Epiphytes in human settlements in rural Panama

Helena Julia Regina Einzmann*a, Lisa Döckeab and Gerhard Zotza,b

*Department of Biology and Environmental Sciences, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany; bSmithsonian Tropical Research Institute, Panamá, República de Panamá

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Background: An ever-increasing proportion of tropical ecosystems are affected by ongoing land-use changes, stressing the importance of understanding how organisms cope with biotic and abiotic challenges outside their natural habitat. An important group in the tropics are vascular epiphytes, whose response to human disturbance is poorly understood.

Aims: Creating a baseline data set of epiphyte diversity in human settlements and assessing differences with assemblages of less disturbed habitats.

Methods: We surveyed the vascular epiphyte assemblages in 25 settlements of south-west Panama along a rainfall gradient. We tested how epiphyte assemblages were affected by human disturbance and climate by comparing our data to that of pastures and forest.

Results: Almost half (238 of 499) of all studied trees hosted at least one epiphyte. Altogether, 10,700 epiphytes of 56 species were found. Rainfall strongly affected both composition and diversity of epiphyte assemblages, whereas geographic proximity did not. In settlements, the species pool was considerably smaller than in pastures and undisturbed forest; however, settlements’ diversity was only significantly lower compared to pastures.

Conclusions: Epiphyte assemblages in settlements had a diminished species pool but diversity per tree was comparable to less disturbed habitats. Unsurprisingly, rainfall seems to be the main determinant of epiphyte diversity in rural settlements.

Keywords: epiphyte diversity; human influence; isolated trees; mistletoes; rainfall gradient; tropical lowlands

Introduction

Vascular epiphytes represent almost 10% of terrestrial plant diversity worldwide (Zotz 2013a). Although some species may establish and grow on man-made structures, such as overhead power cables (Wester and Zotz 2010), epiphytes typically grow on trees, making them sensitive to any alteration of the forest. Even though the global rate of deforestation has slowed in the last decade, it is still alarmingly high in many parts of the world (FAO 2014) with the greatest losses seen in tropical regions (FAO 2010). Human-modified landscapes are not devoid of trees, but in contrast to trees in forests they represent more isolated “habitat islands” (Turner et al. 1994). Today, land-use change is the greatest on-going threat to the epiphytic life form along with climate change (Zotz and Bader 2009). Many recent studies reflect an increased interest in epiphytes in secondary habitats, such as cocoa or coffee plantations (e.g. Andersson and Gradstein 2005; Hietz 2005; Haro-Carrión et al. 2009; Moorhead et al. 2010), or considered the impact of tree monocultures on epiphyte diversity and dependant organisms (Turner and Foster 2009; Boelter et al. 2011). Epiphytes on isolated trees have mostly been studied at higher elevations, but rarely in the lowlands (Hietz-Seifert et al. 1996; Poltz and Zotz 2011), and there is only one study addressing the long-term dynamics of such assemblages (Larrea and Werner 2010). Only recently, some studies considered specific genera in urban environments in Kathmandu Valley and in Mérida, Venezuela (Adhikari et al. 2012; Judith et al. 2013; see also work on hemiepiphytes: Jim 2014); entire assemblages have been described in three different cities (Oliveira Alves et al. 2014; Bhatt et al. 2015; Izuddin and Webb 2015). The latter studies concentrated on host characteristics rather than comparing their findings to epiphyte diversity in pristine habitats.

