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Abstract

In tropical montane forests epiphytes represent a substantial proportion of biodiversity and green biomass, particularly where fog occurs almost daily. Epiphytes play important ecological roles in these ecosystems, for example, in forest hydrology and in amplifying arthropod biodiversity, but quantitative assessments of epiphytic biomass and species diversity are rare. Such data are important, however, for a better understanding on their ecological roles and as a baseline for detecting ecological change due to climate or land-use changes. In a tropical lower montane cloud forest (c. 1,150 m above sea level) in Panama, we identified and weighed all epiphytic matter, which includes vascular plants, bryophytes, lichens, and dead organic matter from the trunks of 22 trees varying in diameters at breast height and 28 canopy branches. Additionally, we collected epiphytic matter in the understory in 22 plots of 2×2 m. A total of 155 species of vascular epiphytes, hemiepiphytes, and nomadic vines were found. Orchidaceae were by far the most species-rich family, followed by Araceae and Bromeliaceae. The vertical distribution of these species in the forest showed species-specific vertical preferences, but species numbers varied little in undergrowth, trunks, and tree crowns. Epiphytic matter was positively related to tree size, and we used tree-size data inventory data from a nearby 1-ha plot to extrapolate our findings to the plot level. The resulting estimate of 16,439 kg ha^{-1} for total epiphytic matter and 6,214 kg ha^{-1} for living plants, the latter representing about 2% of aboveground forest biomass.

Epiphytes germinate and grow on other plants without contact to the soil and, unlike mistletoes, do not parasitize their host (Zotz, 2013b). These plants can play an important role in the hydrology of many tropical forests (Köhler, Tobón, Frumau, & Bruijnzeel, 2007; Veneklaas et al., 1990). They also participate in the regulation of nutrient fluxes (Foster, 2001; Hsu, Horng, & Kuo, 2002; Nadkarni, Schaefer, Matelson, & Solano, 2004); the modification of forest microclimate (Zotz & Bader, 2009); and the provision of habitat for animals, microorganisms, and other plants.

These roles depend, however, on the structure and biomass of the epiphyte communities. Epiphytes, including vascular and nonvascular plants and lichens, can represent a considerable percentage of forest biodiversity and green biomass (Köhler, Hölscher, & Leuschner,

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2008). In addition to this living component, epiphytic matter is composed of plant litter, canopy humus, associated invertebrates, fungi, and microorganisms (Chen, Liu, & Wang, 2010; Freiberg & Freiberg, 2000; Nadkarni et al., 2004; Nadkarni & Solano, 2002). Here, we will use, as suggested by Zotz (2016), the term ''epiphytic matter'' to refer to the mass of all epiphytic components (dead or alive) and epiphytic biomass to refer only to living plants.

In spite of the large contribution of epiphytes to biodiversity and ecosystem functioning in many tropical and subtropical ecosystems, information about the composition and biomass of epiphytic communities is still scarce for most regions of the world (Díaz, Sieving, Peña-Foxon, Larraín, & Armesto, 2010; Zotz, 2005). It is known, however, that epiphytes are particularly prominent in tropical montane cloud forests (TMCFs), where high and constant moisture supply favors the growth of plants even without access to soil water (Gradstein, 2008). TMCFs form at elevations in the condensation zone, where mist or low clouds occur almost daily (Hofstede, Dickinson, & Mark, 2001). Studies in TMCFs documented epiphytic matter amounting to several tons per hectare (Hofstede, Wolf, & Benzing, 1993; Köhler et al., 2007; Nadkarni et al., 2004) although the variation between estimates is huge (Zotz, 2016; Table 1). They range from $370 \, kg \, ha^{-1}$ in a lower montane rain forest in Jamaica (Tanner, 1980) to $44,000 \, kg \, ha^{-1}$ in an upper montane Colombian forest (Hofstede et al., 1993). Considering the large variation between TMCF areas, data on epiphytic matter in these forests are still too scarce to allow regional generalizations or reliable global estimates (Chen et al., 2010). Additionally, some studies about epiphytic matter in TMCFs are based on a very small number of large trees with strong branches (Hofstede et al., 2001, 1993) due to the relatively easy climbing access. These trees tend to have disproportionally large epiphyte loads. Although six to eight large trees can already give a surprisingly representative picture of epiphyte community structure in lowland rain forests (Gradstein, Nadkarni, Krömer, Holz, & Nöske, 2003; Zotz & Bader, 2011), this is not necessarily the case for biomass (Wolf, Gradstein, & Nadkarni, 2009). The community structure may also be less well represented by the largest trees in montane forests, where lower strata in the forest receive more light and support more epiphytes. For example, in a montane forest in Bolivia, ca. 20% of the total epiphytic flora was found in the understory (Krömer, Kessler, & Gradstein, 2007).

Vascular epiphytes represent approximately 10% of all known vascular plant species (Zotz, 2013b) and up to 50% of local plant species richness in tropical forests (Kelly et al., 2004). The lower montane cloud forest of our study area, Fortuna Forest Reserve (FFR) in western Panama, also features a highly diverse epiphyte flora. For example, there are an estimated 80 species of epiphytic bromeliads (Meisner & Zotz, 2012) and about 250 orchid species, most of which are also epiphytic (McPherson et al. unpublished data). Apart from these extremely species-rich families, vascular epiphytes are represented by numerous aroids and ferns, and the local diversity of bryophytes and lichens may even surpass the diversity of vascular plants (Köhler et al., 2007). Currently, quantitative information about epiphyte community composition or biomass in this forest or about their functional roles in the forest ecosystem is entirely lacking.

Even though TMCFs represent just 2.5% of the total tropical forest area (Cayuela, Golicher, & Rey-Benayas, 2006; Chen et al., 2010; Shi & Zhu, 2008), they are disproportionally important due to their high and unique biodiversity and their important ecological functions in mountain areas. Unfortunately, TMCFs are one of the most threatened ecosystems worldwide because of land-use pressure and global climate change (Shi & Zhu, 2008; Zotz & Bader, 2009). In turn, resulting changes in epiphytic biomass and composition are likely to cause cascading effects on forest structure and functioning, with potentially detrimental impacts on ecosystem services. To assess possible consequences, baseline data on the current status of epiphyte diversity and abundance are indispensable.

Here, we present quantitative information on species richness of vascular epiphytes and biomass of vascular and nonvascular epiphytes in a TMCF in western Panama (1,150 m above sea level [asl]). To this end, we sampled trees of many species across a range of stem diameters at breast height (DBH). Taking advantage of existing forest inventories, we scaled up to the level of total epiphytic matter at the forest level.

Method

Study site. Our study was conducted in the TMCF of the FFR, in the central cordillera of western Panama. Our site was located in the Quebrada Honda section of the reserve (8°45'40'' N, 82°14'22'' W, 1,150 m asl), where forest structure and dynamics have been studied extensively by J. Dalling and coworkers (Andersen, Turner, & Dalling, 2010; Heineman et al., 2015; Heineman, Turner, & Dalling, 2016). During the study period, the annual precipitation was c. $5,700 \, mm \, yr^{-1}$ according to our own recordings (HOBO Data logging rain gauge RG3, Onset Computer Corp., Cape Cod, MA, USA) set up c. 20 m outside the forest near the research station from March 2014 to April 2016.

