Epiphytes in Honduras: a geographical analysis of the vascular epiphyte flora and its floristic affinities to other Central American countries

SVEN P. BATKE[1,2,3*], ALFREDO CASCANTE-MARÍN[4] & DANIEL L. KELLY[1,2,3]

[1]*Department of Botany, Trinity College Dublin, College Green, Dublin 2, Ireland*
[2]*Trinity Centre for Biodiversity Research, Trinity College Dublin, Ireland*
[3]*Operation Wallacea, Hope House, Old Bolingbroke, Lincolnshire, UK*
[4]*Escuela de Biología y Herbario USJ, Universidad de Costa Rica*

Abstract: In this paper, we compared epiphyte inventories from Honduras to recent published floristic inventories from other Central American countries including Costa Rica, Panama, Nicaragua and Belize. Previous estimates of vascular epiphytes have revealed that approximately 9 % of all global plants are epiphytes and that in some countries they constitute approximately one quarter of the total plant diversity. Early estimates of vascular epiphytes from the neotropics have mostly overestimated the total number of epiphytes at a given locality, due to systematic misconceptions and or the use of different life-form classification systems. Moreover, some Central American countries such as Honduras have so far been neglected in any epiphyte surveys. Our database for Central America included a total of 2752 flowering-plant epiphytes. We reported a total of 882 vascular epiphytes (Angiosperms and Pteridophytes) from 245 genera and 29 families from Honduras, representing 11.1 % of the country's total vascular flora. Orchidaceae had the highest contribution to the epiphyte flora (54.9 %), followed by Polypodiaceae (18.9 %), and Bromeliaceae (11.3 %). Two distinctive floristic clusters were detected separating South-Central and North-Central countries. Honduras had the most floristic affinity to Nicaragua and Belize. In addition, a detailed floristic survey of Cusuco National Park, Honduras, a montane forest region, revealed that epiphytes in Honduras may contribute over 20 % of the total vascular flora in a particular area. The results of this study highlight the importance of epiphytes in Honduras relative to other Central American countries.

Key words: Biodiversity, composition, Cusuco National Park, Mesoamerica, orchid, species richness.

Handling Editor: Jorge Arturo Meave

Introduction

Honduras remains one of the least botanically studied countries in Central America. Although the number of plant collections have been relatively high in the past, most collection efforts have been very localized (Gentry 1978). Early botanical surveys dating from the nineteenth century include collections by A. Sinclair, G. Barcley and R.B. Hinds of the H.M.S. *Sulphur* voyage (Bentham 1844) and by W.B. Hemsley who published *Biologia Centrali-Americana*, an ency-

---

Corresponding Author; e-mail: batkesp@tcd.ie

clopaedia of the natural history of Mexican and Central American plants (Hemsley 1879 - 1888). Later, there were localized collections by Samuel J. Record (Record 1927), Paul C. Standley (Standley 1930, 1931, 1934) and T.G. Yuncker (Yuncker 1938, 1940). During the 1950's - 1990's botanical contributions to the Honduran Flora were mostly limited, with a few publications describing smaller additions to the Flora. In 1996 Cyril Hardy Nelson Sutherland and colleagues published a catalogue of the Honduran Pteridophytes (Nelson *et al.* 1996), which was followed by the most substantial record of the Honduran Flora to date: the *Catálogo de las plantas vasculares de Honduras* (Nelson 2008). However, Honduras still lacks a published Flora. According to the two published catalogues, the Honduran Flora encompasses 651 species of Pteridophytes (Nelson *et al.* 1996) and 7950 species of Spermatophytes (Angiosperms and Gymnosperms) (Nelson 2008). These numbers need to be revised soon as new discoveries continue to be made (Batke *et al.* 2013; Ulloa *et al.* 2010).

Epiphyte surveys in Honduras are particularly scarce and, to our knowledge, most epiphytes have only been included as part of general vegetation surveys, *e.g.* Standley (1931) on the flora of Lancetilla Valley near Tela; S. V. Zavala-Molina (University of Zamorano 2002 unpublished) on Bromeliaceae in a cloud forest in Department of El Paraíso; R. A. Rivera-Dueñas (University of Zamorano 2002 unpublished) in an orchid guide for 55 species of the Yuscarán Biological Reserve; Piątek *et al.* (2012) on ferns and lycophytes in Celaque National Park. We are only aware of one study that specifically focused on epiphytes, in the Copán region in the SW of Honduras (Decker *et al.* 2011). In geographical comparisons of the Neotropical epiphyte flora, Honduras has so far been entirely neglected (Cascante-Marín & Nivia-Ruíz 2013; Gentry 1982; Gentry *et al.* 1987; Nieder *et al.* 1999). In a recent overview of Neotropical epiphytes diversity, Cascante-Marín & Nivia-Ruíz (2013) included, for Central America, only Panama, Costa Rica, Nicaragua and Belize, with no references to Honduras, El Salvador and Guatemala.

Current estimates of Neotropical epiphyte diversity indicate that approximately 10 - 17 % of all vascular plants are epiphytes (Cascante-Marín & Nivia-Ruíz 2013; Ibisch *et al.* 1996). This is similar to global estimates of 9 - 10 % (Kress 1986; Zotz 2013b). However, the proportion of epiphyte species varies considerably between different
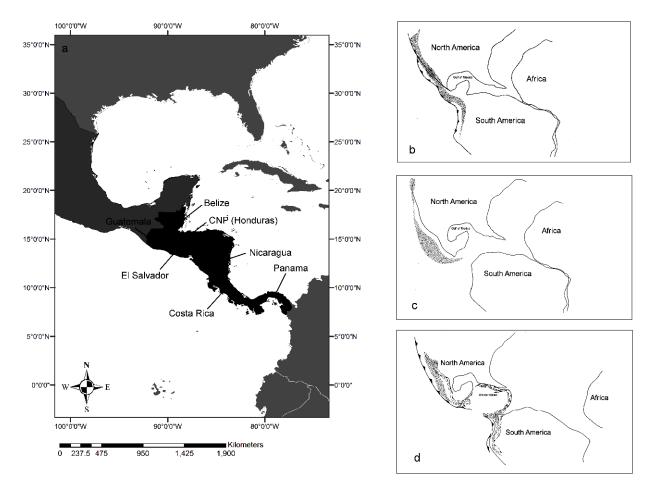
countries (Cascante-Marín & Nivia-Ruíz 2013). As pointed out by Zotz (2013a, b), differences in epiphyte estimates may be partially attributed to differences in the ways in which life-forms are classified (see Zotz 2013b for a more detailed discussion). The classification of plants into the epiphytic life-forms has never been straight-forward and many attempts have been made to encompass the different life-history strategies of different species (Benzing 1987, 1990). Many life-form categories blend into one another as emphasised by Kelly (1985), with examples of the plasticity of individual species, which makes their categorization difficult. Currently, the most useful life-form classification for mechanically dependent plants (Kelly 1985) divides species into six categories: holo-epiphytes, primary hemi-epiphytes, nomadic vines (includes secondary hemi-epiphytes), climbers (lianas and vines), stranglers and hemi-parasites (*i.e.*, mistletoes) (Zotz 2013a, b). Only holo-epiphytes and primary hemi-epiphytes (including stranglers) are accepted by Zotz (2013b) as epiphytes. It is essential, in any study of epiphyte diversity, to be explicit about the classification used to facilitate comparisons (Moffett 2000; Zotz 2013a).