The two main factors that may affect epiphyte assemblages in a fragmented landscape include (1) the isolation of host trees and (2) altered microenvironmental conditions. Isolation of host trees increases dispersal distances, which has been shown to have negative consequences on non-vascular epiphytes (Snäll et al. 2005; Löbel et al. 2006; Hylander 2009), similar negative effects were shown for epiphytic bromeliads (Cascante-Marín et al. 2009) and orchids (Ackerman et al. 1996). By modelling the metapopulation dynamics of lichens, Johansson et al. (2012) could link slow colonisation-extinction dynamics to connectivity, species traits and patch dynamics. In contrast to the findings for bryophytes and lichens, microclimatic changes, not dispersal constraints, seem to be key determinants for vascular epiphyte assemblages in a disturbed landscape (Köster et al. 2009; Werner and Gradstein 2009). A dry microclimate in the host will favour drought-resistant epiphyte taxa, while excluding more mesic taxa (Zotz and Bader 2009). Sensitivity of vascular epiphyte assemblages to microenvironmental changes has also been demonstrated for assemblages on
individual trees within a forest: deciduous trees hosted less diverse epiphyte assemblages and lower epiphyte abundance than did evergreen trees that provided a more humid microclimate (Einzmann et al. 2015). Another aspect of environmental differences is microhabitat diversity. A positive association of tree size and epiphyte diversity has been found repeatedly (e.g. terSteege and Cornelissen 1989; Hietz and Hietz-Seifert 1995; Wolf 2005). Woods et al. (2015) showed that microhabitat heterogeneity increased with tree growth, which, in turn, contributed to structural changes in epiphyte assemblages. More than half the epiphyte species they studied were associated with large trees. Consequently, only a sufficient number of large trees can promote a diverse epiphyte community. This should also hold true in fragmented landscape as the importance of large (native) trees in a human-modified landscape has been demonstrated for at least one epiphytic orchid (Kartzinel et al. 2013). Thus, the global decline of large old trees (Lindenmayer et al. 2012) would arguably have a cascading effect on dependent epiphytes.

For the present study, we assessed entire epiphyte assemblages of isolated and grouped trees in rural settlements in the lowlands of south-western Panama. We chose this area because of the already existing data of epiphyte assemblages on pasture trees, where at the drier end of a fourfold rainfall gradient less diverse epiphyte assemblages were observed (Poltz and Zotz 2011). We expected this to hold true for epiphytes in settlements as well as higher and/or more regular precipitation should buffer the negative microclimatic effect of host isolation on epiphyte assemblages. If an altered microclimate in isolated trees, compared to forest trees, acted as the main filter to epiphyte diversity, we would expect less diverse epiphyte assemblages on single trees than in grouped trees in settlements. Comparing the epiphyte assemblages of a lowland forest plot to those observed on pasture trees, Poltz and Zotz (2011) found a clear decrease in epiphyte richness. We expected that an even higher human influence on assemblages in the settlements should further diminish epiphyte richness (e.g. Werner and Gradstein 2009; Etisa 2010; Carvajal-Hernández et al. 2014). At close ranges of a few kilometres, dispersal constraints seem to play a minor role for vascular epiphytes (Köster et al. 2009; Werner and Gradstein 2009). Since our study region spanned over 250 km, we expected epiphyte assemblages in settlements closer to each other to be more similar than those found further apart. Likewise, we expected the similarity of neighbouring pastures and settlements to be greater than expected by chance.

**Material and methods**

**Study area**

The study was conducted along the Pacific slope of Panama in the lowlands of the provinces Coclé, Herrera, Los Santos, Veraguas and Chiriquí (71°37′–81°32′ N, 80° 12′–82°50′ W). This area has been used for agriculture for many decades, sometimes centuries, and small rural communities are scattered throughout the region. The current vegetation resembles tropical dry to wet savannah. At the beginning of the twentieth century, large parts of the Azuero Peninsula were still covered by forest (Heckadon-Moreno 2009). Tropical dry forests grew on the eastern slope of the western mountain chain of Azuero and tropical wet forest was typical for the region around Tonosi, which is located at the centre of the southern coast of the peninsula. Today, forest fragments are scattered, usually small, and mostly secondary stands. The region features a humidity gradient ranging from ca. 1100–4200 mm mean annual precipitation with a dry season of about 3 months from January to March (Poltz and Zotz 2011). The mean annual temperature varies from 27 °C at the coast to 25 °C inland (Atlas Nacional de la República de Panamá 1988). However, in the drier part of the Azuero Peninsula, the dry season lasts 4–5 months from December to May and the mean annual temperature is around 28 °C (Heckadon-Moreno 2009).

