama/Costa Rica. Central American species have a wide distribution in Central America, but reach their southernmost distribution in Colombia.

of all species), followed by Araceae (18%), Bromeliaceae (12%), and Polypodiaceae (8%), while ferns and fern allies taken together accounted for 27% of all species. The rank abundance data (not shown) revealed low evenness as the high ranked species showed considerably higher abundances than low ranked species, i.e. the first 20 species comprised 75% of all individuals.

Geographical distribution of species

Most epiphyte species found at Río Changuinola have relatively wide geographic ranges: 50% of the encountered species have been recorded in a number of countries throughout Central and South America (Tropicos, 2008). About 21% of the species have a primarily South American distribution and reach their northernmost occurrences in the study region. 29% of all identified species are restricted to Central America. Of the latter group, 14% can be considered more narrowly endemic, i.e. are restricted to Panama and Costa Rica (Fig. 3).

Altitudinal distribution data were available for 350 species from the Tropicos (2008) database. For the majority of epiphyte species (83%), the elevation at Río Changuinola was within the known elevational range. However, 15% of the species occurred at elevations lower than previously known. On average, species were growing 438 ± 173 m (mean ± S.D., $n = 52$) below their previously reported minimum elevation. On the other hand, a few species (2%) were found at higher elevations than reported in the literature. Mean divergence from maximum elevation values here was 134 ± 17 m ($n = 8$).

Floristic similarities to other Neotropical lowland forest sites

The floristic similarity of the epiphyte flora at Río Changuinola with other Neotropical sites was related to geographical distance (Fig. 4). Thus, the epiphyte flora at Río Changuinola showed greatest similarities with La Selva, Costa Rica, located ca. 200 km to the west. The PCoA revealed that together with Barro Colorado Island and San Lorenzo (both Panama) these sites form a distinct Central American lowland cluster (Fig. 5a). A UPGMA cluster analysis was consistent with the PCoA results (Fig. 5b). Next in floristic similarity was the epiphyte community located at Río Palenque in the Andean foothills of Western Ecuador (Gentry and Dodson, 1987). Although this site is geographically closer to Jatun Sacha (Missouri Botanical Garden, 2008) and Tiputini (Kreft et al., 2004), which are at 200 and 360 km distance, respectively, the epiphyte species composition at Río Palenque is more similar to the Central American study sites (about 1100 km distance). In our analysis, montane forests are grouped in a distinct cluster. Although highly separated in terms of geographical distance, they show high species similarity to each

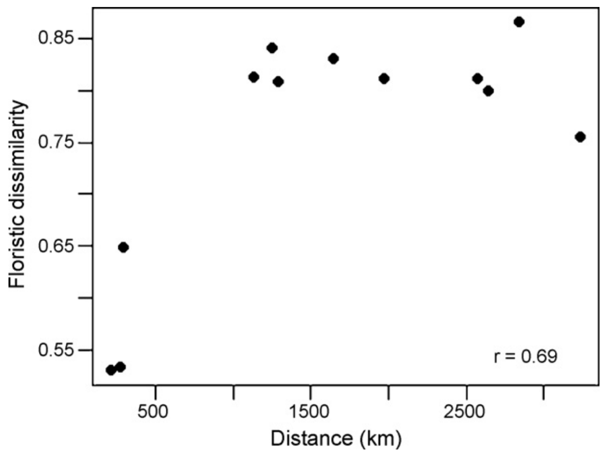

Fig. 4. Analysis of correlation between geographic distance of a lowland forest site from Río Changuinola and other Neotropical sites of comparable floristic documentation and their floristic dissimilarity in vascular epiphytes (β_{sim}). Data sources are shown for sites in Table 1.

other and low similarity to lowland forests (Fig. 5). While the first axis reflects an altitudinal gradient, lowland epiphyte species segregate along the second axis.

Functional diversity

Unequivocal evidence for crassulacean acid metabolism (CAM, $\delta^{13}C > -20‰$) was found in three plant families: all studied cacti were CAM, as were 23% of all studied bromeliads and 11% of all orchids (Table 2; Fig. 6). However, due to their exceedingly high contribution to local species richness, most CAM species in the epiphyte community belonged to the Orchidaceae.

The values of leaf-N varied about threefold and significantly differed among families (Table 2, one-way ANOVA, $p < 0.001$). The highest values (>2% dry mass) were found in Araceae, Rubiaceae, and Dryopteridaceae, the lowest (<0.9% dry mass) in Bromeliaceae, Lycopodiaceae and Ericaceae. Different photosynthetic pathways in the two families Orchidaceae and Bromeliaceae were not associated with differences in leaf-N concentrations (Welch Two Sample *t*-test, $p = 0.77$).

Discussion

The vascular epiphyte flora of the Río Changuinola area is the most species-rich of any Neotropical lowland forest sites studied so far. Although the flora of Panama has been studied intensively for more than 300 years by almost 1000 botanists (Dwyer, 1985), this finding comes as a surprise and highlights the need for closer examination of tropical biodiversity even in comparatively well-studied countries. With 476 vascular epiphyte species found in this study, the species pool at the Río Changuinola site clearly surpasses other lowland forest sites in terms of species richness. One explanation for this high number of species may be the high annual precipitation in the area (3000–4500 mm). First shown in the classic study of Gentry and Dodson (1987) and confirmed and extended in a meta-analysis by Kreft et al. (2004), vascular epiphyte diversity is strongly correlated with the amount of rainfall. High local moisture availability may also explain the shifts towards lower altitudes in 15% of the species by promoting the establishment and growth of species normally restricted to higher and supposedly moister sites. High moisture availability is also reflected in the low proportion of species with the water-saving crassulacean acid metabolism (CAM). Only 23, or 7%, of all species in the Changuinola region were unambiguously CAM, i.e. with $\delta^{13}C$ signatures more positive than $-20‰$. Noteworthy, the latter figure is less than half of those reported for epiphyte assemblages from other moist lowland forest (Zotz and Ziegler, 1997; Zotz, 2004). Other studies which focused on particular taxa, e.g. epiphytic orchids, reported about 25% CAM species (Winter et al., 1983; Earnshaw et al., 1987). Consistent with low overall CAM occurrence in the Changuinola epiphyte flora, the proportion of orchids with CAM (ca. 11%) was also low. The func-

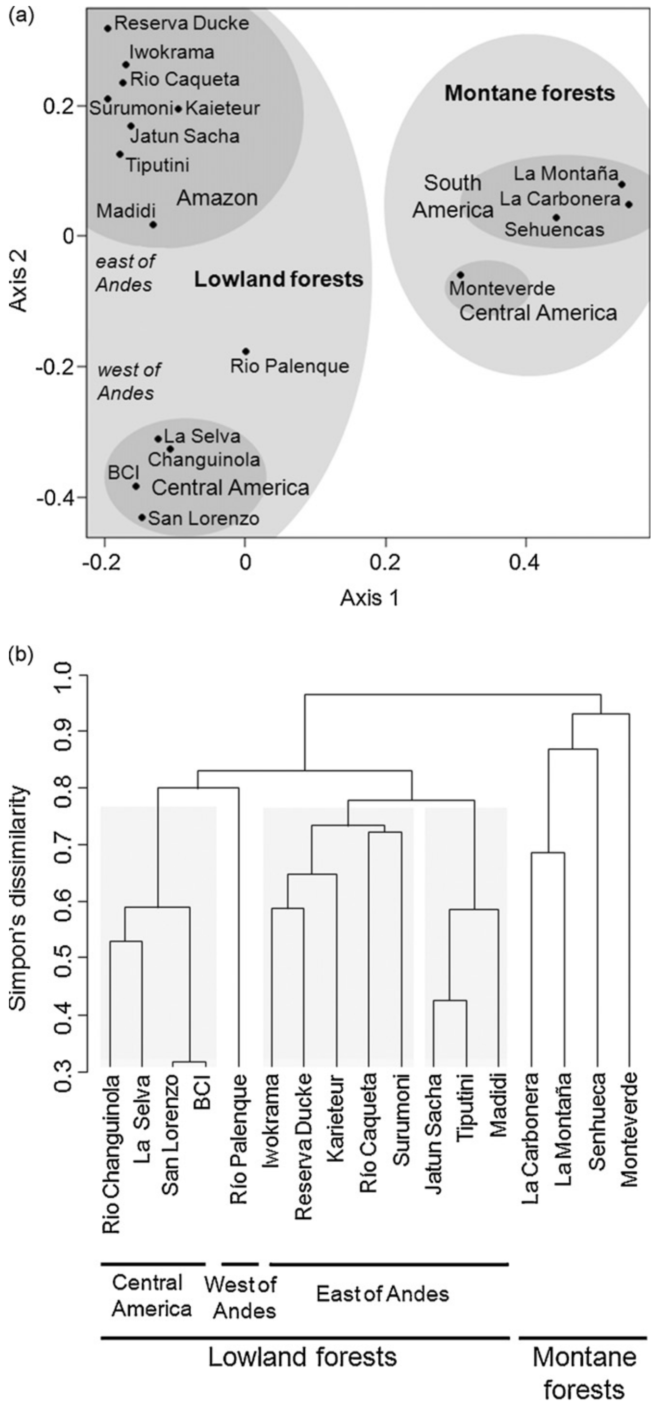

Fig. 5. Analyses of floristic dissimilarity (β_{sim}) of vascular epiphyte communities at Central and South American study sites. In the Principal coordinates analysis (a) similar sites appear close together, and dissimilar sites are far apart. The two axes explain 45% of the variance. In the UPGMA cluster analysis (b) height of the tree refers to the floristic dissimilarity (β_{sim}) used in the analysis. The agglomerate coefficient is 0.37. Data sources are sites in Table 1 plus montane forest sites: Monteverde (Ingram et al., 1996), La Montaña (Kelly et al., 1994), La Carbonera (Engwald, 1999; Barthlott et al., 2001), and Sehuencas (Ibisch, 1996).