In the present study, we amended Cascante-Marín & Nivia-Ruíz (2013) work on the Neotropical vascular epiphytes of Central America, by including floristic information on Honduran epiphytes and by excluding species that do not fall within the definition of Zotz (2013b). We focused our geographical analysis on individual countries rather than biogeographical regions, as the information gained from such an analysis is likely to be more useful in the implementation of national strategies for conservation. The aims of the study were: (1) to present data on the epiphytic diversity of the Cusuco National Park and an overview of the vascular epiphyte plants of Honduras and its contribution to the country's flora, and (2) to evaluate the geographic affinities of the Honduran epiphyte flora in the context of the Central American region.

Materials and methods

Cusuco National Park

Cusuco National Park (CNP) is located in the Departments of Santa Bárbara and Cortés in north-west Honduras (15° 32' 31" N, 88° 15' 49" W; Fig. 1a). Cusuco is situated within a mountainous, high-rainfall region, with a mean annual precipi-

Fig. 1. Maps of Central America including parts of South and North America. The figure on the left (a) presents the current configuration of Central America and the location of Cusuco National Park in Honduras. The figures on the right present late Jurassic (b), early Cretaceous (c) and Eocene (d) plate configurations of North and South America. Barbed lines are subduction zones where one tectonic plate moves under another plate. Dashes show distribution of magmatic arcs. Fig. b-d were adopted from Coney (1982) and Janzen (1983).

tation of approximately 2500 mm (Baker 1994). The wet season is between May and November. Maximum altitude is 2242 m asl. The vegetation in CNP consists of a complex mosaic of forest types, dominated by mixed broadleaved and pine forests in the core zone, with *Liquidambar* (Altingiaceae), *Pinus* (Pinaceae) and *Quercus* (Fagaceae) being among the principal tree genera (maximum forest height is approximately 65 m). The families Melastomataceae, Lauraceae, Rubiaceae and Euphorbiaceae are also well represented. At the highest elevations a well-defined elfin forest is present. The buffer-zone has a minimum altitude of zero meters (data were only collected above 660 m) and consists of secondary vegetation (mostly pine), coffee plantations, small settlements and agricultural pastures.

Epiphyte database

We compiled a database of vascular epiphytes for CNP and for Belize, Honduras, Nicaragua, Costa Rica and Panama. Information for CNP comprised floristic data from two surveys conducted by the lead author in 2012 and 2013, a floristic inventory provided by the Operation Wallacea Botany Team lead by D.L. Kelly (2004-2013; to request data from the inventory please contact http://opwall.com/) and a floristic inventory from C. Nelson from 1993 (Baker 1994). The inventory by the lead author focused on canopy dependent plants; voucher specimens are deposited at the herbaria in Trinity College Dublin (TCD). Rope climbing methods were employed in ten 150 × 150 m plots across the park and the six

largest trees were sampled for all mechanically dependent plants. The inventories by D.L. Kelly and C. Nelson focused on terrestrial life-forms, although opportunistic samples of the dependent flora were also made. The database for Honduras was compiled using published floristic information from the literature. We used the checklists by Nelson (2008) and Nelson *et al.* (1996) to extract the relevant inventory information.

The recent overview by Zotz (2013b) was followed to identify all the families and genera that were known to include epiphytes. To identify the different life-forms, we cross-referenced individual species to the Flora de Nicaragua (Gómez 2009; Stevens *et al.* 2001), Flora of Guatemala (Standley *et al.* 1946), Flora Mesoamericana (Davidse *et al.* 1995) and the TROPICOS Database of the Missouri Botanical Garden (http://www.tropicos.org). The floristic data for other Central American countries including Costa Rica, Nicaragua, Panama and Belize were assembled by A. Cascante-Marín (data summarized in Cascante-Marín & Nivia-Ruíz 2013).

In our database the botanical family and species name was documented for each country. Following Cascante-Marín *et al.* (2013) and Zotz (2013b), we included only records of holo-epiphytes, hemi-epiphytes, stranglers and facultative epiphytes. Accidental epiphytes and hemi-parasitic epiphytes from the families Eremolepidaceae, Loranthaceae and Santalaceae (Viscaceae) were not included. For taxonomic classification at the family level we followed Zotz (2013b), Chase *et al.* (2009) [APG III] and Mabberley (2008). We followed Zotz's (2013b) recommendation and excluded secondary hemi-epiphytes (*i.e.*, nomadic vines) (Moffett 2000; Zotz 2013a). Most of these species in our region belonged to genera from the Araceae such as *Anthurium* Schott, *Monstera* Adans, *Philodendron* Schott and *Syngonium* Schott. Moreover, we also excluded taxa that did not fully satisfy the definition of a primary hemi-epiphyte or holo-epiphyte (Zotz 2013b). These included several taxa from the families Gesneriaceae, Hydrangeaceae and Piperaceae and all taxa from the Marcgraviaceae. The exclusion of these taxa from the database resulted in a substantial reduction (n = 222) in the number of species for each region relative to those included by Cascante-Marín & Nivia-Ruíz (2013). We excluded a total of 177 species from Panama, 170 species from Costa Rica, 72 species from Nicaragua and 29 species from Belize. Records for Honduras that could not be assigned a life-form

category were excluded from the database. This will have led to a more conservative estimate of the number of epiphytes in Honduras. Finally, to avoid taxonomic synonymy or redundancy in our data we used the TROPICOS Database and the third edition of Mabberley (2008).