**Sampling**

We selected 25 settlements (Table S1), which were within <6 km to study sites of an epiphyte inventory on pasture trees (revisiting the plots established by Poltz and Zotz 2011). Human population size ranged from ca. 300 (El Muñoz) to about 13,500 (Las Lomas; de Ramos 2004). Additionally, we studied epiphyte assemblages in the provincial capitals Chitré (8000), Santiago (32,500) and David (78,000). We used the following sampling approach. Per settlement, 10 single trees and one group of trees were chosen via satellite images from Google Earth (Earth Version 7.1.2.2041) at a scale of about 700 m. We chose this sampling approach to find out if grouped trees, in contrast to isolated single trees, provided a more amenable microclimate and/or increased host connectivity conducive to dispersal and establishment. Single trees had to fulfil the following prerequisites: >10 m distance to next tree, and a diameter at breast height (dbh) > 10 cm. Within each tree group, we also chose 10 individual trees with a dbh > 10 cm. Height, crown diameter and distance to next tree (in case of single trees) were estimated visually for each tree (Figure S1). Epiphyte species and their abundance were recorded for each tree via observation from the ground and the additional use of binoculars for larger trees (names follow The Plant List 2013). Voucher specimens were deposited in the Herbarium of the University of Panama. Ground-based censuses are known to yield incomplete results (Flores-Palacios and García-Franco 2001), but given that the epiphyte flora in the lowlands is not as diverse as in the cloud forest studied by these authors and that trees could be inspected from all sides, sampling from the ground with binoculars is likely to introduce only a small error. For trees hosting a large number of epiphytes, abundance was quantified in one 90 degree sector of each tree crown and later extrapolated for the whole tree. The remaining crown was searched for
additional species. Individuals growing on the trunk were also quantified. Since the delimitation of individual plants is often difficult when studying epiphytes, we used the common concept of a “stand” following Sanford (1968): a group of rhizomes, stems and leaves belonging to one species, which is clearly separated from any conspecific. Smaller plants were only included when exceeding ca. 25% of the maximum size of a given species. We recorded holoepiphytes, hemiepiphytes, nomadic vines (as defined by Zotz 2013b) as well as mistletoes (hemiparasites).

Statistical analyses were conducted only with holoepiphytes and hemiepiphytes without ground contact at the time of the inventory. All nomadic vines had ground contact and thus were excluded from the analyses. The degree of drought tolerance of the epiphyte assemblages in the settlements was assessed using δ13C values from the literature distinguishing crassulacean acid metabolism (CAM) and C3 species: δ13C values less negative than −20‰ were taken as an unambiguous indication of CAM (Zotz 2004). Members of genera and families, which are known to use invariably either CAM or C3, were assigned to the respective category, e.g. Cactaceae are CAM (Smith and Winter 1996). Only three species with 82 individuals could not be assigned and were excluded from the comparison.

Climatic influence on epiphyte assemblages

Data on annual rainfall were obtained from the electricity supplier Empresa de Transmisión Eléctrica. S.A. (ETESA). For almost all settlements, there were mean monthly rainfall data from rain gauge stations (Empresa de Transmisión Eléctrica S.A. 2015). For six settlements, there was no nearby station, and the interpolated data from Poltz and Zotz (2011) were used (Table S1).

We tested whether the composition of epiphyte assemblages was related to rainfall and/or tree size parameters via a canonical correspondence analysis (CCA) using Canoco 4.5 (ter Braak and Smilauer 1997–2002). The settlement identity was incorporated in the analysis as qualitative explanatory variable by creating dummy variables, which assigned each tree to the respective settlement. Rainfall and tree size parameters were included as environmental variables and their effect tested using a Monte Carlo permutation test with manual forward selection (9999 runs). The analyses were run with abundance data. Scaling of data was symmetric between inter-species and inter-sample distances. Biplot scaling was used. Tree size parameters correlated with each other (weighted correlation coefficients >0.59), and we included only tree height in the final analysis.

To test if epiphyte diversity correlated with annual rainfall, we calculated the Shannon index including all the individual trees of each settlement, for the 10 grouped trees and finally, for including both the 10 single and the 10 trees of the group. We then carried out linear regressions for all three cases.