The bedrock in Quebrada Honda is Rhyolitic tuff, which is acidic and poor in nutrients, and the topsoil is organic, with an acidic pH < 5.0 (Andersen et al., 2010). Emergent forest trees include *Oreomunnea mexicana* and

Table 1. Epiphytic Matter (Biomass and DOM) in Tropical and Subtropical Montane Forests.

Ecosystem/Location	Elevation m asl	Epiphytic matter (kg)					Method	Source	Comments
		LICH	BRYO	VP	DOM	Total			
Tropical									
TLMCF, primary Costa Rica	1,480		4,058	8,205	20745	33,100	Extrapolated from 16 tree trunks and segments of branches from 9 trees. Not all epiphytic matter was removed from the trees	Nadkarni, Schaefer, Matelson, and Solano (2004)	Lichens with bryophytes
TLMCF, secondary Costa Rica	1,480		115	1.7	3.7	120	Extrapolated from nine trees. Not all epiphytic matter was removed from the trees	Nadkarni et al. (2004)	Lichens with bryophytes
TLMCF, primary Costa Rica	1,490	NS	11,505	2,615	2,095	16,215	Extrapolated from nine trees in different DBH classes. Not all epiphytic matter was removed from the trees.	Köhler et al. (2007)	
TLMCF, secondary Costa Rica	1,620	NS	944	84	7	1,035	Extrapolated from six trees. Not all epiphytic matter was removed from the trees.	Köhler et al. (2006)	
TUMCF Colombia	3,700	727	6,848	8,750	27,662	44,000	Extrapolated from three trees representing three canopy layers.	Hofstede, Wolf, and Benzing (1993)	
Subtropical									
UMCF Yunnan, China	2,600	1	1,663	234	362	2,259	Extrapolated from 77 trees in different DBH classes.	Chen, Liu, and Wang (2010)	VP: only ferns

Note. We considered only sources that allow the distinction between vascular and nonvascular plants. LICH = lichens, BRYO = bryophytes, VP = vascular plants; DOM = dead organic matter; NS = not specified; TUMCF = tropical upper-montane cloud forest; TLMCF = tropical lower-montane cloud forest; DBH = diameters at breast height.

Quercus sp. Other important genera of trees are *Hedyosmum, Faramea, Trichilia, Guettarda, Ardisia*, and *Inga*. The subcanopy and understory vegetation consists of trees and shrubs from the Rubiaceae, Malvaceae, Melastomataceae, Myrtaceae, Meliaceae, and others (C. Rodríguez, unpublished. data). Data are available on stem DBH of all trees >5 cm DBH in a 1-ha permanent forest plot (Prada et al., unpublished data) in the vicinity of our study area, which allowed us to scale up from our census to a plot-level estimation (see below). Stem density was 1,597 (trees >5 cm DBH) and 787 (trees > 10 cm DBH), and the total basal area was 46.3 m^2 ha^{-1} (Prada et al., unpublished data).

Study trees and sampling methods. We censused all epiphytic vascular plants in the 22 selected trees, dividing the trees vertically into six height zones (0–5, 5–10, 10–15, 15–20, 20–25, 25–27 m). The uppermost zones were not present in all trees, the smallest sampled tree being only 9 m tall.

Individual abundance was quantified followed the "stand method" (Sanford, 1968), in which a "stand" is a group of individual shoots belonging to the same species that is spatially isolated or otherwise clearly separated from other groups of plants from the same species. Not all mechanically dependent plants were included in our biodiversity census: We excluded vines (climbing plants that germinate in and stay connected to the ground throughout their lives) and mistletoes (parasitic plants). Juvenile epiphytes less than two thirds of the adult's size were not considered either because of the difficulty of identification.

Epiphytic vascular plants were separated into three categories: vascular epiphytes (plants that germinate on other plants and never establish a connection to the ground), hemiepiphytes (plants that germinate on other plants but later establish contact with the ground via aerial roots), and nomadic vines (climbing plants that germinate on the ground and later may lose their connection to the ground as they ascend) following the terminology outlined by Zotz (2013a). Vascular plants were identified using taxonomic keys and critical cases were identified by specialists. Voucher specimens were deposited in the herbaria of the University of Panama and the University of Chiriqui.

To estimate species richness in the area based on our sampling, we calculated the Chao 1 index (1984), which recognizes the fact that the sampled diversity normally is less than the actual diversity present in an area.

Our sampling strategy for the quantification of epiphytic matter was meant to assure a reliable estimate of the amount, composition, and variability of epiphytic matter on different surface types (branches and trunks) and tree sizes.

The DBH of host trees is usually a good predictor of epiphytic matter across trees of a forest (Chen et al.,

2010). We determined the epiphytic matter on 22 trees with DBH ranging between 9 and 75 cm in order to obtain a wide representation of the available tree sizes to establish the quantitative relationship between epiphyte matter and DBH (Hsu et al., 2002; Wolf et al., 2009). The 22 trees ranged from 9 to 27 m in height with their crown branches starting from 8 to 14 m above the ground. The smallest tree was a palm lacking branches that was included because of the importance of palms in this forest and their inclusion in the tree survey used for extrapolations.

We sampled epiphytes on trunk and branch and additionally on surrounding vegetation up to a height of 2 m in 2×2-m plots around the selected trees. Trees were climbed using single-rope techniques, or ladders were used in the case of smaller trees and lower sections of all trees. The epiphytic matter, that is, all living vascular and nonvascular epiphyte biomass and dead organic matter (DOM), of the 22 trees was sampled from one half of the tree trunk ($180°$ of each trunk).

For estimating epiphytic matter in the tree crowns, we sampled all epiphytes from 28 branches (2–11 cm basal diameter) from 15 trees after cutting and lowering the branches to the ground. This allowed the determination of the relationship between branch diameter and epiphytic matter. We then estimated the diameters of all the primary branches of 19 of the 22 selected trees. Consistent with the approach used by Köhler et al. (2007), the remaining three trees were not taken into account because one of them was a palm without epiphytes in the crown and the other two were small with a strong crown deformation. The numbers and sizes of all branches were used to estimate epiphytic matter for the crown of each of the 19 trees.

For the understory, all epiphytic matter below 2 m in height inside the 2×2-m plots, with the exception of the focal tree, was collected.

In the lab, the epiphytic matter was separated into five categories: DOM, lichens, bryophytes, vascular plants, hemiepiphytes, and nomadic vines. Hemiepiphytes and nomadic vines were lumped for biomass because it was not always clear to which group they belonged. Each group was weighed within 2 hr of collection in order to obtain fresh weight. Subsamples were then oven dried at $80°C$ for 48 hr (for most of the living tissues) and 96 hr for some Araceae and Bromeliaceae (depending on their size and level of succulence) and DOM. After drying, they were reweighed to obtain dry weight.