Data analysis

To allow comparison to other studies, we used the same analytical methods as described by Cascante-Marín & Nivia-Ruíz (2013). The contribution of epiphytic plants between different countries was compared using an 'epiphyte quotient'. The epiphyte quotient expressed the contribution of epiphytes to the total flora and was expressed as a percentage. As the epiphyte quotient does not take into account the areal extent of the region under investigation, we needed to express the relative richness of epiphytes with regards to the total area of each region. We used the model $S = cA^z$ to express the number of species (S) in relation to the countrie's area (A). The letters c and z are exponent values that were defined following Brummitt (2005) as $z = 0.14$ for non-isolated mainland regions and $c = S/A^z$. The relative richness (c) was rescaled using a scale from 0 - 1. A value of one was assigned to the country that had the highest c-value and therefore the highest relative richness (see Cascante-Marín & Nivia-Ruíz [2013] for more detail).

Table 1. Overall life-form composition of the vascular flora for Cusuco National Park, Honduras. The total number of families, genera and species for the different life-forms are presented.

Life-form	Number of families	Number of genera	Number of species
Terrestrial	120	299	607
Holo-epiphyte	14	60	164
Primary hemi-epiphyte	8	10	21
Strangler	1	1	3
Nomadic vine	1	5	20
Climber	35	53	79
Hemi-parasite	2	7	14
Total	181	435	908

The floristic similarity of epiphytes between countries was estimated using Jaccard's similarity

coefficient, Sj (Krebs 1999). This method was used as it allowed comparisons of data sets with unequal numbers of absent species. Only angiosperms were used in the floristic comparison among countries, as we did not have adequate information on Pteridophytes from most Central American countries.

Results

Epiphyte richness at the Cusuco National Park and Honduras

The database for CNP comprised 908 species of vascular plants (Table 1) and nearly 30 % corresponded to epiphytic species. Of the 301 mechanically dependent species recorded, including hemi-parasites, the following three groups accounted for half the total (Supplementary Material 1), 22.7 % (n = 66) were from the family Orchidaceae, 19 % (n = 58) were ferns from the group Polypodiaceae (*s.l.*) and 10.5 % (n = 32) were from the family Bromeliaceae. Most of the dependent flora (61.8 %) in CNP was represented by holo- and hemi-epiphytes. The epiphyte quotient for the CNP was 20.4 %.
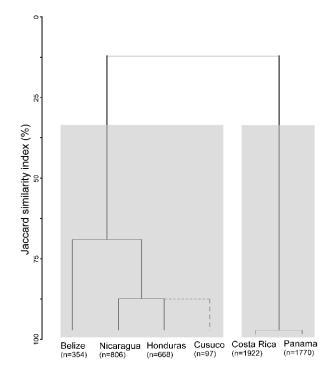
In our database for Honduras we identified a total of 878 species of epiphytes from 245 genera and 29 families. Most of the epiphytes (71.2 %) were represented by only three families: Orchidaceae, Polypodiaceae and Bromeliaceae. Only 13 of the 29 families were represented by more than ten species of epiphytes (Table 2). The epiphyte quotient for Honduras was approximately 11 % of the total flora (Table 2).

Geographic affinities of the Honduran epiphyte flora

The exclusion of 222 species from Cascante-Marín & Nivia-Ruíz (2013) database that did not fulfill Zotz's (2013b) definition of an epiphyte, produced a total of 585 Dicotyledonae (*s.l.*) and 2167 Monocotyledonae. The ten most diverse Central American epiphyte genera comprised 68.9 % of all the species from our database and were mainly represented by orchid genera (Table 3). Costa Rica had the highest epiphyte quotient followed by Panama, Nicaragua, Honduras and Belize. CNP had a high epiphyte quotient, but this was in relation to vegetation that was largely forest (Table 4). Comparing the relative number of epiphytes species (following the power function $S = cA^z$) between Central American countries indicated that Honduras had a similar relative

number of epiphytes to Nicaragua. Costa Rica and Panama had the highest relative numbers of epiphytes and Belize the lowest (Table 4).

The species richness of epiphytes deviated between different countries (χ^2 = 99.1; d.f. = 63; P < 0.01). A strong cluster was observed between South-Central (*i.e.*, Costa Rica and Panama) and North-Central American countries (Belize, Nicaragua and Honduras) (Fig. 2). The greatest similarity was between Costa Rica and Panama (Sj = 98.1 %). The epiphyte flora of Honduras was taxonomically most similar to that of neighboring Nicaragua, with a Sj value of 89.9 % (Fig. 2).

Fig. 2. Comparison of floristic affinities among angiosperm epiphytic floras across Central America. The total number of species is given for each country. A Jaccard similarity index was used as distance measure and flexible beta as a group linkage method for the clustering.

Discussion

The systematic contribution of vascular epiphytes (Angiosperms and Pteridophytes) to the global plant diversity has recently been estimated as approximately 9 %, which represents a total of 27,614 species from 913 genera in 73 families (Zotz 2013b). Similar global estimates have been made elsewhere, with approximations of 10 % (Gentry *et al.* 1987; Kress 1986; Madison 1977). The latter

Table 2. Taxonomic overview of Honduras' epiphyte flora and comparison with Neotropical and global figures. Data for the Neotropics and the global estimates are summarized from the literature. H = Honduras; N = Neotropics; G = Global; (1) = Kress (1986); (2) = Gentry & Dodson (1987); (3) = Wiehler (1983); (4) = Zotz (2013); (5) = Cascante-Marín & Nivia-Ruíz (2013); nd = no data available; asterisk = Pteridophytes.