Human influence on epiphyte assemblages

To compare species richness in habitats with increasing human influence, we used individual-based rarefaction curves, which correct for differences in the numbers of individuals in a sample (Gotelli and Graves 1996). As there are, to our knowledge, no prior data on natural epiphyte vegetation along such a large precipitation gradient, we used data of a 0.4-ha plot within a moist tropical forest located in Panama (San Lorenzo crane site, Zotz and Schultz 2008). As an example of intermediate human influence, we used the data of the recently repeated (2013) epiphyte census of the pasture trees originally described in Poltz and Zotz (2011) (HJR Einzmann, unpubl. data). Because the forest plot receives about 3300 ± 550 mm of annual rainfall (= mean ± sd for 1997–2014, Paton 2014), we only included data of pasture trees and settlements within this precipitation range. Only trees with a dbh > 10 cm and at least one epiphyte (forest: 161 trees; pasture: 190 trees and settlements: 99 trees) were included. As all epiphytes from the included trees of the three habitats were subjected to the rarefaction procedure, the obtained curves showed average numbers of species per habitat type. The significance of the observed differences in species richness (P < 0.05) was assessed by visually comparing rarefaction curves and their 95% confidence intervals.

Geographic proximity

A partial Mantel test was used to evaluate if epiphyte assemblages were more similar in settlements closer to each other. This test allowed the separation of the expected effect of rainfall from a pure distance effect on spatial structure. As recommended by Jost et al. (2011), the Morisita–Horn index was used as similarity index. We also assessed if epiphyte assemblages of randomly paired settlements and pasture plots were less similar than those of settlements and their neighbouring pasture plots. For this test Chitré, Santiago and David were excluded because these lacked neighbouring pasture plots within 6 km. First, the similarity indices of species assemblages of randomly paired settlement and pasture plots were calculated in a bootstrap analysis. Then, the similarity index of species assemblages from settlements and neighbouring pasture plots were calculated. Subsequently, it was tested if the means of the two generated lists differed significantly.

Host tree identity and epiphyte richness

The degree of specificity between epiphytes and hosts has been the subject of many studies (review in Wagner et al. 2015). These authors concluded that vascular epiphytes are largely unrestricted in their host ranges, although a certain level of bias seems common. Thus, it is unlikely that different tree composition in the settlements would be a major confounding factor in our analyses, but it would
have been desirable to analyse habitat-related differences in epiphyte assemblages controlling for tree species. Unfortunately, this was not possible due to the high diversity, low abundance and the dispersed geographical distributions of tree species. It was possible, however, to quantify the differences in tree species composition between habitats. To this end, we quantified species overlap in settlements and pastures, and correlated the host tree ranks from settlements and pastures.

Moreover, we specifically addressed the suitability of Mango (*Magnifera indica* L.) trees for epiphytes. Mango was by far the most abundant host species in our survey (>100 individuals, Table S2) with at least one Mango tree in all but one settlement. There is a long-standing debate whether Mango trees are better or poorer hosts compared to other trees. For example, Mango trees were observed to be “poor” hosts in the West Indies, but “good” host around Rio de Janeiro (Schimper 1888). While the first categorisation was supported in Johansson’s study in Africa (1974), the latter was supported by observations in Costa Rica (Nir 1988). For our analysis, we excluded all trees from other species outside the observed dbh range of Mango trees (20 cm < dbh < 237 cm), distinguishing four dbh classes to ensure that size parameters did not differ significantly between groups. The upper limits of the dbh classes were: (1) 38 cm, (2) 50 cm, (3) 100 cm and (4) 237 cm. Because data were not normally distributed, we used the Kruskal–Wallis rank sum test (KW) and post hoc the Nemenyi–Damico–Wolfé–Dunn test (NDWD). We tested epiphyte abundance and presence/absence data.

### Statistical analyses

If not mentioned otherwise, statistical analyses were conducted with R (R Core Team 2013) with the add-on libraries ade4 (Dray and Dufour 2007), car (Fox and Weisberg 2011), coin (Hothorn et al. 2006), ecodist (Goslee and Urban 2007), MASS (modern applied statistics with S; Venables and Ripley 2002) and vegan (version 2.2–1, Oksanen et al. 2015).