Table 2
Ecophysiological traits of epiphytes by family. Included are all families with at least three species. Given are species numbers (in parentheses the number of analysed species), the proportions of species with CAM in % as deduced from the $\delta^{13}C$ values, of which the ranges are also shown, and the leaf-N concentrations (% DW, mean ± S.D.).

Family	Species number	$\delta^{13}C$ range	CAM species (%)	Leaf N
Araceae	85 (69)	−27.7/−37.8	0	2.1 ± 1.0
Aspleniaceae	6 (6)	−28.7/−34.4	0	1.63 ± 0.6
Bromeliaceae	34 (26)	−14.4/−32.7	23.1	0.91 ± 0.5
Cactaceae	3 (3)	−16.7/−18.6	100	1.31 ± 0.1
Clusiaceae	4 (4)	−30.6/−34.1	0	0.92 ± 0.4
Cyclanthaceae	11 (9)	−27.6/−36.4	0	1.31 ± 0.5
Davalliaceae	3 (1)	−33.5/−33.5	0	1.11
Ericaceae	8 (6)	−29.7/−34.1	0	0.71 ± 0.2
Gesneriaceae	12 (11)	−22/−33.3	0	1.35 ± 0.6
Grammitidaceae	5 (5)	−31.3/−34.8	0	0.95 ± 0.3
Hymenophyllaceae	23 (14)	−28.8/−34.4	0	1.67 ± 0.3
Lomariopsidaceae	16 (13)	−29.7/−36.0	0	1.71 ± 1.0
Lycopodiaceae	4 (2)	−28.2/−31.0	0	0.64 ± 0.3
Marcgraviaceae	7 (5)	−30.2/−34.3	0	1.23 ± 0.4
Melastomataceae	3 (3)	−29.2/−32.5	0	1.38 ± 1.2
Orchidaceae	182 (129)	−14/−34.8	10.9	1.2 ± 0.5
Piperaceae	17 (11)	−23.4/−38	0	1.58 ± 0.6
Polypodiaceae	26 (16)	−26.5/−34.6	0	1.28 ± 0.6
Rubiaceae	4 (3)	−32.8/−36.1	0	2.15 ± 1.0
Vittariaceae	7 (4)	−30/−34.2	0	1.37 ± 0.3

tional importance of CAM species in terms of epiphytic biomass is likely to be even lower than suggested by these numbers because most CAM plants are orchids which are considerably smaller than many massive C3 species in, e.g. the Araceae (compare Zotz, 2004). $\delta^{13}C$ signatures of −22.0 to −24.4‰ are also suggestive of CAM in one *Codonanthe* (Gesneriaceae) and two *Peperomia* species (Piperaceae) (Appendix A). The linear relationship between net carbon gain in the night and plant $\delta^{13}C$ in CAM plants (Winter and Holtum, 2002), indicates that net carbon gain during the night may account for 14–27% of the overall carbon budget in these species. Such weakly expressed CAM has also been demonstrated for a considerable proportion of orchids with $\delta^{13}C$ values indicative of C3 (=more negative than −22‰) in a recent investigation of orchid species in Panama (Silvera et al., 2005). Thus, CAM could play a more important role in this epiphyte community than suggested by our analysis.

Despite the suitable climatic conditions for epiphytic growth, geographic idiosyncrasies might also play an important additional role for local biodiversity since the study site is close to the South American continent which results in a high proportion of species with a principal South American distribution: more than one fifth of the local species pool consists of species that reach their northernmost distribution in Panama and Costa Rica.

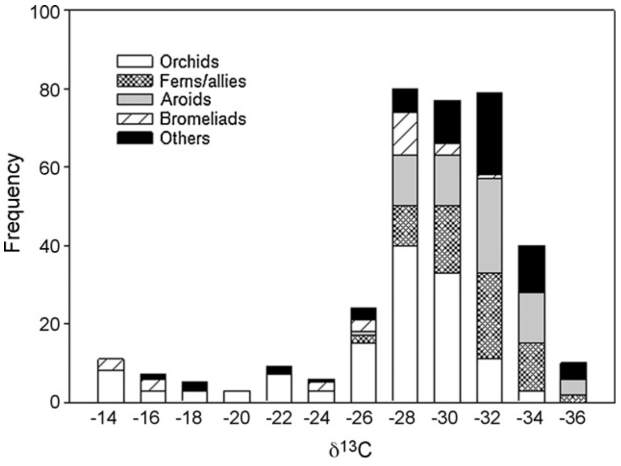

Fig. 6. Frequency (number of species) of leaf $\delta^{13}C$ values of 351 species of vascular epiphytes at Río Changuinola. Each bar represents a 2‰ change of $\delta^{13}C$, i.e. the first bar from −14 to −16‰ (data from Appendix A).

High species richness at Changuinola could also be due to a larger sample area, higher diversity of habitats or greater sampling effort. These factors certainly differ between compared sampling sites and scarcity of information about these factors impedes an evaluation of possible explanations for species richness. However, the site area in this project is in the range of the other high-species-diversity sites with similar precipitation. And sampling effort certainly is less than in the other places that have been subject to botanical studies for long periods.

Endemism does not particularly contribute to species richness in the area, since the observed proportion of 14% regional endemics is in the range of other sites. For example, Küper et al. (2004) report 18% endemic species for Ecuadorian lowland forests, and Kreft et al. (2004) estimate that at least 10% of the epiphyte species of the Yasuní region in Western Amazonia are regional endemics.

The epiphyte community at Río Changuinola shows the greatest floristic similarity with the nearby Central American lowland sites La Selva, Costa Rica, and BCI, Panama. Although equidistant to Río Changuinola, the four Ecuadorian sites varied in similarity. Río Palenque, which is located west of the Andes, had much more species in common with Río Changuinola than with Jatun Sacha, Madidi or Tiputini, which are all located east of the Andes. At the latter sites, the natural barrier of the Andes probably impeded the dispersal of many epiphyte species. In turn, Río Palenque with its westward location from the Andes shares a considerable number of species with Central American sites. Possibly due to the Andean barrier and the geographical distance, Amazonian epiphyte communities had the lowest similarity to the Central American counterparts.

The general taxonomic composition of epiphytic flora at Río Changuinola is consistent with that of many other lowland communities in the Neotropics (Gentry and Dodson, 1987; Kreft et al., 2004). Orchids comprise more than two-thirds of all species at Río Changuinola, i.e. the local species richness is dominated by this family, which is typical for many lowland sites. However, the very high local species richness cannot be attributed to one or few families, all epiphytic families show proportionally high species numbers at Río Changuinola. We assume that a closer inspection would reveal more species and even species new to science, as has happened during the course of this study (Hágsater et al., 2008).

Functional diversity associated with taxonomic affiliation, e.g. the restriction of water-saving CAM to just three families, was also evident in the nutrient contents of leaves. There was a threefold variation in leaf nitrogen concentrations among families (Table 2).

Particularly puzzling were the very low levels of N in Ericaceae, because ericoid mycorrhizas have been detected morphologically in a number of epiphytic family members in a consistent manner in several studies (e.g. Bermudes and Benzing, 1989; Rains et al., 2003). These ericoid mycorrhizas can use complex organic sources of N and P, and we actually expected to find relatively high N concentration in Ericaceae (Cairney and Meharg, 2003; Grelet et al., 2003), quite in contrast to our current findings. However, we can discard the possibility that our results are exceptional because even lower leaf N values have been reported for two epiphytic Ericaceae from a rainforest in New Guinea (mean 0.4% N, Grubb and Edwards, 1982). Currently, we cannot offer a satisfying explanation for our observation, and the functional significance of these mycorrhizal associations is unclear.

Another family with very low N concentrations was the Bromeliaceae. Again, such low leaf N levels have been reported earlier (e.g. Stuntz and Zotz, 2001), and are considered to be unrelated to mycorrhizal associations because nutrient uptake occurs mostly via absorbing leaf scales (Benzing, 2000). However, for this family nutrient concentrations have been related to functional aspects before. Stuntz and Zotz (2001) have shown that bromeliads as a group have very high nitrogen use efficiencies, i.e. achieve much higher rates of net photosynthesis per mol N than co-occurring orchids, ferns or aroids. Taxonomic differences in the use of nutrient elements for different functions are widespread in the plant kingdom (Lambers et al., 1998), but virtually unexplored in vascular epiphytes.

Differences in leaf N concentration may also be discussed in relation to photosynthetic pathway. Theoretically, high internal CO_2 concentrations during the day should allow CAM plants to use N more economically (Raven and Spicer, 1996), but our data do not support this notion, while previous studies gave ambiguous results (e.g. Lüttge, 1987; Hietz et al., 1999).