Total epiphytic matter per tree was regressed against DBH. The same was done for biomass/epiphytic matter by category. The resulting functions were used to estimate total matter per category on each of the trees in a nearby 1-ha forest plot, where tree DBH data were available (Prada et al., unpublished data). Two estimates of epiphytic matter for the whole forest (in kg ha^{-1}) were

calculated, one based on regressions using the total epiphytic matter and one on the sum of the separate categories. All analyses were performed in R version 3.2 (R CORE TEAM 2015).

Results

Epiphyte species richness and floristic structure. Each of the 22 trees hosted numerous bryophytes and at least one vascular epiphyte. We recorded a total of 2,423 stands, belonging to 155 species of vascular epiphytes, 84 of which could be identified to species level (Table A1). From the 155 species, we recorded 47 genera and 18 families. Of these, 133 species (85%) were epiphytes, 9 species (6%) were hemiepiphytes, 6 species (4%) were nomadic vines, and the remaining 7 species (4%) could not unambiguously be assigned to hemiepiphytes or nomadic vines (Table A1). Five species could not be identified even to family level because reproductive organs were lacking. In our analysis, those species not identified to species or genus level were included as morphospecies.

The species accumulation curve for vascular epiphytes in the sampled trees (Figure 1) does not reach an asymptote which indicates that not all species in the area were included in our sample. The Chao 1 estimation of the total number in the study area was 189 ± 16 (*SE*) with a 95% confidence interval of [169, 239] species.

Ferns and fern-allies were represented by 51 species in 17 genera and nine families. The most constant (widespread among trees) epiphyte species was an unidentified *Elaphoglossum* (Dryopteridaceae), which was found on 15 of the 22 sampled trees (Table 2). The most abundant epiphyte species was a filmy fern with 188 stands (*Hymenophyllum axillare Sw.*, Hymenophyllaceae), followed by *Elaphoglossum nigrescens (Hook.) T. Moore ex Diels* (Dryopteridaceae) with 115 stands (Table 2).
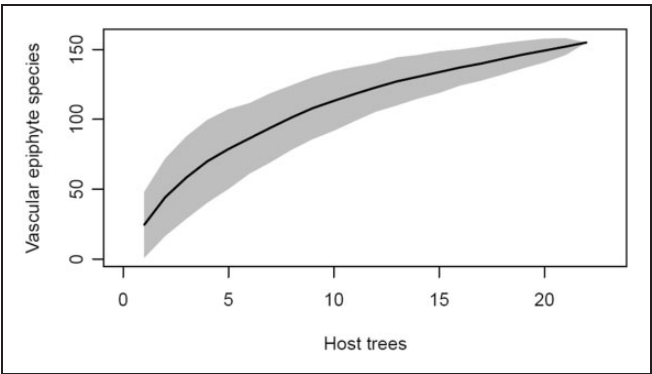
Figure 1. Epiphyte species accumulation curve (155 species, 22 trees) in a montane cloud forest in western Panama (Quebrada Honda, Fortuna). The shaded area indicates the 95% confidence interval.

Although the dominant species in terms of constancy and abundance were ferns, angiosperms were more species rich, with 104 species in 53 genera and nine families, representing five eudicotyledonous and four monocotyledonous families (Table A1). The vascular epiphyte assemblages were dominated by Orchidaceae with 38 species, contributing 25% (Figure 2) to epiphyte species diversity, and 494 stands, representing 20% of total abundance (Figure 3). Furthermore, orchids were found on 19 trees with *Pleurothallis* as the most species-rich genus of the family occurring in nine trees (Table 2). *Pleurothallis dentipetala* was the most abundant orchid species, with 57 stands (Table 2). Other species-rich families were Araceae with 23 species (15%), also documented on 19 trees, Hymenophyllaceae (9%), Dryopteridaceae and Polypodiaceae (each 8%), and Bromeliaceae (7%, Figure 2).

Anthurium (Araceae) and *Elaphoglossum* (Dryopteridaceae) were the most species-rich genera (each 10% of the total), followed by *Pleurothallis* (Orchidaceae, 6%), *Guzmania* (Bromeliaceae), *Peperomia* (Piperaceae), and *Trichomanes* (Hymenophyllaceae; each 5%).

Table 2. Most Important Epiphyte Species Sorted by Constancy.

Species	Number of trees	Number of individuals
Elaphoglossum sp.2 (Dryopteridaceae)	15	63
Elaphoglossum erinaceum (Dryopteridaceae)	13	78
Elaphoglossum nigrescens (Dryopteridaceae)	12	115
Werauhia kathyae (Bromeliaceae)	11	93
Elaphoglossum sp.4 (Dryopteridaceae)	10	61
Hymenophyllum axillare (Hymenophyllaceae)	9	188
Pleurothallis sp.3 (Orchidaceae)	9	32
Guzmania cf. *nicaraguensis* (Bromeliaceae)	9	16
Trichomanes punctatum (Hymenophyllaceae)	7	86
Cochlidium serrulatum (Polypodiaceae)	7	80
Tillandsia sp.2 (Bromeliaceae)	7	55
Asplenium holophlebium (Aspleniaceae)	5	80
Pleurothallis dentipetala (Orchidaceae)	2	57