### Results

We inspected 499 trees in human settlements, of which 238 (48%) hosted at least one epiphyte. In total, we observed almost 10,900 individual epiphytes (holoepiphytes and hemiepiphytes, e.g. *Clusia* sp., without ground contact) and >160 mistletoes (for a complete list of epiphyte and trees species see Table 1 and Table S2, respectively). We also found ca. 100nomadic vines, of two morphospecies (*Monstera* sp. and *Philodendron* sp.), invariably with ground contact. The holoepiphytes belonged to 56 species of 12 families. Most prominent were Bromeliaceae (almost 4000 individuals, 36%) and Orchidaceae (> 3000 individuals, 30%). About 60% of the individuals grew on single trees and only 40% grew in grouped trees. This pattern did not change when the larger settlements (population >10,000) were excluded.

Almost 40% of the epiphyte species and almost 45% of the individuals (4710) used CAM (Table 1). There tended to be more CAM plants on single trees than in grouped trees, although this difference was not significant (KW: $\chi^2 = 2.77$, df = 1, $P = 0.10$). As expected, the proportion of CAM individuals per settlement was inversely related to rainfall (Spearman’s rank correlation: $P < 0.001$, $r = −0.8$).

The 499 host trees belonged to 28 families and >70 species (Table S2). More than 90% of all trees could be identified at least to genus level, but for 30 trees (27 species) we were unable to determine even the family affiliation. Anacardiaceae (144 individuals) and Leguminosae (53 individuals) were the most common families. *Magnifera indica* L. was by far the most abundant species (113 individuals, Anacardiaceae), followed by *Byrsonima crassifolia* (L.) Kunth with 26 individuals (Malpighiaceae). Individual trees were up to ~26 m tall and their projected crown area ranged from 7 m² to ~1600 m². Dbh of single trees was slightly larger than that of grouped trees (mean: 62 vs. 56 cm), but not significantly (KW: $\chi^2 = 1.6$, df = 1, $P = 0.20$). Crown diameter did not differ significantly either (mean: 12 vs. 13 m; KW: $\chi^2 = 1.2$, df = 1, $P = 0.27$). Single trees were significantly shorter (mean: 8 vs. 11 m; KW: $\chi^2 = 61.8$, df = 1, $P < 0.001$).

#### Climatic influence on epiphyte assemblages

Of the environmental variables included rainfall explained 68% of the variation in the multivariate analysis and tree size explained about 32%. The scatter of the settlement centroids along the first axis of the diagram mainly reflected the rainfall gradient, which correlated strongly with the first axis (−0.79, Figure 1). In line with the influence of rainfall on assemblage composition in the CCA, epiphyte diversity correlated significantly with rainfall: for single trees (linear model: $F_{(1,23)} = 56.2$, $P < 0.001$, adjusted $R^2 = 0.7$), grouped trees (linear model: $F_{(1,23)} = 40.1$, $P < 0.001$, adjusted $R^2 = 0.6$) and both groups combined (linear model: $F_{(1,23)} = 70.1$, $P < 0.001$, adjusted $R^2 = 0.7$). Excluding settlements with a population >10,000 did not change the pattern of the multivariate analysis nor the trends related to rainfall (data not shown).

#### Human influence on epiphyte assemblages

Estimated species richness diminished gradually as human influence increased, being highest in the forest plot, intermediate in pastures, and lowest in settlements (Figure 2). Note that forest data stem from a single discrete plot, while the sampled trees in pastures and settlements were distributed over a large geographic area. Thus, epiphyte richness in forests is certainly underestimated relative to the two other habitats.

In the forest plot, 83% of the trees (dbh > 10 cm) hosted epiphytes compared to 93% in the pastures. In the settlements, 72% of the trees acted as hosts. While the
### Table 1. Epiphyte species (including hemiepiphytes* and nomadic vines** with established ground contact) found in 25 rural settlements in Panama. Also given are mistletoes, which are grouped at the end of the table. Numbers of individuals found are separated according to single ($n = 249$) and grouped trees ($n = 250$). The distinction of C3/CAM species is based on published $\delta^{13}C$ values for particular species (1) or derived from data on congenerics (2). (Zotz and Ziegler 1997; Crayn et al. 2004; Zotz 2004; Silvera et al. 2010; Einzmann et al. 2015).