In conclusion, the epiphyte flora of the Río Changuinola region is more species-rich than that of any other lowland forest investigated so far, and extended fieldwork will doubtlessly reveal more species. Along with the finding of species new to science, we report a low percentage of CAM species for a tropical lowland forest, and present some puzzling observations concerning the nutrient relationships of different taxonomic groups of epiphytes.

Acknowledgements

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Appendix A. Species list of vascular epiphytes found in the Río Changuinola area. Given are taxonomic data, life form of a species as either true epiphtye (e) or hemi-epiphyte (he), proportional incidence of a species in a total of 23 thoroughly studied sites (eigtheen 400 m^2 plots, one 1-ha plot, four field camp vicinities of different size; * indicates that species was found elsewhere at one occurrence), $\delta^{13}C$ value and nitrogen content (% N) of dried leaf samples, and photosynthetic pathway (pp).

Family	Genus	Epitheton	Author	Life form	Incidence	$\delta^{13}C$	% N	pp
Araceae	*Anthurium*	*acutangulum*	Engl.	e	0.04			n/a
Araceae	*Anthurium*	*bakeri*	Hook. f.	e	0.57			n/a
Araceae	*Anthurium*	*bicollectivum*	Croat	e	0.04			n/a
Araceae	*Anthurium*	cf. obtusifolium	Schott	e	0.04	−32.3	1.7	C3
Araceae	*Anthurium*	*clavigerum*	Poepp.	e	0.43	−33.4	3.1	C3
Araceae	*Anthurium*	*clidemioides*	Standl.	e	0.22	−34.7	4	C3
Araceae	*Anthurium*	*cuneatissimum*	(Engl.) Croat	e	0.22			n/a
Araceae	*Anthurium*	*cuspidatum*	Mast.	e	0.52	−32.7	1.4	C3
Araceae	*Anthurium*	*fatoense*	K. Krause	e	0.57	−32.1	2.3	C3
Araceae	*Anthurium*	*flexile*	Schott	e	0.3	−32.4	2.9	C3
Araceae	*Anthurium*	*formosum*	Schott	e	0.52	−32.5	1.7	C3
Araceae	*Anthurium*	*friedrichsthalii*	Schott	e	0.61	−29.7	1.1	C3
Araceae	*Anthurium*	*garagaranum*	Standl.	e	0.13			n/a
Araceae	*Anthurium*	*gracile*	(Rudge) Schott	e	0.35	−30.4	2.4	C3
Araceae	*Anthurium*	*hacumense*	Engl.	e	0.17	−32	0.8	C3
Araceae	*Anthurium*	*hoffmannii*	Schott	e	0.04	−31.9	0.9	C3
Araceae	*Anthurium*	*interruptum*	Sodiro	e	0.43	−30.5	1	C3
Araceae	*Anthurium*	*kallunkiae*	Croat	e	0.09	−33.4	0.9	C3
Araceae	*Anthurium*	*kunthii*	Poepp.	e	0.09	−34.4	2.6	C3
Araceae	*Anthurium*	*lancifolium*	Schott	e	0.04			n/a
Araceae	*Anthurium*	*michelii*	Guillaumin	e	0.17	−33.1	1.8	C3
Araceae	*Anthurium*	*ochranthum*	K. Koch	e	0.04			n/a
Araceae	*Anthurium*	*pageanum*	Croat	e	0.13	−29.8	1.1	C3
Araceae	*Anthurium*	*paludosum*	Engl.	e	0.22	−29.5	0.6	C3
Araceae	*Anthurium*	*panamense*	Croat	e	0.13	−33.1	2.2	C3
Araceae	*Anthurium*	*pentaphyllum* var. *bombacifolium*	(Aubl.) G. Don	e	0.13			n/a
Araceae	*Anthurium*	*pittieri*	Engl.	e	0.04	−29.4	0.6	C3
Araceae	*Anthurium*	*prolatum*	Croat & R.A. Baker	e	0.39			n/a
Araceae	*Anthurium*	*protensum*	Schott	e	0.04			n/a
Araceae	*Anthurium*	*purpureospathum*	Croat	e	0.26	−31.4	1.5	C3
Araceae	*Anthurium*	*ramonense*	Engl. ex K. Krause	e	0.04	−31.7	0.5	C3
Araceae	*Anthurium*	*ravenii*	Croat & R.A. Baker	e	0.22	−29.9	2.7	C3
Araceae	*Anthurium*	*redolens*	Croat	e	0.04	−33.4	2.1	C3

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Araceae	*Anthurium*	*salviniae*	Hemsl.	e	0.13	−29.9	2	C3
Araceae	*Anthurium*	*sanctifidense*	Croat	e	0.04	−27.7	2.2	C3
Araceae	*Anthurium*	*scandens*	(Aubl.) Engl.	e	0.3			n/a
Araceae	*Anthurium*	*seibertii*	Croat & R.A. Baker	e	0.04	−28.8	1.9	C3
Araceae	*Anthurium*	sp. (489)		e	0.04	−35	2.6	C3
Araceae	*Anthurium*	sp. (84)		e	0.09	−32.1	1.9	C3
Araceae	*Anthurium*	sp. nov. (367)		e	0.09	−32.2	0.9	C3
Araceae	*Anthurium*	sp. nov. (506)		e	0.04	−32.6	0.7	C3
Araceae	*Anthurium*	*tilaranense*	Standl.	e	0.13	−31.5	1.1	C3
Araceae	*Anthurium*	*trinerve*	Miq.	e	0.35	−28.3	1.2	C3
Araceae	*Monstera*	cf. adansonii	Schott	he	0.04	−37.8	2.6	C3
Araceae	*Monstera*	cf. dubia	(Kunth) Engl. & K. Krause	he	0.13	−34.2	5.9	C3
Araceae	*Monstera*	cf. spruceana	(Schott) Engl.	he	0.13			n/a
Araceae	*Monstera*	cf. tenuis	K.Koch	he	0.04			n/a
Araceae	*Monstera*	*dilacerata*	Schott	he	0.09	−35.9	4.7	C3
Araceae	*Monstera*	*obliqua*	Miq.	he	0.09	−33.5	2.5	C3
Araceae	*Monstera*	sp. (145)		he	0.04	−29.8	2.5	C3
Araceae	*Monstera*	sp. (162)		he	0.04	−32.9	1.7	C3
Araceae	*Philodendron*	*alliodorum*	Croat & Grayum	he	0.04	−36.3	2.3	C3
Araceae	*Philodendron*	*aurantiifolium*	Schott	he	0.09	−32.5	2	C3
Araceae	*Philodendron*	cf. cretosum	Croat & Grayum	he	0.04			n/a
Araceae	*Philodendron*	cf. elegantulum	Croat & Grayum	he	0.04	−29.4	4.2	C3
Araceae	*Philodendron*	cf. wendlandii	Schott	he	0.3	−28.8	1.5	C3
Araceae	*Philodendron*	*correae*	Croat	he	0.04	−31.7	2.5	C3
Araceae	*Philodendron*	*ensifolium*	Croat & Grayum	he	0.04	−33.1	2	C3
Araceae	*Philodendron*	*fragrantissimum*	(Hook.) G. Don	he	0.04	−29.5	2	C3
Araceae	*Philodendron*	*grandipes*	K. Krause	he	0.09	−34.8	1.7	C3
Araceae	*Philodendron*	*grayumii*	Croat	he	0.13	−33.8	1.7	C3
Araceae	*Philodendron*	*inaequilaterum*	Liebm.	he	0.09	−37.4	3.4	C3
Araceae	*Philodendron*	*jodavisianum*	G.S. Bunting	he	0.17	−30.5	2.8	C3
Araceae	*Philodendron*	*pterotum*	K. Koch & Augustin	he	0.04	−34.2	2.9	C3
Araceae	*Philodendron*	*radiatum*	Schott	he	0.52	−29.3	2.7	C3
Araceae	*Philodendron*	*rhodoaxis*	G.S. Bunting	he	0.04	−31.9	2.1	C3
Araceae	*Philodendron*	*rothschuhianum*	(Engl.) Croat & Grayum	he	0.04			n/a
Araceae	*Philodendron*	*sagittifolium*	Liebm.	he	0.09	−35.4	1.7	C3
Araceae	*Philodendron*	*sulcatum*	K. Krause	he	0.22	−31.2	1.4	C3
Araceae	*Philodendron*	*tripartitum*	(Jacq.) Schott	he	0.22			n/a
Araceae	*Philodendron*	*verrucosum*	L. Mathieu ex Schott	he	0.09	−34.6	3	C3
Araceae	*Rhodospatha*	cf. brachypoda	G.S.Bunting	he	0.04			n/a
Araceae	*Rhodospatha*	*pellucida*	Croat & Grayum	he	0.09	−36.3	2.1	C3
Araceae	*Rhodospatha*	*wendlandii*	Schott	he	0.13	−34.6	2.5	C3
Araceae	*Stenospermation*	*angustifolium*	Hemsl.	he	0.26	−31	1.6	C3
Araceae	*Stenospermation*	*marantifolium*	Hemsl.	he	0.13	−33.6	1.5	C3
Araceae	*Stenospermation*	*multiovulatum*	(Engl.) N.E. Br.	he	0.09	−31.3	1.4	C3
Araceae	*Stenospermation*	*robustum*	Engl.	he	0.04	−31.1	0.7	C3
Araceae	*Syngonium*	*hoffmannii*	Schott	he	0.61	−34.9	2	C3
Araceae	*Syngonium*	*macrophyllum*	Engl.	he	0.17	−33.7	2.1	C3
Araceae	*Syngonium*	*peliocladum*	Schott	e	0.04	−32.4	2.9	C3
Araceae	*Syngonium*	*podophyllum*	Schott	he	0.52	−32.4	3.6	C3
Araceae	*Syngonium*	*schottianum*	H. Wendl. ex Schott	he	0.26	−33.3	2.2	C3
Araceae	*Syngonium*	sp. (147)		he	0.3	−34.3	2.5	C3
Araceae	*Syngonium*	*triphyllum*	Birdsey ex Croat	he	0.09	−34.7	2.6	C3
Araliaceae	*Schefflera*	cf. caduca	M.J. Cannon & Cannon	e	0.04	−34	2.3	C3
Araliaceae	*Schefflera*	sp. (780)		e	0.04			n/a
Aspleniaceae	*Asplenium*	*auritum*	Sw.	e	0.7	−30.1	1.8	C3
Aspleniaceae	*Asplenium*	*juglandifolium*	Lam.	e	0.04	−30.5	2.6	C3
Aspleniaceae	*Asplenium*	*serra*	Langsd. & Fisch.	e	0.04	−31.9	1.6	C3
Aspleniaceae	*Asplenium*	*serratum*	L.	e	0.39	−28.7	0.8	C3
Aspleniaceae	*Asplenium*	sp. (123)		e	0.04	−32.8	1.5	C3
Aspleniaceae	*Asplenium*	sp. (261)		e	0.09	−34.4	1.5	C3
Begoniaceae	*Begonia*	*glabra*	Aubl.	e	0.39	−32.5	2.5	C3
Bignoniaceae	*Gibsoniothamnus*	sp. (775)		e	0.04	−35.8	1.3	C3
Bignoniaceae		sp. (783)		e	0.04			n/a
Bromeliaceae	*Aechmea*	*angustifolia*	Poepp. & Endl.	e	0.22	−16	1.1	CAM
Bromeliaceae	*Aechmea*	*mariae-reginae*	H. Wendl.	e	0.04			n/a
Bromeliaceae	*Aechmea*	*nudicaulis*	(L.) Griseb.	e	0.04			n/a
Bromeliaceae	*Aechmea*	*pubescens*	Baker	e	0.09	−15.2	1.8	CAM
Bromeliaceae	*Aechmea*	sp. (773)		e	0.04			n/a
Bromeliaceae	*Aechmea*	*tillandsioides*	(Mart. ex Schult. & Schult. f.) Baker	e	0.39	−16.5	1.9	CAM
Bromeliaceae	*Catopsis*	*morreniana*	Mez	e	0.04	−28.5	0.4	C3
Bromeliaceae	*Catopsis*	*sessiliflora*	(R. & P.) Mez in DC.	e	0.13	−25.3	0.9	C3
Bromeliaceae	*Guzmania*	*lingulata*	(L.) Mez	e	0.17	−29.9	0.9	C3
Bromeliaceae	*Guzmania*	*monostachia*	(L.) Rusby ex Mez	e	0.35	−28.8	0.7	C3
Bromeliaceae	*Guzmania*	*scherzeriana*	Mez	e	0.52	−31.9	0.3	C3
Bromeliaceae	*Guzmania*	*subcorymbosa*	L.B. Sm.	e	0.65	−30.4	0.9	C3
Bromeliaceae	*Racinaea*	*contorta*	(Mez & Pittier) M.A. Spencer & L.B. Sm.	e	0.04	−30	1.3	C3