Family	No. of genera with epiphytes[H]	No. of epiphytic species[H]	Total no. of species[H]	Epiphyte quotient (%)[H]	Epiphyte quotient (%)[N]	Epiphyte quotient (%)[G]
Orchidaceae	153	484	641	76.5	67[2]	69[4]
Bromeliaceae	13	100	125	80.0	46[1]	56[4]
Polypodiaceae*	17	44	76	57.9	93[1]	86[4]
Piperaceae	1	36	164	21.9	24[2]	25[4]
Hymenophyllaceae*	2	36	48	75.0	67[1]	55[4]
Aspleniaceae*	4	24	59	40.7	59[1]	55[4]
Dryopteridaceae*	4	21	38	55.3	15[2]	20[4]
Cactaceae	9	18	59	30.5	7[2]	8[4]
Gesneriaceae	5	15	57	26.3	20[3]	14[4]
Moraceae	1	13	67	19.4	37[2]	36[4]
Lycopodiaceae*	2	13	20	65.0	50[1]	49[4]
Araceae	2	12	95	12.6	42[2]	8[4]
Pteridaceae*(Vittariaceae)	8	11	14	78.6	100[2]	9[4]
Clusiaceae (Guttiferae)	1	8	31	25.8	9[2]	38[4]
Begoniaceae	1	7	32	21.9	nd	3[4]
Ericaceae	5	6	32	18.8	23[2]	15[4]
Nephrolepidaceae*	1	6	10	60.0	nd	67[4]
Melastomataceae	2	4	149	2.7	14[2]	6[4]
Solanaceae	2	4	173	2.3	nd	2[4]
Lomariopsidaceae*	1	4	4	100.0	nd	0.4[4]
Selaginellaceae*	1	3	33	9.1	nd	2[4]
Araliaceae	1	2	27	7.4	10[2]	4[4]
Rubiaceae	2	2	266	0.8	4[2]	1[4]
Blechnaceae*	1	2	18	11.1	nd	Nd
Asteraceae (Compositae)	2	2	414	0.5	nd	0.2[4]
Psilotaceae*	1	2	2	100.0	nd	100[4]
Oleandraceae*	1	1	1	100.0	nd	50[4]
Crassulaceae	1	1	3	33.3	nd	2 [4]
Asparagaceae	1	1	88	1.1	nd	0.5[4]
Total (all)	245	882	7950	11.1	10[2]-17.5[5]	9.0[4]
Total (Angiosperms)	202	715	7298	9.0	10.9[2]	10.1[4]
Total (Pteridophytes)	43	167	652	2.1	1.1[2]	1.2[4]

figure appears to correspond to early Neotropical estimates (Gentry *et al.* 1987; Ibisch *et al.* 1996) but has been demonstrated to vary significantly between different countries (Cascante-Marín & Nivia-Ruíz 2013). It is important to note that early estimates of Neotropical epiphytes often included other mechanically dependent plants such as secondary hemi-epiphytes. As previously pointed out by Moffett (2000) and more recently by Zotz

(2013a), the term "secondary hemi-epiphyte" has often been misused in the literature and has resulted in much confusion in the categorization of species. Secondary hemi-epiphytes differ in their ecology from species that are truly epiphytic (Holbrook *et al.* 1996; Zotz 2013a, b). Many estimates for epiphytes are thus likely to be exaggerated using the criteria of Zotz (2013b).

Our analysis, which excluded secondary hemi-

epiphytes and other taxa that did not fully satisfy Zotz's criteria (*e.g.*, Marcgraviaceae), differed from earlier Central American estimates between 0.8 % and 1.8 % (Cascante-Marín & Nivia-Ruíz 2013). The exclusion of species (total number of excluded species = 222) across the countries did not affect the overall observed epiphyte quotient patterns, but somewhat changed the floristic affinities among countries. In Central America, the highest number of epiphytes was recorded from Costa Rica, followed by Panama, Nicaragua, Honduras and Belize. This is still in agreement with Cascante-Marín & Nivia-Ruíz (2013). However, floristically they found that Nicaragua was relatively close to Costa Rica and Panama in southern Central America, whereas our study found that Nicaragua was more similar to north Central American countries. Including Honduras into the analysis resulted in a split of Nicaragua from the South-Central American group. The exclusion of certain species (*e.g.*, nomadic vines) resulted in an approximately 14 % decreases in floristic similarity between the South-Central and North-Central American countries. The decrease in floristic similarity can be attributed to the high diversity and degree of endemism of certain species such as nomadic aroids (Araceae) in South-Central America (Croat 1998; Grayum 1990). Our analysis excluded most species of the Araceae. We omitted a total of 127 nomadic species from Panama, 107 from Costa Rica, 47 from Nicaragua and 24 from Belize. Of the 150 species of Araceae reported from Panama, 55 % are endemic to the country, whereas Honduras and Nicaragua have each only a single endemic species (Croat 1998).

The floristic difference among Central American countries reflects the differing representation of biogeographical elements from North and South American floras. Past geological, climatic and biogeographical events are recognized to have played important roles in the current distribution of epiphytes in the Neotropics and between different countries (Cascante-Marín & Nivia-Ruíz 2013; Gentry 1982, 1988; Graham 2011; Haffer 1969; Knapp *et al.* 2003; Morawetz *et al.* 2007). During the late Jurassic the Caribbean-Middle American region formed, as part of the super-continent Pangaea (Fig. 1b). South America was still attached to Africa at that point, which predetermined South America's position with respect to North America. By the early Cretaceous South America started separating from North America (Fig. 1c). In the late Cretaceous a chain of magmatic arcs formed, connecting Central America

Table 3. Composition of the Central American epiphytic flora (flowering plants) as represented by the ten most important, in terms of species number, epiphyte families and genera. Note: *Maxillaria* (*sensu lato*) includes species of the genera *Camaridium* and *Ornithidium*. *Pleurothallis* (*sensu lato*) includes species of the genera *Anathallis*, *Specklinia*, *Stelis* and *Trichosalpinx*.

Family composition		Generic composition	
Family	Total epiphytes	Genera	Total epiphytes
Orchidaceae	1693	*Epidendrum* (Orchidaceae)	221
Bromeliaceae	266	*Anthurium* (Araceae)	145
Araceae	160	*Maxillaria* (Orchidaceae)	140
Piperaceae	113	*Lepanthes* (Orchidaceae)	123
Ericaceae	81	*Peperomia* (Piperaceae)	113
Gesneriaceae	74	*Stelis* (Orchidaceae)	91
Melastomataceae	65	*Pleurothallis* (Orchidaceae)	84
Moraceae	42	*Tillandsia* (Bromeliaceae)	73
Cyclanthaceae	41	*Werauhia* (Bromeliaceae)	64
Cactaceae	39	*Oncidium* (Orchidaceae)	55

with Ecuador (Coney 1982). Thus, the connection between nuclear Central America and South America was reestablished by mostly interrupted island arcs in the late Cretaceous (Gentry 1982). The degree of connectivity and the number of islands that were above sea level however, are not known. In the late Neogene with the formation of the Central American trench and the associated uplifting of new volcanic islands (Fig. 1d), the land bridge between South and Central America coalesced forming a land connection across the Isthmus of Panama (Graham 1973, 2011). Of particular importance to the migration of plant species was the uplift of the Andes during the Neogene, which resulted in a rapid increase in plants from the Gondwanan families in South America. With the closing of the Panamanian Isthmus, Laurasian taxa migrated southwards and Gondwanan families migrated northwards. This

Table 4. Species richness of vascular epiphytes (including Pteridophytes) from selected countries of Central America. Data from Nicaragua, Costa Rica, Panama and Belize were modified from Cascante-Marín & Nivia-Ruíz (2013). The relative number of species represents the number of epiphytic (*i.e.*, holo-epiphytes, primary hemi-epiphytes, stranglers and facultative) species in relation to the area of the region (S = cA^z).