Note. Also shown is abundance (from a total of 155 species and 2,423 individuals/stands) recorded on 22 trees in western Panama (Quebrada Honda, Fortuna).
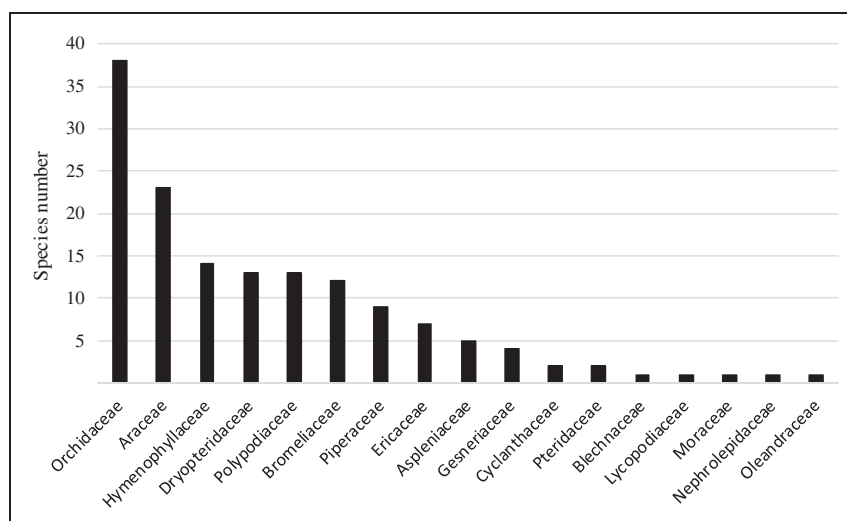
Figure 2. Species richness of epiphyte families recorded on 22 trees in western Panama (Quebrada Honda, Fortuna). For a complete species list, see Table A1.
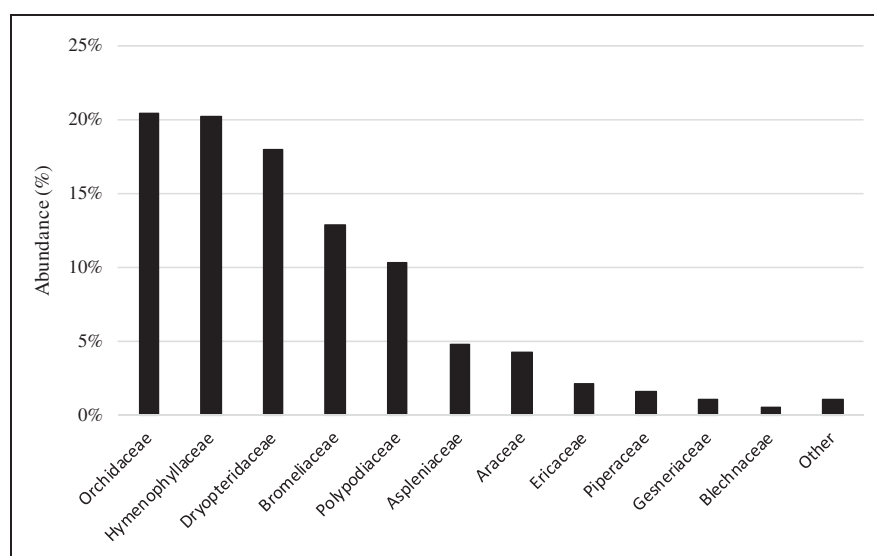
Figure 3. Proportional abundance of epiphytes by family (from a total of 2,423 individuals) recorded on 22 trees in western Panama (Quebrada Honda, Fortuna).

Epiphytic biomass. A total of 28 kg of epiphytic matter was removed from the 22 sampled tree trunks. From the 28 branches in the crowns, 25 kg of epiphytic matter was removed and 12 kg from the understory. Taken together, 62% of epiphytic matter was DOM and the remaining 38% were vascular and nonvascular epiphytes (Table 3). Vascular epiphyte biomass was dominated by bromeliads (73% of total vascular plants), with a lower contribution of ferns (12%) and orchids (8%). The remaining vascular epiphytes, mostly Araceae and Piperaceae, contributed just 7% to the total.

Epiphytic matter increased exponentially with DBH as well as with branch diameter ($R^2 = .65$; $p < .001$; Figure A1). The total epiphytic matter per tree was estimated by adding the calculated epiphytic matter on all branches per tree to the measured epiphytic matter on the trunks for each of the 22 sampled trees. This epiphytic matter per tree (on trunk plus branches) increased exponentially with tree size (DBH) (linear regression analysis with log [epiphyte matter]: $R^2 = .53$; $p < .01$; Figure 4). Similar relationships were found for individual categories: DOM ($R^2 = .59$; $p < .001$; Figure A2), lichens

Table 3. Epiphytic Matter Components in the Tropical Montane Forest (1,150 m asl) of Quebrada Honda, Fortuna Forest Reserve, western Panama (kg cm^{-2}).

Epiphytic matter	Epiphytic matter on branches and trunks (kg ha^{-1})	Epiphytic matter on undergrowth <2 m (kg ha^{-1})	Total epiphytic matter (kg ha^{-1})
Dead organic material	10,136	89	10,225
Lichens	3	0	3
Bryophytes	1,012	50	1,062
Vascular epiphytes	4,258	147	4,405
Hemiepiphytes/nomadic vines	744	0	744
Total	16,153	286	16,439

Note. Data are based on diameters at breast height–based extrapolations from of 22 trees plus area-based extrapolation from twenty-two 2 × 2-m plots in the undergrowth.
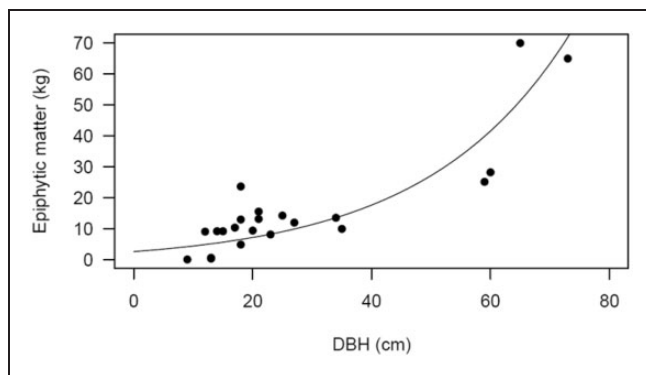
Figure 4. Relationship of epiphytic matter and trunk diameter at breast height (DBH; cm), based on epiphytes on the branches and trunks of 22 trees in western Panama: Quebrada Honda, Fortuna (log 10 epiphyte matter) = 1.26 + 0.04 DBH, R^2 = .53; p < .001).

(linear relationship, R^2 = .60; p < .001; Figure A3), bryophytes (R^2 = .71; p < .001; Figure A4), and vascular epiphytes (R^2 = .53; p < .001; Figure A5). For hemiepiphytes, the relationship was not significant (R^2 = .26; p > .001; Figure A6).

Based on these regression equations (or the mean in the case of hemiepiphytes) for each epiphyte group and the DBH of all trees in a nearby 1-ha forest plot (Prada et al. unpublished data), plus an extrapolation of the overall mean biomass in the understory in the 2 × 2-m plots, we estimated the total epiphytic matter in this forest to be 16,439 kg ha^{-1} (Table 3). We obtained a somewhat higher estimate (18,974 kg ha^{-1}) based on the direct regression of total epiphytic matter per tree with DBH, shown in Figure 4.

Discussion

Epiphyte species richness. The epiphytic community in the studied forest is rich in species and comparable to other primary tropical lower montane forests between 1,000 and 2,000 m asl (Table 4). It is characterized by a high proportion of rare species, so that the species abundance curve did not saturate. The real number of species in the forest is expected to be considerably higher than the observed number (189 vs. 155) according to our Chao 1 index estimate. Interestingly, the estimated number of vascular epiphyte species roughly equals the observed number of tree species (>5 DBH cm) in the 1-ha census used for our extrapolation (190 species; Prada et al. unpublished data).

For dominant epiphyte families, the registered species represented only 9% (Orchidaceae) or 15% (Bromeliaceae) of the estimated number of species in the FFR. This indicates that apart from the high α-diversity found in this study, the β-diversity is also likely very high in this heterogeneous mountain reserve, which ranges from 700 to over 2,000 m asl, stressing its conservation value. Many of the orchid and bromeliad species occurred in a small number of trees. This high proportion of uncommon species may also explain why the 22 sampled trees hosted quite a low percentage of the species reported in the reserve (McPherson unpublished data, Meisner & Zotz, 2012).