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Bromeliaceae		sp. (764)		e	0.04	–25	0.6	C3
Bromeliaceae	*Tillandsia*	*acostae*	Mez & Tonduz	e	0.57			n/a
Bromeliaceae	*Tillandsia*	*anceps*	G. Lodd.	e	0.35	–29.5	0.7	C3
Bromeliaceae	*Tillandsia*	*bulbosa*	Hook.	e	0.04	–15	0.7	CAM
Bromeliaceae	*Tillandsia*	*fasciculata*	Sw.	e	0.3			n/a
Bromeliaceae	*Tillandsia*	*festucoides*	Brongn. ex Mez	e	0.22	–14.4	0.5	CAM
Bromeliaceae	*Tillandsia*	*juncea*	(Ruiz & Pav.) Poir.	e	0.35	–27.8	0.8	C3
Bromeliaceae	*Tillandsia*	*leiboldiana*	Schltdl.	e	0.3	–28.5	1.4	C3
Bromeliaceae	*Tillandsia*	*monadelpha*	(E. Morren) Baker	e	0.22	–29.2	1.1	C3
Bromeliaceae	*Tillandsia*	*pruinosa*	Sw.	e	0.17	–17.4	1.6	CAM
Bromeliaceae	*Tillandsia*	*singularis*	Mez & Wercklé	e	0.04	–28.6	0.4	C3
Bromeliaceae	*Tillandsia*	sp. (303)		e	0.09	–28.8	0.6	C3
Bromeliaceae	*Tillandsia*	*venusta*	Mez & Wercklé	e	0.04	–26.2	0.4	C3
Bromeliaceae	*Vriesea*	*chontalensis*	(Baker) L.B. Sm.	e	0.39			n/a
Bromeliaceae	*Vriesea*	*gladioliflora*	(H. Wendl.) Antoine	e	0.09			n/a
Bromeliaceae	*Vriesea*	*heliconioides*	(Kunth) Hook. ex Walp.	e	0.22	–32.7	1.6	C3
Bromeliaceae	*Werauhia*	*kupperiana*	(Suess.) J.R.Grant	e	*	–29.1	0.4	C3
Bromeliaceae	*Werauhia*	*marnier-lapostollei*	(L.B.Sm.) J.R.Grant	e	0.04	–29.5	1	C3
Bromeliaceae	*Werauhia*	*singuliflora*	(Mez & Wercklé) J.R. Grant	e	*			n/a
Bromeliaceae	*Werauhia*	sp. (627)		e	0.3	–29.5	1	C3
Bromeliaceae	*Werauhia*	*vittata*	(Mez & Wercklé) J.R.Grant	e	0.04	–26.3	0.5	C3
Cactaceae	*Epiphyllum*	*phyllanthus*	(L.) Haw.	e	0.48	–16.7	1.4	CAM
Cactaceae	*Hylocereus*	sp. (170)		e	0.04	–18.1	1.2	CAM
Cactaceae	*Rhipsalis*	*baccifera*	(J.S. Muell.) Stearn	e	0.26	–18.6	1.3	CAM
Cecropiaceae	*Coussapoa*	*villosa*	Poepp. & Endl.	he	0.04			n/a
Clusiaceae	*Clusia*	*gracilis*	Standl.	he	0.13	–33.9	1.4	C3
Clusiaceae	*Clusia*	*loranthacea*	Planch & Triana	he	0.04	–30.6	0.6	C3
Clusiaceae	*Clusia*	sp. (549)		he	0.04	–31.8	0.7	C3
Clusiaceae	*Clusiella*	*isthmensis*	Hammel	e	0.04	–34.1	0.9	C3
Cyclanthaceae	*Asplundia*	*brunneistigma*	Hammel	he	0.3	–34.7	0.8	C3
Cyclanthaceae	*Asplundia*	cf. ceci	Hammel	he	0.04	–36.4	2.1	C3
Cyclanthaceae	*Asplundia*	cf. ferruginea	Grayum & Hammel	he	0.09			n/a
Cyclanthaceae	*Asplundia*	cf. multistaminata	Harling	e	0.13	–28.7	0.9	C3
Cyclanthaceae	*Asplundia*	*euryspatha*	Harling	e	0.04	–34.5	1.7	C3
Cyclanthaceae	*Asplundia*	*ferruginea*	Grayum & Hammel	e	0.22	–33.7	1.7	C3
Cyclanthaceae	*Asplundia*	*vagans*	Harling	e	0.04	–34.6	1.9	C3
Cyclanthaceae	*Chorigyne*	*pendula*	(Hammel) R. Erikss.	e	0.26	–33.7	1	C3
Cyclanthaceae	*Evodianthus*	*funifer*	(Poit.) Lindm.	he	0.3	–34.3	1	C3
Cyclanthaceae	*Ludovia*	*integrifolia*	(Woodson) Harling	he	0.3			n/a
Cyclanthaceae	*Sphaeredenia*	cf. alleniana	Harling	e	0.04	–27.6	0.7	C3
Davalliaceae	*Nephrolepis*	*biserrata*	(Sw.) Schott	e	0.04			n/a
Davalliaceae	*Nephrolepis*	*pectinata*	(Willd.) Schott	e	0.35	–33.5	1.1	C3
Davalliaceae	*Oleandra*	*articulata*	(Sw.) Presl.	he	0.09			n/a
Dryopteridaceae	*Polybotrya*	*caudata*	Kunze	he	0.09	–33.7	2.2	C3
Dryopteridaceae		sp. (98)		e	0.04	–37.1	2.9	C3
Ericaceae	*Cavendishia*	*axillaris*	A.C. Sm.	e	0.09			n/a
Ericaceae	*Cavendishia*	*capitulata*	Donn. Sm.	e	0.04	–31.6	0.5	C3
Ericaceae	*Cavendishia*	sp. (300)		e	0.09	–34.1	1.1	C3
Ericaceae	*Cavendishia*	sp. (570)		e	0.04			n/a
Ericaceae	*Macleania*	*smithiana*	Luteyn	e	0.09	–29.7	0.5	C3
Ericaceae	*Macleania*	sp. (292)		e	0.09	–32.9	0.7	C3
Ericaceae	*Satyria*	*panurensis*	(Benth. ex Meisn.) Hook. f. ex Nied.	e	0.17	–32.1	0.7	C3
Ericaceae	*Sphyrospermum*	*buxifolium*	Poepp. & Endl.	e	0.35	–33.8	0.8	C3
Gesneriaceae	*Codonanthe*	*crassifolia*	(H. Focke) C.V. Morton	e	0.35	–22	0.6	C3
Gesneriaceae	*Codonanthe*	*uleana*	Fritsch	e	0.09	–27.7	2.2	C3
Gesneriaceae	*Columnea*	*hirta*	Klotzsch & Hanst.	e	0.09	–29.4	1.5	C3
Gesneriaceae	*Columnea*	*maculata*	C.V. Morton	e	0.22	–33.3	1.5	C3
Gesneriaceae	*Columnea*	*purpurata*	Hanst.	e	*	–28.9	0.9	C3
Gesneriaceae	*Columnea*	*sanguinolenta*	(Klotzsch ex Oerst.) Hanst.	e	0.09	–33.2	1.4	C3
Gesneriaceae	*Columnea*	sp. (515)		e	0.04	–32.8	0.6	C3
Gesneriaceae	*Columnea*	sp. (568)		e	0.04	–26.5	0.8	C3
Gesneriaceae	*Columnea*	*tulae* var. *tomentulosa*	(Morl.) Morley	e	0.43	–30.8	1.4	C3
Gesneriaceae	*Drymonia*	*conchocalyx*	Hanst.	e	0.09			n/a
Gesneriaceae	*Drymonia*	*coriacea*	(Oerst. ex Hanst.) Wiehler	e	0.17	–32.1	1.5	C3
Gesneriaceae	*Drymonia*	*pilifera*	Wiehler	e	0.04	–32.6	2.5	C3
Grammitidaceae	*Ceradenia*	cf. pruinosa	(Maxon) L.E. Bishop	e	0.04	–32.8	0.7	C3
Grammitidaceae	*Cochlidium*	*serrulatum*	(Sw.) L.E. Bishop	e	0.22	–31.3	1	C3
Grammitidaceae	*Enterosora*	*parietina*	(Klotzsch) L.E. Bishop	e	0.04	–31.9	0.5	C3
Grammitidaceae	*Lellingeria*	*phlegmaria* var. *phlegmaria*	A.R. Sm. & R.C. Moran	e	0.04	–33.5	1.3	C3
Grammitidaceae	*Terpsichore*	cf. chrysleri	(Proctor ex Copel.) A.R. Sm.	e	0.04	–34.8	1.3	C3
Hymenophyllaceae	*Hymenophyllum*	*brevifrons*	Kunze	e	0.04	–28.8	1.3	C3
Hymenophyllaceae	*Hymenophyllum*	*elegans*	Sw.	e	0.04	–32.3	1.7	C3
Hymenophyllaceae	*Hymenophyllum*	*elegans*	Sw.	e	0.09			n/a
Hymenophyllaceae	*Hymenophyllum*	*maxonii*	H. Christ ex C.V. Morton	e	0.04	–29.7	1.4	C3
Hymenophyllaceae	*Hymenophyllum*	*plumosum*	Kaulf.	e	0.04	–30.4	1.6	C3
Hymenophyllaceae	*Hymenophyllum*	*polyanthos*	(Sw.) Sw.	e	0.13	–29.4	1.3	C3