Country or CNP	Elevation (m a.s.l.)	Area (km^2)	Epiphyte flora	Epiphyte quotient (%)	Relative number of species
Costa Rica	0 - 3820	51,100	2430	25.50	1.00
Panama	0 - 3475	78,200	1804	20.55	0.70
Nicaragua	0 - 2438	129,794	977	18.58	0.35
Honduras	0 - 2870	112,492	878	11.04	0.32
Belize	0 - 1124	22,963	381	11.14	0.18
CNP	660 - 2242	234	185	20.35	0.16

migration, particularly from the south, resulted in Gondwanan elements observed in South-Central America (Gentry 1982). The flora of Panama and Costa Rica are therefore more influenced by Godwanan families, whereas North-Central American countries such as Honduras have much stronger Laurasian and north temperate floristic elements (Graham 2011). This was also reflected in our results, as our cluster analysis identified one distinctive South-Central and another North-Central American group.

The strong South-North floristic dissimilarity of epiphytes was also reflected in individual taxonomic groups. For example, within the Ericaceae the genera *Anthopteropsis* A.C.Sm., *Didonica* Luteyn & Wilbur and *Utleya* Luteyn & Wilbur were characteristic of the South-Central American group. These genera have mostly been associated with low-elevation and permanent cloud forests in Panama and Costa Rica (Luteyn 2002). Similar, the North-Central American group was characterized by the genus *Satyria* Klotzsch. Kron *et al.* (2005) pointed out that *Satyria* has undergone more recent speciation in North-Central America than most Ericaceae following the introduction via dispersal from the northern Andes (Kron *et al.* 2005). Similarly, we found evidence that the number of epiphytic species from the genus *Columnea* L. (Gesneriaceae) decreased from the South-Central (mainly Costa Rica) to the North-Central American group (60 % difference in the number of species between Costa Rica and Belize). DNA chloroplast analysis of *Columnea* has suggested that the radiation of this genus has most likely occurred in Central America and that the epiphytic habit arose more than once (Smith *et al.* 1994b). Bird dispersal has been attributed to be one of the most likely contributing factors to

explain the distribution of *Columnea* in some Central America regions (Smith *et al.* 1994a). This was also reported for other families, where biotic and long-distant dispersal are believed to be more important than past plate-tectonic activities (Christenhusz *et al.* 2013; Pennington *et al.* 2004; Renner *et al.* 2001). Other geographical features such as the Talamancan montane range in Costa Rica and Panama could also have been important in the radiation of some species (Kohlmann *et al.* 2010; Perret *et al.* 2013).

We focused our analysis on national floras and thus limited our analysis to political boundaries. We believe that such an approach can be of similar importance to studies that assess floras within a biogeographical framework. Many conservation efforts for woodlands across Central America are still much limited by regional and national policy strategies (Duffy 2005). Globally, only approximately 10 % of protected areas are part of trans-boundary conservation efforts (Agrawal 2000), which highlights the importance of studies that focus on floras at a national level. Our results are therefore very important to help with the implementation of national strategies for conservation (Mondragón *et al.* 2015), as they give insight into the contribution of epiphytes to national floras. However, we are acknowledging the importance of biogeographical studies on epiphytes, particularly in the Neotropics, as information derived from such studies can give further insight into how evolutionary processes have shaped their current distribution (Givnish *et al.* 2014).

In our database for Honduras we recognized a total of 878 epiphytes species from 245 different genera and 29 different families. As expected, epiphytism was mostly restricted to a small

number of taxonomic groups including Orchidaceae (n = 484), Pteridophytes (n = 167) and Bromeliaceae (n = 100). The dominance of these groups from Honduras is consistent with other studies (Cascante-Marín & Nivia-Ruíz 2013; Gentry *et al.* 1987; Kreft *et al.* 2004; Küper *et al.* 2004; Zotz 2013b). Orchidaceae in particular is the most dominant family in Neotropical inventories. Of the 2752 angiosperm epiphyte species reported here from Central America, orchids alone contributed to over 60 % of the total vascular epiphyte flora. The high numbers of epiphytic orchids in many tropical inventories reflect the orchids' high genetic and morphological variation, their short life-cycle and the higher niche differentiation in tropical forest canopies compared to forest floors (Ackerman *et al.* 1999; Benzing 1990; Gravendeel *et al.* 2004). Globally almost 25,000 orchid species have been described, of which approximately 18,000 are epiphytic (Gravendeel *et al.* 2004). Members of Polypodiaceae, a Pteridophyte family, were the second largest epiphytic group from Honduras. Pteridophytes, in general, accounted for approximately 2.1 % of all vascular epiphytic plants in Honduras, which was slightly above Neotropical (1.1 %) and global (1.2 %) estimates for that group (Gentry *et al.* 1987; Zotz 2013b).

Honduras had an epiphyte quotient of approximately 11 %, which was similar to Belize, but only half that of Panama (approximately 20 %) and less than half that of Costa Rica (approximately 25 %). Compared to Nicaragua, Honduras had a similar relative number of epiphytes for its land-surface area, whereas the relative numbers of epiphytes for Costa Rica and Panama were much higher. Although Honduras is almost twice the size of Panama and Costa Rica, it had a much lower number of epiphyte species. As epiphytes mostly occur in humid forest habitats, the variation in the relative number of species observed could be a result of differences in forest cover among countries. According to the FAO (2010), Honduras had a forest cover of approximately 50,000 km^2 (46 %) in 2010, whereas forest cover in Nicaragua (26 %) and Panama (44 %) was lower. Belize had the highest forest cover (61 %), followed by Costa Rica (51 %). Botanical efforts in documenting the flora of Central American countries may also account for the observed differences in epiphyte diversity; the botanical exploration and documentation of Costa Rica and Panama's flora have received more attention during the last decades.

Moreover, it is important to note that the epiphyte quotient in a particular locality depends on the number of non-epiphytic taxa sampled. For example, CNP had an epiphyte quotient of approximately 20 % and a relatively low number of species for its size. The high epiphyte quotient is likely the result of a survey bias towards terrestrial woodland species and the relative number of species was consequently based on an area that was mainly forest.