| Taxon                     | Abundance in single trees (number of host trees) | Abundance in grouped trees (number of host trees) | CAM/C3 |
|---------------------------|--------------------------------------------------|--------------------------------------------------|--------|
| **Araceae**               |                                                  |                                                  |        |
| Anthurium schlechtendalii Kunth | 37 (7)                                           | 23 (11)                                          | C3     |
| Monstera sp.**            | 34 (12)                                          | 47 (39)                                          | C3     |
| Philodendron sp.**        | 3 (3)                                            | 13 (11)                                          | C3     |
| Aspleniaceae              |                                                  |                                                  |        |
| Asplenium sulcatum Lam.   | 98 (7)                                           | 155 (5)                                          | C3     |
| **Bromeliaceae**          |                                                  |                                                  |        |
| Catopsis nutans (Sw.) Griseb. | 297 (21)                                         | 32 (7)                                           | C3     |
| Catopsis sp.              | 36 (1)                                           | 0 (0)                                            | C3     |
| Tillandsia balbisiana Schult. & Schult.f. | 456 (33)                                         | 137 (17)                                         | CAM    |
| Tillandsia brachycaulos Schltdl. | 81 (14)                                          | 168 (11)                                         | CAM    |
| Tillandsia caput-medusae E.Morren | 86 (10)                                          | 38 (6)                                           | CAM    |
| Tillandsia elongata Kunth  | 199 (12)                                         | 38 (5)                                           | CAM    |
| Tillandsia fasciculata Sw. | 659 (50)                                         | 241 (29)                                         | CAM    |
| Tillandsia flexuosa Sw.   | 305 (18)                                         | 0 (0)                                            | CAM    |
| Tillandsia juncea (Ruiz & Pav.) Poir. | 20 (2)                                            | 0 (0)                                            | CAM    |
| Vriesea sanguinolenta Cogn. & Marchal | 630 (43)                                         | 466 (32)                                         | C3     |
| **Cactaceae**             |                                                  |                                                  |        |
| Disocactus phyllanthoides (DC.) Barthlott | 6 (2)                                              | 0 (0)                                            | CAM    |
| Hylocereus costaricensis (F.A.C.Weber) Britton & Rose | 156 (25)                                         | 143 (12)                                         | CAM    |
| **Clusiaceae**            |                                                  |                                                  |        |
| Clusia sp.*               | 6 (5)                                            | 15 (4)                                           | C3     |
| **Gesneriaceae**          |                                                  |                                                  |        |
| Codonanthe crassifolia (H.Focke) C.V.Morton | 80 (8)                                            | 0 (0)                                            | C3     |
| **Lycopodiaceae**         |                                                  |                                                  |        |
| Huperzia sp.              | 0 (0)                                            | 5 (1)                                            | C3     |
| **Moraceae**              |                                                  |                                                  |        |
| Ficus sp.*                | 15 (12)                                          | 9 (9)                                            | C3     |
| **Orchidaceae**           |                                                  |                                                  |        |
| Aspasia epidendroides Lindl. | 0 (0)                                           | 6 (1)                                            | C3     |
| Brassavola nodosa (L.) Lindl. | 52 (13)                                          | 20 (6)                                           | CAM    |
| Bulbophyllum pachyrachis (A.Rich.) Griseb. | 57 (1)                                            | 0 (0)                                            | C3     |
| Camaridium ochroleucum Lindl. | 50 (7)                                           | 183 (9)                                          | C3     |
| Catasetum sp.             | 15 (3)                                           | 129 (9)                                          | C3     |
| Cattleya sp.              | 65 (11)                                          | 36 (10)                                          | CAM    |
| Caularthron bilamellatum (Rchb.f.) R.E.Schult. | 19 (3)                                           | 0 (0)                                            | C3     |
| Dimerandra emarginata (G.Mey.) Hoehne | 341 (24)                                          | 213 (22)                                         | C3     |
| Encyclia cordigera (Kunth) Dressler | 176 (23)                                          | 371 (24)                                         | CAM    |
| Encyclia sp.              | 2 (1)                                            | 0 (0)                                            | CAM    |
| Encycliastellata (Lindl.) Schlr. | 167 (5)                                          | 13 (3)                                           | CAM    |
| Epidendrum difforme Jacq. | 519 (49)                                         | 317 (33)                                         | CAM    |
| Epidendrum scultpnum Rchb.f. | 1 (1)                                             | 3 (3)                                            | CAM    |
| Epidendrum strobiliferum Rchb.f. | 0 (0)                                           | 5 (2)                                            | C3     |
| Heterotaxis sesslis (Sw.) F.Barros | 10 (4)                                           | 119 (3)                                          | CAM    |
| Notylia albida Klotzsch    | 45 (1)                                           | 0 (0)                                            | CAM    |
| Oncidium sp.              | 10 (1)                                           | 0 (0)                                            | C3     |
| Orchidaceae sp.           | 0 (0)                                            | 4 (1)                                            | C3     |
| Polystachya foliosa (Hook.) Rchb.f. | 70 (14)                                          | 89 (13)                                          | C3     |
| Prosthechea chacaensis (Rchb.f.) W.E.Higgins | 68 (7)                                           | 10 (2)                                           | C3     |
| Rossioglossum ampiatium (Lindl.) M.W.Chase & N.H.Williams | 1 (1) | 0 (0) | CAM |
| Scaphyglottis behrii (Rchb.f.) Benth. & Hook.f. ex Hemsl. | 5 (3) | 5 (2) | C3 |
| Scaphyglottis bidentata (Lindl.) Dressler | 4 (2) | 1 (1) | C3 |
| Scaphyglottis imbricata (Lindl.) Dressler | 9 (2) | 4 (2) | C3 |