The representation of angiosperms families in this study agrees very well with general patterns of epiphytes diversity in the Neotropics, the most common taxon being Orchidaceae, followed by Araceae and Bromeliaceae (Gentry & Dodson, 1987). However, taking into account all species, some fern families were more species rich than the Bromeliaceae. According to previous studies, Araceae are the second-most species rich group after orchids in tropical lowland forests, while in montane forests, ferns tend to become more important than Araceae (Kreft, Köster, Küper, Nieder, & Barthlott, 2004; Krömer, Kessler, Gradstein, & Acebey, 2005). However, in our study area, both groups show similar species richness. The Neotropical epiphytic eudicotyledonous flora is more diverse in families but much less diverse in species compared to the monocots

Table 4. Number of Species of Vascular Epiphytes Recorded in Tropical Montane Forests.

Ecosystem/location	Elevation	Number of species	Sampled trees	Source
TLMCF, Costa Rica	1,000	215	Ten emergent trees	Cardelus et al. (2006)
TLMCF, Los Cedros Ecuador	1,400	31	Five emergent trees	Freiberg and Freiberg (2000)
TLMCF, Costa Rica	1,480–1,530	65	10 trees > 50 cm DBH	Ingram and Nadkarni (1993)
TLMCF, Costa Rica	1,600	171	Ten emergent trees	Cardelus et al. (2006)
TLMCF, Bolivian Andes	1,600	175	Eight trees and nearby 20x20 m plots	Krömer and Gradstein (2003)
TLMCF, Otonga, Ecuador	1,800	42	Four emergent trees	Freiberg and Freiberg (2000)
TLMCF, México	1,980	39	36 trees > 10 cm DBH	Hietz and Hietz (1995)

Note. Included only studies in forests between 1,000 and 2,000 m that were referred to as cloud forest. TLMCF = tropical lower-montane cloud forest; DBH = diameters at breast height.

(Zotz, 2016). The largest eudicot epiphyte family globally is the Piperaceae, which also contributed 6% (nine species) to the total species count in this study, occupying the first place of eudicotyledonous families, followed by Ericaceae and Gesneriaceae. The large contribution of the Orchidaceae to epiphyte species richness confirms patterns found in forests from both the tropical lowlands and montane primary and secondary forests (Barthlott, Schmit-Neuerburg, Nieder, & Engwald, 2001; Kreft et al., 2004; Küper, Kreft, Nieder, Köster, & Barthlott, 2004). On a global scale, orchids account for ca. 68% of all species and 59% of all genera of epiphytes (Zotz, 2013b).

The epiphyte species and families were not randomly distributed in the forest, but most showed clear preferences for height zones. The lower strata were preferred by aroids and several fern families, especially the filmy ferns (Hymenophyllaceae). Eight of the 14 species of Hymenophyllaceae were exclusively recorded in the lower zone (0–5 m), six were found in more than one zone, but just one, a *Trichomanes* species, was found in the upper forest canopy. In contrast, the Orchidaceae as a family preferred the higher strata of the forest, whereby this general preference differed considerably between species (Table A1). Orchids were less common on understory shrubs than on the lower 2 m of the trunks. One explanation could be that they prefer thick branches because these offer a different substrate, another that trunks have been available for colonization for a longer (Hietz & Hietz-Seifert, 1995).

Epiphytic matter. Because of differences in the estimation methods in previous studies, comparisons are not straightforward. For example, the 2-fold difference in the epiphytic matter estimates of Köhler et al. (2007) and Nadkarni et al. (2004) for a montane cloud forest of Monte Verde, Costa Rica (16,215 kg ha^{-1} vs. 33,100 kg ha^{-1}) may be explained by the different number and different limits of DBH classes, different stratification of the trees, and different sampling methods (Table 1). Alternatively, the results may reflect real differences between plots or may be explained by a mixture of biological and methodological reasons. The epiphytic matter estimate of the present study was 16,439 kg ha^{-1} and coincides with that of Köhler et al. (2007). Taken together, informed tentative estimate of typical epiphytic matter in this type of forest would be in the range of c. 20,000 kg ha^{-1}.

The highest estimation of epiphytic loads so far is from an upper montane forest in Colombia (Hofstede et al., 1993) with an estimation of 44,000 kg ha^{-1} of epiphytic matter. This estimate was based on sampling data from three trees, chosen as representative of three canopy strata. This approach may easily yield an overestimate, but epiphyte loads are indeed very high in the wet upper montane forest sampled, with large (c. 1-m diameter) balls of bryophytes covering the trees (M.Y. Bader, personal observation). In comparison, the moss layer in our study area was modest, though still considerable. In the montane forest, low temperatures probably favor both bryophyte growth and reduce decomposition rates (Conant et al., 2011), which may explain the high fraction of DOM (63%). Similarly high estimates of DOM are reported by Nadkarni et al. (2004) and Kanzaki & Sri-Ngernyuang (2012), which also coincidence with the values of our study (62%).

The estimated 6,214 kg ha^{-1} epiphytic biomass (all epiphytic matter excl. DOM) contributes about 2% to the total aboveground biomass in the Quebrada Honda forest, which is estimated at 360,000 kg ha^{-1} based on tree survey used for our extrapolations (K. Heineman, unpublished data). Considering total forest biomass, that is, aboveground and belowground biomass, this relative contribution is even lower and represents only a very modest fraction. Only few studies

report direct estimations of both tree leaves and epiphytes foliage from tropical forests (Kanzaki & Sri-Ngernyuang, 2012; Socher, Vellozo Roderjan, & Galvão, 2008) with c. 13%. For a lowland rain forest in Panama, in turn, the contribution to green biomass was estimated to be much lower with only 0.02% (Golley, McGinnis, Clements, Child, & Duever, 1969). This difference, even after taking possible methodological biases into account, illustrates the great importance of epiphytes in tropical montane forests compared to lowland forests.

Reported epiphyte biomass values for tropical montane forests in the literature cover a very wide range, and our estimate lies roughly in the middle of this range. Some of the previous estimates may be considered unreliable because of the very limited sampling (e.g., three trees only) and simple extrapolation methods (Hofstede et al., 1993; Nadkarni, 1984). In spite of the uncertainties related to the epiphyte biomass versus DBH relationships in our study, the extensive sampling and the detailed information about forest structure used for the extrapolation makes our estimate relatively robust. Our data show that epiphytic matter increased exponentially with tree size (DBH, linear regression analysis) consistent with other reports Díaz et al. (2010). For future surveys, we would suggest using this tree-size based method with some modifications. Studying a range of tree sizes is necessary, as there is a strong relationship between epiphyte load and DBH. However, as the smaller trees were more similar in their biomass, fewer trees in the smaller size classes would need to be sampled. On the other hand, as large trees have high but also very variable epiphyte loads, we recommend including more large trees to improve the regression model in this influential size range. Sampling the understory is not necessary for estimating the biomass per hectare, as this part of the forest contributed only about 2% to total epiphytic matter, which is much less than the uncertainty associated with the biomass-size model. This recommendation does not, however, hold for biodiversity studies, as conditions specific for the understory might support specific species not found in higher strata (Krömer et al., 2007; Zotz, 2007).