Our data suggest a decreasing geographic trend in vascular epiphyte diversity in Central America, from Panama to Belize. It is possible that some of the floristic difference, which was observed between the South-Central and North-Central American countries, is attributed to low specialized collection efforts particularly in North-Central American countries. Our database did not include all Central American floras and it is likely that the total number of epiphytes in northern Central America would be higher if Guatemala and El Salvador were included. Guatemala in particular has a very rich flora (Standley *et al.* 1946) and it is believed that Guatemala's flora is the most species-rich flora for angiosperms in Central America (Morawetz *et al.* 2007). As most epiphytes have a very small distribution range (Küper *et al.* 2004), including epiphyte inventories from Guatemala and El Salvador would most certainly increase the total number of epiphytes found in North-Central America. Belize, El Salvador and Honduras have currently no complete published floras and even the checklists for vascular plants in El Salvador (Calderón *et al.* 1941) and Guatemala (with the exception of orchids [Cameron 2000]) require substantial revisions.

Most research on the mechanically-dependent flora in Central America has been conducted in South-Central American countries such as Panama and Costa Rica (Cáceres González *et al.* 2011, 2013; Cascante-Marín *et al.* 2009; Laube *et al.* 2006; Marín *et al.* 2008; Nadkarni and Mateleon 1992; Patiño *et al.* 1999; Zotz *et al.* 2008), with less focus on North-Central American countries such as Nicaragua (Atwood 1984), Belize (Catling 1997), El Salvador (Méndez *et al.* 2010), Guatemala (Catling *et al.* 1989; Nesheim *et al.* 2007) and Honduras (Decker *et al.* 2011). The only country in Mesoamerica that has been covered relatively well in epiphyte studies is Mexico (Hietz *et al.* 2002; Hietz *et al.* 1995; Scheffknecht *et al.* 2010; Vergara-Torres *et al.* 2010; Wolf 2005; Wolf *et al.* 2006; Wolf *et al.* 2001). Collections in

Honduras have mostly been sporadic and have generally focused on the terrestrial flora. Although local herbaria contain some good collections of epiphytes, many species, particularly widely distributed species, are still absent from collections or require taxonomic revisions. Botanical collections have often focused on the southern and north-western coast, with little contribution from mountainous regions (Gentry 1978). It has been shown that sites that are located in mountain cloud forest are often more epiphyte rich (Cardelús *et al.* 2006), highlighting the need to have more targeted collections efforts in such areas.

It is likely that the number of epiphytes in Honduras, and other 'epi-floristically' neglected countries such as El Salvador, Guatemala and Belize, will rise with more targeted sampling efforts. For example, our survey in CNP discovered previously unknown epiphytes in the Park, Honduras and/or Mesoamerica (*e.g.*, Batke *et al.* 2013). This is important given current anthropogenic pressures on many forests in Honduras and elsewhere in Central America (Bonta 2005; Southworth *et al.* 2001). We therefore propose that future epiphyte sampling efforts in Honduras focus more on moist montane forests, as these locations have been less impacted by forest degradation and are more likely to reveal further additions to the Honduran epiphyte flora.

Acknowledgments

References

Ackerman, J. D. & S. Ward. 1999. Genetic variation in a widespread, epiphytic orchid: where is the evolutionary potential? *Systematic Botany* **24**: 282-291.

Agrawal, A. 2000. Adaptive management in transboundary protected areas: the Bialowieza National Park and Biosphere Reserve as a case study. *Environmental Conservation* **27**: 326-333.

Atwood, J. T. 1984. A floristic study of Volcán Mombacho Department of Granada, Nicaragua. *Annals of the Missouri Botanical Garden* **71**: 191-209.

Baker, D. S. (ed.). 1994. *Evaluación Ecológica Rápida, Parque Nacional El Cusuco y Cordillera del Merendón, Honduras.* The Nature Conservancy, Washington.

Batke, S. & N. Hill. 2013. First record of *Serpocaulon lasiopus* (Polypodiaceae) from Mesoamerica. *American Fern Journal* **103**: 182-184.

Bentham, G. (ed.). 1844. *The Botany of the Voyage of H.M.S. Sulphur, Under the Command of Captain Sir Edward Belcher, R., N., C., B., F., R., G., S., etc. During the Year 1836-1842.* Smith, Elder & Co., London.

Benzing, D. H. 1987. Vascular epiphytism: taxonomic participation and adaptive diversity. *Annals of the Missouri Botanical Garden* **74**: 183-204.

Benzing, D. H. (ed.). 1990. *Vascular Epiphytes. General Biology and Related Biota.* Cambridge University Press, Cambridge.

Bonta, M. 2005. Becoming-forest, becoming-local: transformations of a protected area in Honduras. *Geoforum* **36**: 95-112.

Brummitt, N. A. 2005. Plant diversity and complexity patterns: local, regional and global dimensions. pp. 539-564. *In:* N. A. Brummitt (ed). *Plant Diversity and Complexity Patterns: Local, Regional and Global Dimensions.* Biologiske Skrifter 55, The Royal Danish Academy of Sciences and Letters, Copenhagen.

Cáceres González, D. A., K. Schulte, M. Schmidt & G. Zizka. 2011. A synopsis of the Bromeliaceae of Panama, including new records for the country. *Willdenowia - Annals of Botanic Garden and Botanical Museum Berlin-Dahlem* **41**: 357-369.

Cáceres González, D. A., K. Schulte, M. Schmidt & G. Zizka. 2013. Diversity and levels of endemism of the

Bromeliaceae of Costa Rica - an updated checklist. *PhytoKeys* **29**: 17-62.

Calderón, S. & P. C. Standley (eds.). 1941. *Flora Salvadoreña: Lista Preliminar de Plantas de El Salvador*. Imprenta Nacional, San Salvador.

Cameron, K. M. 2000. Orchids of Guatemala: a revised annotated checklist. *Brittonia* **52**: 365-365.

Cardelús, C. L., R. K. Colwell & J. E. Watkins. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* **94**: 144-156.

Cascante-Marín, A. & A. Nivia-Ruíz. 2013. Neotropical flowering epiphyte diversity: local composition and geographic affinities. *Biodiversity and Conservation* **22**: 113-125.