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Hymenophyllaceae	*Hymenophyllum*	sp. (355)		e	0.04	−30.2	1.3	C3
Hymenophyllaceae		sp. (40)		e	0.04	−32.3	1.7	C3
Hymenophyllaceae	*Trichomanes*	aff. galeottii	E. Fourn.	e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	cf. hymenoides	Hedw.	e	0.04	−33.1	2.1	C3
Hymenophyllaceae	*Trichomanes*	cf. ovale	(E. Fourn.) Wess. Boer	e	0.09			n/a
Hymenophyllaceae	*Trichomanes*	cf. punctatum	Poir.	e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	*collariatum*	Bosch	e	0.35	−31.7	1.7	C3
Hymenophyllaceae	*Trichomanes*	*crispum*	L.	e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	*curtii*	Rosenst.	e	0.09	−32.1	1.7	C3
Hymenophyllaceae	*Trichomanes*	*delicatum*	Bosch	e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	*lucens*	Sw.	e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	*membranaceum*	L.	e	0.43	−33.2	1.8	C3
Hymenophyllaceae	*Trichomanes*	*ovale*	(E. Fourn.) Wess. Boer	e	0.17	−34.4	1.9	C3
Hymenophyllaceae	*Trichomanes*	*polypodioides*	L.	e	0.17	−31.9	1.4	C3
Hymenophyllaceae	*Trichomanes*	sp. (260)		e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	sp. (784)		e	0.04			n/a
Hymenophyllaceae	*Trichomanes*	*tuerckheimii*	H. Christ	e	0.04	−29.4	2.5	C3
Lentibulariaceae	*Utricularia*	sp. (577)		e	0.04			n/a
LomaRíopsidaceae	*Bolbitis*	*lindigii*	(Mett.) C. Chr.	he	0.09	−33.7	3.2	C3
LomaRíopsidaceae	*Bolbitis*	*nicotianifolia*	(Sw.) Alston	e	0.17	−36	3.5	C3
LomaRíopsidaceae	*Elaphoglossum*	*amygdalifolium*	(Mett. ex Kuhn) H. Christ	e	0.04	−32.6	1.8	C3
LomaRíopsidaceae	*Elaphoglossum*	*herminieri*	(Bory ex Fee) T. Moore	e	0.61	−33	0.6	C3
LomaRíopsidaceae	*Elaphoglossum*	*heterochroum*	Mickel	e	0.13	−33	1	C3
LomaRíopsidaceae	*Elaphoglossum*	*latifolium*	(Sw.) J. Sm.	e	0.09			n/a
LomaRíopsidaceae	*Elaphoglossum*	*latum*	(Mickel) Atehortúa ex Mickel	e	0.04	−31.3	0.6	C3
LomaRíopsidaceae	*Elaphoglossum*	*montgomeryi*	Mickel	e	0.39	−30	0.8	C3
LomaRíopsidaceae	*Elaphoglossum*	*palmense*	H. Christ	e	0.43	−29.7	0.6	C3
LomaRíopsidaceae	*Elaphoglossum*	*peltatum* ssp. *peltatum*	(Sw.) Urb.	e	0.52	−30.6	1.6	C3
LomaRíopsidaceae	*Elaphoglossum*	*productum*	Rosenst.	e	0.04			n/a
LomaRíopsidaceae	*Elaphoglossum*	sp. (242)		e	0.04			n/a
LomaRíopsidaceae	*Elaphoglossum*	sp. (426)		e	0.04	−34.7	1.2	C3
LomaRíopsidaceae	*LomaRíopsis*	*japurensis*	(Mart.) J. Sm.	e	0.09	−34.7	2.5	C3
LomaRíopsidaceae	*LomaRíopsis*	sp. (115)		e	0.04	−34.6	2.1	C3
LomaRíopsidaceae	*LomaRíopsis*	*vestita*	E. Fourn.	he	0.61	−34.7	2.7	C3
Lycopodiaceae	*Huperzia*	*dichotoma*	(Jacq.) Trevis.	e	0.3			n/a
Lycopodiaceae	*Huperzia*	*funiformis*	(Cham. ex Spring) Trevis.	e	0.04	−28.2	0.4	C3
Lycopodiaceae	*Huperzia*	*linifolia*	(L.) Trevis.	e	0.26	−31	0.9	C3
Lycopodiaceae	*Huperzia*	sp. (469)		e	0.04			n/a
Marcgraviaceae	*Marcgravia*	cf. sarcopera		he	0.04	−33.8	1.1	C3
Marcgraviaceae	*Marcgravia*	*nervosa*	Triana & Planch	he	0.09	−30.2	1.5	C3
Marcgraviaceae	*Marcgravia*	sp. (352)		he	0.04			n/a
Marcgraviaceae	*Marcgravia*	sp. (47)		he	0.04	−34.3	1.7	C3
Marcgraviaceae	*Marcgravia*	sp. (72)		he	0.43	−33.5	1	C3
Marcgraviaceae	*Ruyschia*	*tremadena*	(Ernst) Lundell	he	0.09	−31.5	0.8	C3
Marcgraviaceae	*Souroubea*	*sympetala*	Gilg	he	0.04			n/a
Melastomataceae	*Aciotis*	sp. (285)		e	0.04	−32.5	0.5	C3
Melastomataceae	*Blakea*	cf. calycosa	Gleason	he	0.04	−32.2	0.9	C3
Melastomataceae	*Blakea*	*foliacea*	Gleason	he	0.09	−29.2	2.8	C3
Moraceae	*Ficus*	sp. (527)		he	0.04	−34.4	1.5	C3
Myrsinaceae	*Cybianthus*	sp. (284)		e	0.09	−30.2	1	C3
N/A		sp. (406)		e	0.04			n/a
N/A		sp. (569)		e	0.04			n/a
Orchidaceae	*Acianthrea*	*ellipsophylla*	(L.O. Williams) Pridgeon & M.W. Chase	e	0.04	−19	1	CAM
Orchidaceae	*Aspasia*	*principissa*	Rchb. f.	e	0.04	−34.2	1.4	C3
Orchidaceae	*Bulbophyllum*	*oerstedii*	(Rchb. f.) Hemsl.	e	0.04	−29.8	1	C3
Orchidaceae	*Campylocentrum*	*micranthum*	(Lindl.) Rolfe	e	0.04	−18.5	0.7	CAM
Orchidaceae	*Campylocentrum*	*tyrridion*	Garay & Dunst.	e	0.04			n/a
Orchidaceae	*Catasetum*	*maculatum*	Hook.	e	0.09	−30.9	1.8	C3
Orchidaceae	*Cattleya*	sp. (750)		e	0.04	−30.7	1.1	C3
Orchidaceae	*Comparettia*	*falcata*	Poepp. & Endl.	e	*	−15.9	0.9	CAM
Orchidaceae	*Coryanthes*	*speciosa*	(Hook.) Hook.	e	0.04			n/a
Orchidaceae	*Crossoglossa*	cf. elliptica	Dressler	e	0.04	−27.6	4.1	C3
Orchidaceae	*Cryptarrhena*	*guatemalensis*	Schltr.	e	0.04	−27.2	1.5	C3
Orchidaceae	*Dichaea*	*brachypoda*	Rchb. f.	e	0.35	−31.5	1.6	C3
Orchidaceae	*Dichaea*	cf. eligulata	Folsom	e	0.43	−28.5	1.6	C3
Orchidaceae	*Dichaea*	cf. tuerckheimii	Schltr.	e	*	−30	1.4	C3
Orchidaceae	*Dichaea*	*fragrantissima subsp. eburnea*	Folsom	e	0.04	−30.1	1.2	C3
Orchidaceae	*Dichaea*	*panamensis*	Lindl.	e	0.09	−31	1.3	C3
Orchidaceae	*Dichaea*	sp. (112)		e	0.04	−29.2	1.2	C3
Orchidaceae	*Dichaea*	sp. (774)		e	*			n/a
Orchidaceae	*Dichaea*	*trulla*	Rchb. f.	e	0.13	−30	1.3	C3
Orchidaceae	*Elleanthus*	*cynarocephalus*	(Rchb. f.) Rchb. f.	e	0.13	−28.6	0.7	C3
Orchidaceae	*Elleanthus*	*graminifolius*	(Barb. Rodr.) Løjtnant	e	0.04	−30.5	0.6	C3
Orchidaceae	*Elleanthus*	*hymenophorus*	(Rchb. f.) Rchb. f.	e	0.26	−31.9	0.9	C3
Orchidaceae	*Encyclia*	*cochleata*	(L.) Dressler	e	0.09	−29.7	0.5	C3
Orchidaceae	*Encyclia*	sp. (680)		e	0.04	−26	1.8	C3
Orchidaceae	*Encyclia*	sp. (786)		e	0.04			n/a