Even though bryophytes were found in all trees, they contributed relatively little to the total epiphytic matter, at variance with some other montane forests (e.g., bryophytes contributed nearly 75% of green epiphyte biomass in Hofstede et al., 1993). However, their role in the ecosystem may be much larger than suggested by this low contribution to biomass. For instance, their contribution to DOM is important since most of the DOM is derived from bryophytes (Turetsky, 2003). They may also contribute to the maintenance of high epiphyte biomass by facilitating vascular-epiphyte germination, establishment, and survival (Zamfir, 2000). Additionally, their poikilohydric nature and large water-holding capacities are probably very important in their regulatory potential for water fluxes and microclimate in the forest (Cornelissen, Lang, Soudzilovskaia, & During, 2007).

Epiphytes and climate change. Because of their existence at the interface of vegetation and atmosphere, epiphytes have been called particularly vulnerable to climate change. In contrast, at least in seasonal climates, epiphytes are well adapted to survive irregular access to water and appear relatively insensitive to, for example, increased drought in lowland forests (Zotz & Bader, 2009). In montane cloud forests, however, epiphytes thrive because of the humid conditions and may indeed be quite susceptible to drought. As a result, changes in microclimate due to forest disturbance have been linked to a floristic turnover in the epiphyte vegetation of tropical montane forests (Larrea & Werner, 2010). Climatic changes, especially changes in atmospheric water inputs, are therefore expected to have detrimental consequences for cloud-forest epiphytes.

To date, information on biomass or biodiversity of epiphytes is lacking for the great majority of tropical montane forests. Thus, any less than catastrophic change may easily go unnoticed. With this study, we created a baseline for a diverse montane forest and contribute to the still-small body of epiphytic matter estimates in tropical forest ecosystems. More studies are needed to understand and quantify the current and future role that epiphytic plants play in these forests.

Implications for Conservation

Changes in vascular and nonvascular epiphyte communities and associated biotic communities can disturb ecosystem functioning and affect the ecological and economic services the forest provides. These services include the regulation of water flows, provision of diverse habitats for other organisms, as well as direct economic uses like the extraction of ornamental plants. This study provides a baseline for the monitoring of such changes in epiphyte communities due to climate- or land-use changes. Such a baseline is a first prerequisite to become aware of changes and for designing mitigation or adaptation strategies. Additionally, we show that local diversity can be very high for epiphytic plants at our study site, but that a small area of forest represents only a small fraction of the epiphyte diversity in the larger reserve (as shown for bromeliads and orchids, where estimates of the species numbers for the whole FFR are available). This indication of a high α as well as β diversity provides support for the conservation of the entire reserve. Extrapolating beyond our study area, it underlines the value of large conservation areas in topographically heterogeneous TMCFs.

Appendix

Table A1. Vascular Epiphytes and Other Mechanically Dependent Species Recorded on 22 Trees in a Tropical Montane Cloud Forest, Western Panama.

Group	Family	Species	Habit	Height zone					
				A	B	C	D	E	F
FERNS AND ALLIES	Aspleniaceae	*Asplenium harpeodes* Kunze	EP	X	X				
		Asplenium holophlebium Baker	EP	X					
		Asplenium sp. 1	EP	X					
		Asplenium sp. 2	EP	X	X				
		Asplenium sp. 3	EP	X	X				
	Blechnaceae	*Salpichlaena volubilis* (Kaulf.) J. Sm.	NV	X	X	X			
	Dryopteridaceae	*Elaphoglossum atrobarbatum* Mickel	EP			X	X		
		Elaphoglossum ciliatum (C. Presl) T. Moore	EP	X	X	X			
		Elaphoglossum erinaceum (Fée) T. Moore	EP	X	X	X	X		
		Elaphoglossum cf. *grayumii* Mickel	EP		X		X		
		Elaphoglossum lanceiforme Mickel	EP	X	X	X			
		Elaphoglossum nigrescens (Hook.) T. Moore ex Diels	EP	X	X	X	X		
		Elaphoglossum sp. 1	EP	X	X	X			
		Elaphoglossum sp. 2	EP	X	X			X	
		Elaphoglossum sp. 3	EP	X	X	X	X		
		Elaphoglossum sp. 4	EP	X	X	X	X		
		Elaphoglossum sp. 5	EP			X	X		
		Elaphoglossum sp. 6	EP	X					
		Polybotrya sp.	NV	X					
	Hymenophyllaceae	*Hymenophyllum fucoides* (Sw.) Sw.	EP	X					
		Hymenophyllum lineare (Sw.) Sw.	EP	X					
		Hymenophyllum axillare Sw.	EP	X	X	X	X	X	
		Hymenophyllum hirsutum (L.) Sw.	EP	X					
		Trichomanes diaphanum Kunth.	EP	X	X	X			
		Trichomanes hymenophylloides Bosch	EP	X	X				
		Trichomanes ovale (E. Fourn.) Wess. Boer	EP	X					
		Trichomanes polypodioides L.	EP	X					
		Trichomanes punctatum Poir.	EP	X					
		Trichomanes punctatum subsp. *labiatum* (Jenman) Wess. Boer	EP	X	X				
		Trichomanes sp.	EP					X	
		Hymenophyllaceae 1	EP	X	X	X			
		Hymenophyllaceae 2	EP	X					
		Hymenophyllaceae 3	EP	X					

(continued)

Table A1. Continued

Group	Family	Species	Habit	Height zone					
				A	B	C	D	E	F
	Lycopodiaceae	*Phlegmariurus acerosus* (Sw.) B. Øllg.	EP		X				
	Davalliaceae	*Nephrolepis* sp.	EP	X					
	Oleandraceae	*Oleandra articulata* (Sw.) C. Presl	EP	X	X	X			
	Polypodiaceae	*Campyloneurum angustifolium* (Sw.) Fée	EP		X				
		Enterosora trifurcata (L.) L. E. Bishop	EP		X				
		Micropolypodium hyalinum (Maxon) A. R. Sm. *	EP	X	X	X	X		
		Micropolypodium taenifolium (Jenman) A. R. Sm.	EP	X	X				
		Serpocaulon levigatum (Cav.) A.R. Sm	EP		X				
		Polypodium sp. 1	EP	X	X		X		
		Polypodium sp. 2	EP		X				
		Polypodium sp. 3	EP	X	X				
		Terpsichore sp. 1	EP	X					
		Terpsichore sp. 2	EP		X				
		Cochlidium serrulatum (Sw.) L.E. Bishop	EP	X	X	X	X		
		Polypodiaceae 1	EP	X	X	X	X		
		Polypodiaceae 2	EP	X					
	Pteridaceae	*Vittaria costata* Kunze *	EP	X	X				
		Vittaria graminifolia Kaulf.	EP		X				
MONOCOTS	Araceae	*Anthurium bakeri* Hook. f. *	EP	X	X				
		Anthurium chiapasense Standl.	EP		X				
		Anthurium cf. *davidsoniae* Standl.	NV	X	X	X			
		Anthurium dichrophyllum Croat	EP		X	X			
		Anthurium formosum Schott	EP	X	X	X			
		Anthurium cf. *interruptum* Sodiro	EP		X	X			
		Anthurium lentii Croat & R. A. Baker	EP				X		
		Anthurium longistipitatum Croat	EP	X	X	X	X	X	
		Anthurium cf. *microspadix* Schott	HE	X	X				
		Anthurium obtusilobum Schott	EP		X	X			
		Anthurium sect. *Porphyrochitonium* Schott	EP					X	
		Anthurium sp.	EP	X	X	X			
		Monstera sp.	HE	X	X				
		Philodendron jodavisianum G. S. Bunting	HE/NV	X		X			
		Philodendron wilburii Croat & Grayum	HE/NV	X		X			
		Philodendron sp.	HE/NV	X					