Cascante-Marín, A., N. von Meijenfeldt, H. M. H. de Leeuw, J. H. D. Wolf, J. G. B. Oostermeijer & J. C. M. den Nijs. 2009. Dispersal limitation in epiphytic bromeliad communities in a Costa Rican fragmented montane landscape. *Journal of Tropical Ecology* **25**: 63-73.

Catling, P. M. 1997. Influence of aerial *Azteca* nests on the epiphyte community of some Belizean orange orchards. *Biotropica* **29**: 237-242.

Catling, P. M. & L. P. Lefkovitch. 1989. Associations of vascular epiphytes in a Guatemalan cloud forest. *Biotropica* **21**: 35-40.

Chase, M. W. & J. L. Reveal. 2009. A phylogenetic classification of the land plants to accompany APG III. *Botanical Journal of the Linnean Society* **161**: 122-127.

Christenhusz, M. J. M. & M. W. Chase. 2013. Biogeographical patterns of plants in the Neotropics - dispersal rather than plate tectonics is most explanatory. *Botanical Journal of the Linnean Society* **171**: 277-286.

Coney, P. J. 1982. Plate tectonic constraints on the biogeography of Middle America and the Caribbean region. *Annals of the Missouri Botanical Garden* **69**: 432-443.

Croat, T. B. 1998. History and current status of systematic research with Araceae. *Aroideana* **21**: 26-145.

Davidse, G., M. S. Sousa & S. Knapp (eds.). 1995. *Flora Mesoamericana*. Universidad Nacional Autónoma de México, Mexico City.

Decker, M., T. Benjamin, F. Casanoves & F. DeClerck. 2011. Composición y diversidad de epífitas y aves en distintos tipos y densidades de árboles dispersos en sistemas silvopastoriles en la subcuenca del río Copán, Honduras. *Agroforestería en las Américas* **48**: 46-53.

Duffy, R. 2005. The politics of global environmental governance: the powers and limitations of transfrontier conservation areas in Central America. *Review of International Studies* **31**: 307-323.

FAO. 2010. *Global Forest Resources Assessment*. Food and Agriculture Organization of the United Nations, Rome.

Gentry, A. H. 1978. Floristic knowledge and needs in Pacific tropical America. *Brittonia* **30**: 134-153.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* **69**: 557-593.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* **75**: 1-34.

Gentry, A. H. & C. H. Dodson. 1987. Diversity and biogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden* **74**: 205-233.

Givnish, T. J., M. H. J. Barfuss, B. V. Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, R. S. Jabaily, D. M. Crayn, J. A. C. Smith, K. Winter, G. K. Brown, T. M. Evans, B. K. Holst, H. Luther, W. Till, G. Zizka, P. E. Berry & K. J. Sytsma. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. *Molecular Phylogenetics and Evolution* **71**: 55-78.

Gómez, L. D. (ed.). 2009. *Flora de Nicaragua: Tomo IV, Helechos*. Missouri Botanical Garden Press, Saint Louis.

Graham, A. (ed.). 1973. *Vegetation and Vegetational History of Northern Latin America*. Elsevier, New York.

Graham, A. (ed.). 2011. *A Natural History of the New World*. The University of Chicago Press, Chicago.

Gravendeel, B., A. Smithson, F. J. W. Slik & A. Schuiteman. 2004. Epiphytism and pollinator specialization: drivers for orchid diversity? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**: 1523-1535.

Grayum, M. H. 1990. Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Garden* **77**: 628-697.

Haffer, J. 1969. Speciation in Amazonian forest birds. *Science* **165**: 131-137.

Hemsley, W. B. (ed.). 1879-1888. *Biologia Centrali-Americana*. R.H. Porter & Dulau & Co., London.

Hietz, P., J. Ausserer & G. Schindler. 2002. Growth, maturation and survival of epiphytic bromeliads in a Mexican humid montane forest. *Journal of Tropical Ecology* **18**: 177-191.

Hietz, P. & U. Hietz-Seifert. 1995. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science* **6**: 487-498.

Holbrook, N. M. & F. E. Putz. 1996. Physiology of tropical vines and hemiepiphytes: plants that climb up and plants that climb down. pp. 363-394. *In:* N. M. Holbrook & F. E. Putz (eds.) *Physiology of Tropical Vines and Hemiepiphytes: Plants that Climb Up and Plants that Climb Down.* Springer, Berlin.

Ibisch, P. L., A. Boegner, J. Nieder & W. Barthlott. 1996. How diverse are neotropical epiphytes? An analysis based on the 'Catalogue of the flowering plants and gymnosperms of Peru'. *Ecotropica* **2**: 13-28.

Janzen, D. H. (ed.). 1983. *Costa Rican Natural History.* University of Chicago Press, Chicago.

Kelly, D. L. 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories. *Journal of Biogeography* **12**: 223-241.

Knapp, S. & J. Mallet. 2003. Refuting refugia? *Science* **300**: 71-72.

Kohlmann, B., D. Roderus, O. Elle, Á. Solís, X. Soto & R. Russo. 2010. Biodiversity conservation in Costa Rica: a correspondence analysis between identified biodiversity hotspots (Araceae, Arecaceae, Bromeliaceae, and Scarabaeinae) and conservation priority life zones. *Revista Mexicana de Biodiversidad* **81**: 511-559.

Krebs, C. J. (ed.). 1999. *Ecological Methodology.* Benjamin/Cummings, Menlo Park.

Kreft, H., N. Koster, W. Kuper, J. Nieder & W. Barthlott. 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Ecuador. *Journal of Biogeography* **31**: 1463-1476.

Kress, W. J. 1986. The systematic distribution of vascular epiphytes: an update. *Selbyana* **9**: 2-22.

Kron, K. A. & J. L. Luteyn. 2005. Origins and biogeographic patterns in Ericaceae: new insights from recent phylogenetic analyses. *Biologiske Skrifter* **55**: 479-500.

Küper, W., H. Kreft, J. Nieder, N. Köster & W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *Journal of Biogeography* **31**: 1477-1487.

Laube, S. & G. Zotz. 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* **97**: 1103-1114.

Luteyn, J. 2002. Diversity, adaptation, and endemism in neotropical Ericaceae: biogeographical patterns in the Vaccinieae. *The Botanical Review* **68**: 55-87.

Mabberley, D. J. (ed.). 2008. *A Portable Dictionary of Plants, their Classification and Use.* Cambridge University Press, Cambridge.

Madison, M. 1977. Vascular epiphytes: their systematic occurrence and salient features. *Selbyana* **2**: 1-13.