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Orchidaceae	*Epidendrum*	*acunae*	Dressler	e	0.04	−15.7	1	CAM
Orchidaceae	*Epidendrum*	*anceps*	Jacq.	e	0.04			n/a
Orchidaceae	*Epidendrum*	*angustisegmentum*	(L.O. Williams) Hágsater	e	0.04	−26.7	1	C3
Orchidaceae	*Epidendrum*	cf. lockhartioides	Schltr.	e	0.04	−20.2	0.7	C3
Orchidaceae	*Epidendrum*	cf. ramosum	Jacq.	e	0.04			n/a
Orchidaceae	*Epidendrum*	*circinatum*	Ames	e	0.04	−26.9	0.8	C3
Orchidaceae	*Epidendrum*	*guanacastense*	Ames & C. Schweinf.	e	0.04			n/a
Orchidaceae	*Epidendrum*	*hunterianum*	Schltr.	e	0.09	−30.1	1.3	C3
Orchidaceae	*Epidendrum*	*isomerum*	Schltr.	e	0.52	−24.1	0.8	C3
Orchidaceae	*Epidendrum*	*laterale*	Rolfe	e	0.04			n/a
Orchidaceae	*Epidendrum*	*macroclinium*	Hágsater	e	0.04	−20.4	1.3	C3
Orchidaceae	*Epidendrum*	*nocturnum*	Jacq.	e	0.13	−22.7	1.1	C3
Orchidaceae	*Epidendrum*	*octomeRíoides*	Schltr.	e	0.04	−25.9	0.7	C3
Orchidaceae	*Epidendrum*	*raniferum*	Lindl.	e	0.04	−22.6	0.9	C3
Orchidaceae	*Epidendrum*	*repens*	Cogn.	e	0.04	−23.2	0.5	C3
Orchidaceae	*Epidendrum*	schistostemum sp. nov. (563)	Hágsater, Laube & Sánchez	e	0.22	−28.7	0.8	C3
Orchidaceae	*Epidendrum*	*schlechterianum*	Ames	e	0.04			n/a
Orchidaceae	*Epidendrum*	sp. (68)		e	0.09			n/a
Orchidaceae	*Epidendrum*	sp. (691)		e	0.04	−28.4	3	C3
Orchidaceae	*Epidendrum*	sp. (700)		e	0.04			n/a
Orchidaceae	*Epidendrum*	sp. (753)		e	0.04	−28.5	1.1	C3
Orchidaceae	*Epidendrum*	sp. (754)		e	0.26	−23	1.1	C3
Orchidaceae	*Epidendrum*	sp. (84)		e	0.04			n/a
Orchidaceae	*Epidendrum*	sp. nov. (468)		e	0.09			n/a
Orchidaceae	*Epidendrum*	*strobiliferum*	Rchb. F.	e	0.04	−22.5	1.4	C3
Orchidaceae	*Epidendrum*	*trialatum*	Hágsater	e	0.04	−15.9	0.5	CAM
Orchidaceae	*Galeottia*	*grandiflora*	A. Rich. & Galeotti	e	0.04	−32.4	1.7	C3
Orchidaceae	*Gongora*	*boracayanensis*	R.Jenny, Dalström & W.E.Higgins	e	0.04			n/a
Orchidaceae	*Gongora*	*quinquenervis*	Ruiz & Pavon	e	0.3			n/a
Orchidaceae	*Homalopetalum*	*pumilio*	(Rchb. f.) Dodson & Dressler	e	0.04			n/a
Orchidaceae	*Ionopsis*	*satyríoides*	(Sw.) Rchb. f.	e	0.09	−16.4	0.7	CAM
Orchidaceae	*Ionopsis*	*utricularíoides*	(Sw.) Lindl.	e	0.04			n/a
Orchidaceae	*Isochilus*	cf. chiriquensis	Schltr.	e	0.04	−32.4	1.8	C3
Orchidaceae	*Jaquiniella*	*globosa*	(Jacq.) Schltr.	e	0.04	−26.7	0.6	C3
Orchidaceae	*Jaquiniella*	sp. (705)		e	0.04	−31.4	1.3	C3
Orchidaceae	*Jaquiniella*	sp.(741)		e	0.09			n/a
Orchidaceae	*Leochilus*	*labiatus*	(Sw.) Kuntze	e	0.04			n/a
Orchidaceae	*Lepanthes*	sp. (576)		e	0.04			n/a
Orchidaceae	*Lepanthes*	sp. (628)		e	0.04			n/a
Orchidaceae	*Lockhartia*	*pittieri*	Schltr.	e	0.09	−21.3	1.1	C3
Orchidaceae	*Maxillaria*	*bicallosa*	(Rchb. f.) Garay	e	0.04	−14	0.7	CAM
Orchidaceae	*Maxillaria*	*brachybulbon*	Schltr.	e	0.09	−32.7	0.9	C3
Orchidaceae	*Maxillaria*	*brunnea*	Linden & Rchb. f.	e	0.09	−33.2	1.3	C3
Orchidaceae	*Maxillaria*	cf. longipetiolata	Ames & C. Schweinf.	e	0.04	−27.7	1.5	C3
Orchidaceae	*Maxillaria*	*chartacifolia*	Ames & C. Schweinf.	e	0.09	−34.8	1.1	C3
Orchidaceae	*Maxillaria*	*dendrobioides*	(Schltr.) L.O. Williams	e	0.09			n/a
Orchidaceae	*Maxillaria*	*discolor*	(G. Lodd. ex Lindl.) Rchb. f.	e	0.26	−32.3	1	C3
Orchidaceae	*Maxillaria*	*diuturna*	Ames & C. Schweinf.	e	0.13	−27.9	0.9	C3
Orchidaceae	*Maxillaria*	*fulgens*	(Rchb. f.) L.O. Williams	e	0.04	−28.4	0.6	C3
Orchidaceae	*Maxillaria*	*neglecta*	(Schltr.) L. O. Williams	e	0.57	−32.7	1	C3
Orchidaceae	*Maxillaria*	*sanguinea*	Rolfe	e	0.04	−27.7	1.2	C3
Orchidaceae	*Maxillaria*	sp. (544)		e	0.04	−29.9	0.6	C3
Orchidaceae	*Maxillaria*	sp. (672)		e	0.09	−31.4	0.9	C3
Orchidaceae	*Maxillaria*	sp. (676)		e	0.04	−33.1	1.6	C3
Orchidaceae	*Maxillaria*	sp. (736)		e	0.04			n/a
Orchidaceae	*Maxillaria*	sp. (737)		e	0.04			n/a
Orchidaceae	*Maxillaria*	sp. (745)		e	0.17	−24.6	0.9	C3
Orchidaceae	*Maxillaria*	sp. (762)		e	0.04	−29.7	0.8	C3
Orchidaceae	*Maxillaria*	sp. (756)		e	0.04	−30.1	1	C3
Orchidaceae	*Maxillaria*	*uncata*	Lindl.	e	0.13	−28.8	0.8	C3
Orchidaceae	*Maxillaria*	*valenzuelana*	(A. Rich.) Nash	e	0.04	−14.7	0.6	CAM
Orchidaceae	*Mormodes*	*skinneri*	Rchb. f.	e	0.04	−29.9	2.7	C3
Orchidaceae	*Myoxanthus*	*scandens*	(Ames) Luer	e	0.09	−28.9	1	C3
Orchidaceae	*Myoxanthus*	sp. (547)		e	0.04			n/a
Orchidaceae	*Myoxanthus*	*uncinatus*	(Fawc.) Luer	e	0.04	−28.1	1.1	C3
Orchidaceae	*Nidema*	*boothii*	Schltr.	e	0.3	−29.9	1	C3
Orchidaceae	*Octomeria*	*costaricensis*	Schltr.	e	0.04	−23.2	0.6	C3
Orchidaceae		sp. (747, Oncidiinae)		e	*	−29.7	0.9	C3
Orchidaceae		sp. (668, Oncidiinae)		e	0.04			n/a
Orchidaceae		sp. (764, Oncidiinae)		e	0.04	−27.9	1	C3
Orchidaceae	*Oncidium*	*bracteatum*	Warsz. ex Rchb. f.	e	*	−27.6	1.3	C3
Orchidaceae	*Oncidium*	sp. (726)		e	0.04	−28.3	1.7	C3
Orchidaceae	*Ornithocephalus*	*powellii*	Schltr.	e	0.09			n/a
Orchidaceae	*Ornithocephalus*	sp. (361)		e	0.13	−23.4	1.3	C3
Orchidaceae	*Ornithocephalus*	sp. (653)		e	0.09	−14.6	1.3	CAM
Orchidaceae	*Panmorphia*	*funerea*	(Barb. Rodr.) Luer	e	*	−28.4	1.5	C3
Orchidaceae	*Platystele*	cf. brenneri	Luer	e	0.04	−30.8	1.6	C3