Table A1. Continued

Group	Family	Species	Habit	Height zone					
				A	B	C	D	E	F
		Stenospermation sessile Engl.	HE	X		X			
		Syngonium cf. *schottianum* H. Wendl. ex Schott	HE/NV	X					
		Syngonium sp.	HE/NV	X					
		Araceae 1	HE	X	X				
		Araceae 2	HE	X	X				
		Araceae 3	HE	X	X				
		Araceae 4	EP		X				
	Bromeliaceae	*Guzmania angustifolia* (Baker) Wittm.	EP	X	X				
		Guzmania desautelsii Read. & L. B. Sm.	EP	X	X	X			
		Guzmania loraxiana j. R. Grant	EP		X	X			
		Guzmania musaica (Linden & André) Mez	EP	X	X	X			
		Guzmania cf. *nicaraguensis* Mez & C. F. Baker	EP	X	X	X	X		
		Guzmania sanguínea (André) André ex Mez	EP		X				
		Guzmania scandens H. Luther & W. J. Kress	EP	X					
		Racinaea contorta (Mez & Pittier) M. A. Spencer & L. B. Sm.	EP	X	X	X	X		
		Tillandsia sp.	EP	X	X	X			
		Werauhia kathyae (Utley) J.R. Grant	EP	X	X	X	X	X	X
		Werauhia vittata (Mez & Wercklé) J. R. Grant	EP				X		
		Werauhia sp.	EP		X	X			
	Cyclanthaceae	Cyclanthaceae 1	NV	X					
		Cyclanthaceae 2	NV	X					
	Orchidaceae	*Camaridium aurantiacum* (Schltr.) M. A. Blanco	EP			X			
		Camaridium minus Schltr.	EP		X	X	X		
		Camaridium dendrobioides Schltr.	EP		X	X	X	X	X
		Dichaea poicillantha Schltr.	EP	X					
		Dichaea sp. 1	EP		X				
		Dichaea sp. 2	EP	X	X				
		Dichaea sp. 3	EP	X	X		X	X	
		Elleanthus jimenezii (Schltr.) C. Schweinf.	EP					X	
		Elleanthus poiformis Schltr.	EP	X	X	X	X	X	
		Elleanthus stolonifer Barringer	EP		X	X	X	X	
		Epidendrum maduroi Hágsater & García-Cruz	EP	X					

(continued)

Table A1. Continued

Group	Family	Species	Habit	Height zone					
				A	B	C	D	E	F
		Epidendrum turialvae Rchb. f. *	EP	X	X				
		Epidendrum sp.	EP	X	X	X			
		Jacquiniella globosa (Jacq.) Schltr.	EP		X	X	X	X	
		Jacquiniella standleyi (Ames) Dressler	EP	X	X	X	X		X
		Lankesteriana sp.	EP		X		X		
		Lepanthes pexa Luer	EP			X			
		Maxillaria variabilis Bateman ex Lindl.	EP		X	X			
		Pleurothallis bivalvis Lindl.	EP	X	X	X	X		
		Pleurothallis crocodiliceps Rchb. f.	EP			X	X		
		Pleurothallis dentipetala Rolfe ex Ames	EP	X	X		X		
		Pleurothallis eumecocaulon Schltr.	EP		X	X	X		
		Pleurothallis ruscifolia (Jacq.) R. Br.	EP	X					
		Pleurothallis sp. 1	EP	X			X		
		Pleurothallis sp. 2	EP		X	X	X		
		Pleurothallis sp. 3	EP	X	X	X	X		
		Prosthechea pygmaea (Hook.) W. E. Higgins	EP				X	X	
		Scaphyglottis amparoana (Schltr.) Dressler	EP		X	X	X	X	X
		Scaphyglottis densa (Schltr.) B. R. Adams	EP				X		
		Sobralia sp.	EP	X	X	X	X	X	
		Stelis microchila Schltr. *	EP		X	X		X	X
		Stelis sp.	EP			X		X	
		Trichopilia galeottiana A. Rich. & Galeotti *	EP	X	X	X	X		
		Trichosalpinx cedralensis (Ames) Luer	EP	X	X	X	X		
		Trichosalpinx memor (Rchb. f.) Luer	EP		X		X		
		Xylobium sulfurinum (Lem.) Schltr.	EP	X	X	X			
		Orchidaceae 1	EP		X	X	X	X	
		Orchidaceae 2	EP				X		
EUDICOT	Ericaceae	*Disterigma* cf. *humboldtii* (Klotzsch) Nied.	EP		X	X	X	X	X
		Ericaceae 1	EP				X		
		Ericaceae 2	EP		X				
		Ericaceae 3	EP		X	X	X		
		Ericaceae 4	EP			X			
		Ericaceae 5	EP	X					
		Ericaceae 6	EP	X					
	Gesneriaceae	*Drymonia* cf. *pilifera* Wiehler	EP	X	X			X	

(continued)

Table A1. Continued

| Group	Family	Species	Habit	Height zone					
				A	B	C	D	E	F
		Gesneriaceae 1	EP	X		X	X		
		Gesneriaceae 2	NV	X					
		Gesneriaceae 3	EP				X		
	Marcgraviaceae	*Marcgravia nepenthoides* Seem.	HE	X	X		X		
		Marcgravia sp.	HE		X			X	
		Marcgraviaceae	HE	X	X	X			
	Moraceae	*Ficus* sp.	HE	X		X		X	
	Piperaceae	*Peperomia hernandiifolia* (Vahl) A. Dietr.	EP			X	X		
		Peperomia pittieri C. DC.	EP	X	X				
		Peperomia sp. 2	EP	X	X	X	X		
		Peperomia sp. 3	EP	X	X				
		Peperomia sp. 4	EP	X	X	X	X		
		Peperomia sp. 5	EP			X			
		Peperomia sp. 6	EP			X			
		Piper sp. 1	HE/NV	X				X	
		Piper sp. 2	HE/NV	X					
	Morphospecies	Morphospecies 1	EP	X					
		Morphospecies 2	EP	X	X	X		X	X
		Morphospecies 3	EP		X	X	X		
		Morphospecies 4	EP						X
		Morphospecies 5	EP					X	