Marín, A. C., J. H. D. Wolf, J. G. B. Oostermeijer & J. C. M. Den Nijs. 2008. Establishment of epiphytic bro-meliads in successional tropical premontane forests in Costa Rica. *Biotropica* **40**: 441-448.

Méndez, V. E., C. M. Bacon, M. Olson, K. S. Morris & A. Shattuck. 2010. Agrobiodiversity and shade coffee smallholder livelihoods: a review and synthesis of ten years of research in Central America. *The Professional Geographer* **62**: 357-376.

Moffett, M. W. 2000. What's "up"? A critical look at the basic terms of canopy biology. *Biotropica* **32**: 569-596.

Mondragón, D., T. Valverde & M. Hernández-Apolinar. 2015. Population ecology of epiphytic angiosperms: a review. *Tropical Ecology* **56**: 1-39.

Morawetz, W. & C. Raedig. 2007. Angiosperm biodiversity, endemism and conservation in the Neotropics. *Taxon* **56**: 1245-1254.

Nadkarni, N. M. & T. J. Matelson. 1992. Biomass and nutrient dynamics of epiphytic litterfall in a neotropical montane forest, Costa Rica. *Biotropica* **24**: 24-30.

Nelson, C. H. S. (ed.). 2008. *Catálogo de las plantas vasculares de Honduras.* Secretaría de Recursos Naturales y Ambiente, Tegucigalpa.

Nelson, C. H. S., R. Gamarra Gamarra & J. Fernández Casas. 1996. Hondurensis plantarum vascularium catalogus. Pteridophyta. *Fontqueria* **43**: 143.

Nesheim, I. & R. H. Økland. 2007. Do vine species in neotropical forests see the forest or the trees? *Journal of Vegetation Science* **18**: 395-404.

Nieder, J., S. Engwald & W. Barthlott. 1999. Patterns of neotropical epiphyte diversity. *Selbyana* **20**: 66-75.

Patiño, S., G. S. Gilbert, G. Zotz & M. T. Tyree. 1999. Growth and survival of aerial roots of hemiepiphytes in a lower montane tropical moist forest in Panama. *Journal of Tropical Ecology* **15**: 651-665.

Pennington, R. T. & C. W. Dick. 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **359**: 1611-1622.

Perret, M., A. Chautems, A. O. De Araujo & N. Salamin. 2013. Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. *Botanical Journal of the Linnean Society* **171**: 61-79.

Piątek, K., P. Naks, W. Heise, M. Wayda, O. Reyes Calderón & G. Sandoval. 2012. Ferns and Lycophytes of Celaque National Park, Honduras. *Fern Gazette* **19**: 11-23.

Record, S. J. 1927. Trees of Honduras. *Tropical Woods* **10**: 10-47.

Renner, S. S., G. Clausing & K. Meyer. 2001. Historical biogeography of Melastomataceae: the roles of Tertiary migration and long-distance dispersal.

American Journal of Botany **88**: 1290-1300.

Scheffknecht, S., M. Winkler, K. Hülber, M. M. Rosas & P. Hietz. 2010. Seedling establishment of epiphytic orchids in forests and coffee plantations in Central Veracruz, Mexico. *Journal of Tropical Ecology* **26**: 93.

Smith, J. F. & K. J. Sytsma. 1994a. Evolution in the Andean epiphytic genus *Columnea* (Gesneriaceae). I. Morphological variation. *Systematic Botany* **19**: 220-235.

Smith, J. F. & K. J. Sytsma. 1994b. Evolution in the Andean epiphytic genus *Columnea* (Gesneriaceae). II. Chloroplast DNA restriction site variation. *Systematic Botany* **19**: 317-336.

Southworth, J. & C. Tucker. 2001. The influence of accessibility, local institutions, and socioeconomic factors on forest cover change in the mountains of western Honduras. *Mountain Research and Development* **21**: 276-283.

Standley, P. C. 1930. A second list of the trees of Honduras. *Tropical Woods* **21**: 9-41.

Standley, P. C. (ed.). 1931. *Flora of the Lancetilla Valley, Honduras*. Field Museum of Natural History, Chicago.

Standley, P. C. 1934. Additions to the trees of Honduras. *Tropical Woods* **37**: 27-38.

Standley, P. C. & J. A. Steyermark (eds.). 1946. *Flora of Guatemala*. Chicago Natural History Museum, Chicago

Stevens, W. D., C. U. Ulloa, A. Pool & O. M. Montiel (eds.). 2001. *Flora de Nicaragua: Tomo I-III* Missouri Botanical Garden Press, Saint Louis.

Ulloa, C. U., D. L. Nickrent, C. Whitefoord & D. L. Kelly. 2010. *Hondurodendron*, a new monotypic genus of Aptandraceae from Honduras. *Annals of the Missouri Botanical Garden* **97**: 457-467.

Vergara-Torres, C. A., M. C. Pacheco-Álvarez & A. Flores-Palacios. 2010. Host preference and host limitation of vascular epiphytes in a tropical dry forest of central Mexico. *Journal of Tropical Ecology* **26**: 563-570.

Wiehler, H. 1983. A synopsis of the neotropical Gesneriaceae. *Selbyana* **6**: 1-249.

Wolf, J. H. D. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest Ecology and Management* **212**: 376-393.

Wolf, J. H. D. & A. Flamenco-S. 2006. Vascular epiphytes and their potential as a conservation tool in pine-oak forest of Chiapas, Mexico. pp. 375-395. *In:* J. H. D. Wolf & A. Flamenco-S. (eds.). *Ecology and Conservation of Neotropical Montane Oak Forests*. Ecological Studies, Vol. 185. Springer, Heidelberg.

Wolf, J. H. D. & C. J. F. Konings. 2001. Toward the sustainable harvesting of epiphytic bromeliads: a pilot study from the highlands of Chiapas, Mexico. *Biological Conservation* **101**: 23-31.

Yuncker, T. G. (ed.). 1938. *A contribution to the Flora of Honduras*. Field Museum of Natural History, Chicago.

Yuncker, T. G. (ed.). 1940. *Flora of the Aguan Valley and the Coastal Regions near La Ceiba, Honduras*. Field Museum of Natural History, Chicago.

Zotz, G. 2013a. 'Hemiepiphyte': a confusing term and its history. *Annals of Botany* **111**: 1015-1020.

Zotz, G. 2013b. The systematic distribution of vascular epiphytes - a critical update. *Botanical Journal of the Linnean Society* **171**: 453-481.