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Orchidaceae	*Platystele*	*compacta*	(Ames) Ames	e	0.04	−29.2	0.8	C3
Orchidaceae	*Platystele*	sp. (491)		e	0.04	−34.3	1.6	C3
Orchidaceae	*Platystele*	*stenostachia*	(Rchb. f.) Garay	e	0.04			n/a
Orchidaceae	*Platystele*	*taylorii*	Luer	e	0.04	−30.4	1.4	C3
Orchidaceae	*Pleurothallis*	*allenii*	L. Wms.	e	0.04	−29.1	0.9	C3
Orchidaceae	*Pleurothallis*	*cardiothallis*	Rchb. f.	e	0.3	−33.2	1.1	C3
Orchidaceae	*Pleurothallis*	cf. aristata	Ames	e	0.04			n/a
Orchidaceae	*Pleurothallis*	cf. peperomioides	Ames	e	0.04	−30.5	1.1	C3
Orchidaceae	*Pleurothallis*	*decipiens*	Ames & C. Schweinf.	e	0.09			n/a
Orchidaceae	*Pleurothallis*	*isthmica*	Luer	e	0.17	−33	0.9	C3
Orchidaceae	*Pleurothallis*	*pantasmi*	Rchb. f.	e	0.3	−19.9	1.4	CAM
Orchidaceae	*Pleurothallis*	*rhodoglossa*	Schltr.	e	0.04			n/a
Orchidaceae	*Pleurothallis*	sp. (246)		e	0.22			n/a
Orchidaceae	*Pleurothallis*	sp. (522)		e	0.09			n/a
Orchidaceae	*Pleurothallis*	sp. (688)		e	0.04	−27.8	1.2	C3
Orchidaceae	*Pleurothallis*	sp. (689)		e	0.04	−16.6	3.5	CAM
Orchidaceae	*Pleurothallis*	sp. (714)		e	0.04	−29.5	0.8	C3
Orchidaceae	*Pleurothallis*	sp. (776)		e	0.04	−29.9	0.8	C3
Orchidaceae	*Pleurothallis*	sp. (777)		e	0.09	−28.3	1.4	C3
Orchidaceae	*Pleurothallis*	sp. (778)		e	0.13	−27.9	0.5	C3
Orchidaceae	*Pleurothallis*	sp. (779)		e	0.04			n/a
Orchidaceae	*Polystachia*	*foliosa*	(Hook.) Rchb. f.	e	0.09			n/a
Orchidaceae	*Prosthechea*	*pygmaea*	(Hook.) W.E. Higgins	e	0.09	−29.7	0.9	C3
Orchidaceae	*Psygmorchis*	*pumilio*	(Rchb. f.) Dodson & Dressler	e	*			n/a
Orchidaceae	*Rodriguezia*	*compacta*	Schltr.	e	0.17	−14.4	0.6	CAM
Orchidaceae	*Scaphyglottis*	*gracilis*	(Schltr.) Schltr.	e	0.09	−30.5	1.1	C3
Orchidaceae	*Scaphyglottis*	*longicaulis*	S.Watson	e	0.04	−32.1	1.5	C3
Orchidaceae	*Scaphyglottis*	*minutiflora*	Ames & Correll	e	0.22	−28.1	1.7	C3
Orchidaceae	*Scaphyglottis*	*prolifera*	(Sw.) Cogn.	e	0.39	−29.5	1.3	C3
Orchidaceae	*Scaphyglottis*	sp. (658)		e	0.13			n/a
Orchidaceae	*Sievekingia*	*suavis*	Rchb. f.	e	*	−31.2	1.6	C3
Orchidaceae	*Sigmatostalix*	*integrilabris*	Pupulin	e	0.04			n/a
Orchidaceae	*Sobralia*	*atropubescens*	Ames & C. Schweinf.	e	0.22	−30.1	0.8	C3
Orchidaceae	*Sobralia*	*fragrans*	Lindl.	e	0.52	−33.3	1	C3
Orchidaceae	*Sobralia*	sp. (5)		e	0.04			n/a
Orchidaceae	*Sobralia*	sp. (702)		e	0.04	−31.6	1.2	C3
Orchidaceae	*Sobralia*	sp. (781)		e	0.04			n/a
Orchidaceae	*Sobralia*	sp. (782)		e	0.04			n/a
Orchidaceae		sp. (4)		e	0.04	−29.5	1.9	C3
Orchidaceae		sp. (553)		e	0.04			n/a
Orchidaceae		sp. (645)		e	0.04	−29.8	1.5	C3
Orchidaceae		sp. (652)		e	0.04	−31.7	1.1	C3
Orchidaceae		sp. (683)		e	0.09	−31.3	1.6	C3
Orchidaceae		sp. (716)		e	0.04	−29.1	1.6	C3
Orchidaceae		sp. (727)		e	0.04			n/a
Orchidaceae		sp. (728)		e	0.04			n/a
Orchidaceae		sp. (771)		e	0.04	−28.8	1.8	C3
Orchidaceae		sp. (772)		e	0.04			n/a
Orchidaceae		sp. (785)		e	0.09			n/a
Orchidaceae		sp. (787)		e	0.04			n/a
Orchidaceae	*Specklinia*	*microphylla*	(A.Rich. & Galeotti) Pridgeon & M.W.Chase	e	0.04			n/a
Orchidaceae	*Specklinia*	*simmleriana*	(Rendle) Luer	e	0.17	−29.3	0.6	C3
Orchidaceae	*Stanhopea*	*ecornuta*	Lem.	e	0.13	−31.2	1	C3
Orchidaceae	*Stanhopeastrum*	*pullum*	(Rchb. f.) Szlach.	e	*	−29.4	2.1	C3
Orchidaceae		sp. (650, Stanhopeinae)		e	0.09			n/a
Orchidaceae		sp. (659, Stanhopeinae)		e	0.04	−28.7	1.5	C3
Orchidaceae		sp. (651, Stanhopeinae)		e	*	−31.4	1.6	C3
Orchidaceae		sp. (692, Stanhopeinae)		e	0.04	−30	1.7	C3
Orchidaceae		sp. (748, Stanhopeinae)		e	0.04	−31.3	2	C3
Orchidaceae	*Stelis*	*argentata*	Lindl.	e	0.04	−31	0.9	C3
Orchidaceae	*Stelis*	sp. (306)		e	0.04	−31.4	1	C3
Orchidaceae	*Stelis*	sp. (313)		e	0.04			n/a
Orchidaceae	*Stelis*	sp. (357)		e	0.04			n/a
Orchidaceae	*Stelis*	sp. (461)		e	0.04	−29	0.5	C3
Orchidaceae	*Stelis*	sp. (462)		e	0.04	−30.2	1.2	C3
Orchidaceae	*Stelis*	sp. (465)		e	0.09	−28.1	0.7	C3
Orchidaceae	*Stelis*	sp. (531)		e	0.13			n/a
Orchidaceae	*Stelis*	sp. (664)		e	0.04	−29.2	1	C3
Orchidaceae	*Stelis*	sp. (738)		e	0.04	−29.7	1.8	C3
Orchidaceae	*Stelis*	sp. (739)		e	*	−27.7	0.6	C3
Orchidaceae	*Stelis*	sp. (752)		e	0.04	−28	1.4	C3
Orchidaceae	*Stelis*	sp. (757)		e	0.04	−28.4	0.8	C3
Orchidaceae	*Stelis*	sp. (758)		e	0.09	−31.8	0.8	C3
Orchidaceae	*Stelis*	sp. (1)		e	0.04	−27.9	1.5	C3
Orchidaceae	*Telipogon*	*bullpenense*	(J.T. Atwood) N.H. Williams & Dressler	e	*			n/a
Orchidaceae	*Trichosalpinx*	*orbicularis*	(Lindl.) Luer	e	0.13	−31.1	1.3	C3
Orchidaceae	*Trigonidium*	*egertonianum*	Bateman ex Lindl.	e	0.3	−30.5	0.6	C3