Note. Shown is the presence of the species in six height zones on the trees: A = 0–5 m; B = 5–10 m; C = 10–15 m; D = 15–20 m; E = 20–25 m; F = 25–30 m. Nomenclature according to tropicos.org (December 2016). NV = nomadic vine; EP = epiphyte; HE = hemiepiphyte.
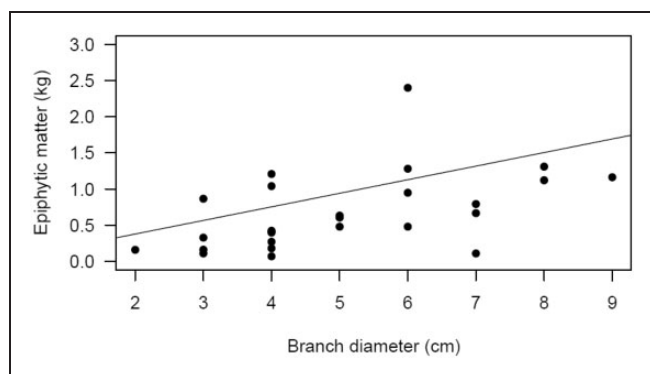

Figure A1. Relationship of epiphytic matter and branch diameter (cm) of 22 trees in western Panama: Quebrada Honda, Fortuna = (0.18, R^2 = .65; p < .001).
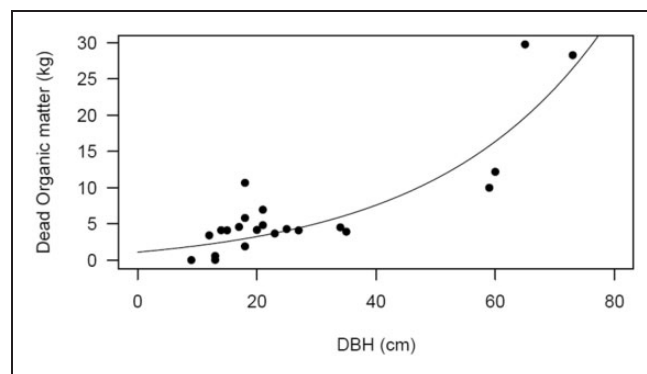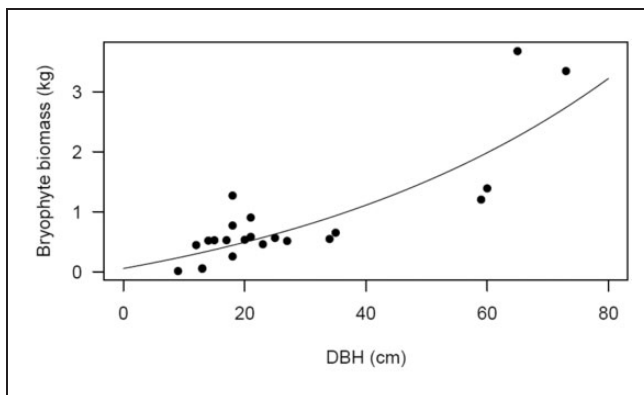

Figure A2. Relationship of dead organic matter and trunk diameter at breast height (DBH, cm) of 22 trees in western Panama: Quebrada Honda, Fortuna (log dead organic matter) = 0.73 + 0.03 DBH, R^2 = .59; p < .001).
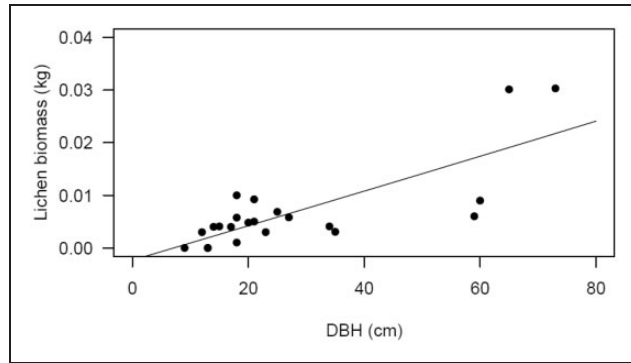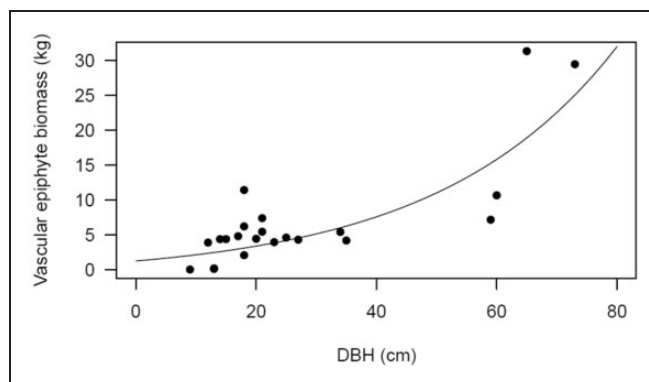
Figure A3. Relationship of lichen biomass and trunk diameter at breast height (DBH, cm) of 22 trees in western Panama: Quebrada Honda, Fortuna (log bryophytes) $= 0.002 + 0.003$ DBH, $R^2 = .60$; $p < .001$.
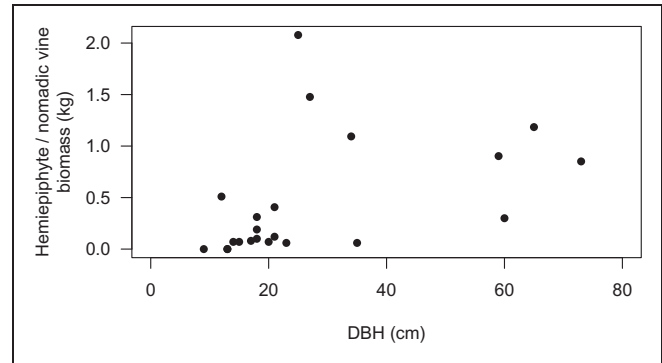
Figure A6. Relationship of hemiepiphyte/nomadic-vine biomass and trunk diameter at breast height (cm) of 22 trees in western Panama: Quebrada Honda, Fortuna. No significant relationship was found.

Figure A4. Relationship of bryophyte biomass and trunk diameter at breast height (DBH, cm) of 22 trees in western Panama: Quebrada Honda, Fortuna (log bryophytes) $= 0.05 + 0.01$ DBH, $R^2 = .71$; $p < .001$.

Figure A5. Relationship of vascular epiphyte biomass and trunk diameter at breast height (DBH, cm) of 22 trees in western Panama: Quebrada Honda, Fortuna (log vascular plants) $= 0.79 + 0.03$ DBH, $R^2 = .53$; $p < .001$.

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