Appendix A (*Continued*)

Family	Genus	Epitheton	Author	Life form	Incidence	δ^{13}C	% N	pp
Orchidaceae	*Trisetella*	*triglochin*	(Rchb. f.) Luer	e	0.13	−30.9	1.4	C3
Orchidaceae	*Vanilla*	*planifolia*	Andrews	e	0.04	−16.4	1.6	CAM
Orchidaceae	*Vanilla*	sp. (514)		e	0.04	−15.9	1.8	CAM
Piperaceae	*Peperomia*	*cordulata*	C. DC.	e	0.04			n/a
Piperaceae	*Peperomia*	*ebingeri*	Yunck.	e	0.04	−31.7	1.9	C3
Piperaceae	*Peperomia*	*elata*	C. DC. ex L.J. Schroeder	e	0.17	−36.9	2.1	C3
Piperaceae	*Peperomia*	*emarginella*	(Sw. ex Wikstr.) C. DC.	e	0.17	−33.3	1.8	C3
Piperaceae	*Peperomia*	*flexinervia*	Yunck.	e	0.09	−38	2.9	C3
Piperaceae	*Peperomia*	*glabella*	(Sw.) A. Dietr.	e	0.3	−32.3	0.5	C3
Piperaceae	*Peperomia*	*hernandiifolia*	(Vahl) A. Dietr.	e	0.04			n/a
Piperaceae	*Peperomia*	*macrostachya*	(Vahl) A. Dietr.	e	0.39	−23.4	1.5	C3
Piperaceae	*Peperomia*	*montium*	C. DC.	e	0.22	−30.6	1.8	C3
Piperaceae	*Peperomia*	*obtusifolia*	(L.) A. Dietr.	e	0.57	−33.9	1.3	C3
Piperaceae	*Peperomia*	*oerstedii*	C. DC.	e	0.57			n/a
Piperaceae	*Peperomia*	*pernambucensis*	Miq.	e	0.22	−35.8	1.6	C3
Piperaceae	*Peperomia*	*portobellensis*	Beurl.	e	0.13	−24.4	1.3	C3
Piperaceae	*Peperomia*	*rotundifolia*	(L.) Kunth	e	0.78	−30.9	0.9	C3
Piperaceae	*Peperomia*	*serpens*	(Sw.) Loudon	e	0.57			n/a
Piperaceae	*Peperomia*	sp. (210)		e	0.04			n/a
Piperaceae	*Peperomia*	*urocarpa*	Fisch. & C.A. Mey.	e	0.09			n/a
Polypodiaceae	*Campyloneurum*	*angustifolium*	(Sw.) Fée	e	0.13	−30.6	0.6	C3
Polypodiaceae	*Campyloneurum*	*aphanophlebium*	(Kunze) T. Moore	e	0.13			n/a
Polypodiaceae	*Campyloneurum*	*costatum*	(Kunze) C. Presl	e	0.09			n/a
Polypodiaceae	*Campyloneurum*	*fasciale*	(Humb. & Bonpl. ex Willd.) C. Presl	e	0.04	−33.9	2.5	C3
Polypodiaceae	*Campyloneurum*	*occultum*	(H. Christ) L. D. Gomez	e	0.13			n/a
Polypodiaceae	*Campyloneurum*	*phyllitidis*	(L.) C. Presl	e	0.61	−32	1.9	C3
Polypodiaceae	*Campyloneurum*	sp. (286)		e	0.04	−33.4	1.3	C3
Polypodiaceae	*Ceradenia*	*jungermannioides*	(Klotzsch) L.E. Bishop	e	0.04	−34.2	0.8	C3
Polypodiaceae	*Dicranoglossum*	*panamense*	(C. Chr.) L.D. Gómez	e	0.26	−30.4	0.8	C3
Polypodiaceae	*Microgramma*	*lycopodioides*	(L.) Copel.	e	0.43	−26.5	0.4	C3
Polypodiaceae	*Microgramma*	*reptans*	(Cav.) A.R. Sm.	e	0.48	−27.9	0.6	C3
Polypodiaceae	*Niphidium*	*crassifolium*	(L.) Lellinger	e	0.04			n/a
Polypodiaceae	*Pecluma*	*hygrometrica*	(Splitg.) M.G. Price	e	0.22	−33.5	1.9	C3
Polypodiaceae	*Pecluma*	*pectinata*	(L.) M.G. Price	e	0.26	−33.2	1.5	C3
Polypodiaceae	*Pecluma*	sp. (4)		e	0.04			n/a
Polypodiaceae	*Pleopeltis*	*panamensis*	(Weath.) Pic. Serm.	e	0.13	−33.1	1.2	C3
Polypodiaceae	*Pleopeltis*	*percussa*	(Cav.) Hook. & Grev.	e	0.39	−29.5	0.8	C3
Polypodiaceae	*Polypodium*	*dissimile*	L.	e	0.17	−31.1	1.5	C3
Polypodiaceae	*Polypodium*	*furfuraceum*	Schltdl. & Cham.	e	0.35	−28.9	1.1	C3
Polypodiaceae	*Polypodium*	*giganteum*	Desv.	e	0.22	−34.6	1.9	C3
Polypodiaceae	*Polypodium*	*loriciforme*	Rosenst.	e	0.04			n/a
Polypodiaceae	*Polypodium*	*rhodopleuron*	Kunze	e	0.04			n/a
Polypodiaceae	*Polypodium*	*sororium*	Humb. & Bonpl. ex Willd.	e	0.09			n/a
Polypodiaceae	*Polypodium*	*subviride*	Lellinger	e	0.17			n/a
Polypodiaceae	*Polypodium*	*triseriale*	Sw.	e	0.13			n/a
Polypodiaceae	*Serpocaulon*	*maritimum*	Hieron.	e	0.35	−29.3	1.7	C3
Pteridophyta		sp. (104)		e	0.04	−35.5	2.5	C3
Rubiaceae	*Hillia*	cf. allenii	C.M. Taylor	e	0.04			n/a
Rubiaceae	*Notopleura*	sp. (73)		e	0.04	−32.8	1	C3
Rubiaceae		sp. (119)		e	0.04	−36.1	2.7	C3
Rubiaceae		sp. (167)		e	0.04	−35.8	2.8	C3
Solanaceae	*Cyphomandra*	sp. (386)		e	0.04	−32.5	2.5	C3
Urticaceae		sp. (583)		e	0.04	−31.9	0.9	C3
Vittariaceae	*Ananthacorus*	*angustifolius*	(Sw.) Underw. & Maxon	e	0.26	−30	1.1	C3
Vittariaceae	*Antrophyum*	*anetioides*	H. Christ	e	0.13	−34.2	1.6	C3
Vittariaceae	*Antrophyum*	*cajenense*	(Desv.) Spreng.	e	0.52	−32.1	1.2	C3
Vittariaceae	*Antrophyum*	*lanceolatum*	(L.) Kaulf.	e	0.35			n/a
Vittariaceae	*Antrophyum*	*lineatum*	(Sw.) Kaulf.	e	0.09			n/a
Vittariaceae	*Vittaria*	*lineata*	(L.) Sm.	e	0.09	−32	1.6	C3
Vittariaceae	*Vittaria*	*stipitata*	Kunze	e	0.17			n/a

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