(Continued)
### Table 1. (Continued).

| Taxon                          | Abundance in single trees (number of host trees) | Abundance in grouped trees (number of host trees) | CAM/C3 |
|-------------------------------|-----------------------------------------------|------------------------------------------------|--------|
| *Trigonidium egertonianum* Bateman ex Lindl. | 0 (0)                                         | 1 (1)                                          | C3     |
| *Trizeuxis falcata* Lindl. | 19 (2)                                        | 26 (2)                                         | CAM    |
| **Piperaceae**                |                                               |                                                |        |
| *Peperomia glabella* (Sw.) A.Dietr. | 3 (1)                                         | 0 (0)                                          | C3     |
| *Peperomia rotundifolia* (L.) Kunth | 201 (25)                                       | 185 (32)                                       | C3     |
| *Peperomia sp.1*              | 48 (4)                                        | 0 (0)                                          | C3     |
| *Peperomia sp.2*              | 0 (0)                                         | 4 (1)                                          | C3     |
| **Polypodiaceae**             |                                               |                                                |        |
| *Campyloneurum phyllitidis* (L.) C. Presl | 51 (8)                                        | 24 (7)                                         | C3     |
| *Pecluma pectinata* (L.) M.G. Price | 98 (19)                                       | 154 (11)                                       | C3     |
| *Pleopeltis astroplepis* (Liebm.) E. Fourn. | 445 (49)                                       | 59 (12)                                        | C3     |
| *Polypodium furfuraceum* Schltdl. & Cham. | 140 (18)                                       | 19 (11)                                        | C3     |
| *Polypodium polypodoides* (L.) Watt | 380 (41)                                       | 183 (16)                                       | C3     |
| *Serpocaulon maritimum* (Hieron.) A.R. Sm. | 35 (12)                                       | 19 (7)                                         | C3     |
| **Pteridaceae**               |                                               |                                                |        |
| *Ananthacorus angustifolius* (Sw.) Underw. & Maxon | 306 (11)                                       | 433 (21)                                       | C3     |
| *Vittaria lineata* (L.) Sm. | 20 (1)                                        | 0 (0)                                          | C3     |
| **Mistletoes**                |                                               |                                                |        |
| **Loranthaceae**              |                                               |                                                |        |
| *Loranthaceae sp.*            | 5 (3)                                         | 0 (0)                                          |        |
| *Oryctanthus occidentalis* (L.) Eichler | 1 (1)                                         | 0 (0)                                          |        |
| *Struthanthus orbicularis* (Kunth) Eichler | 62 (16)                                       | 12 (4)                                         |        |
| **Santalaceae**               |                                               |                                                |        |
| *Phoradendron quadrangulare* (Kunth) Griseb. | 79 (7)                                        | 8 (3)                                          |        |

Figure 1. Triplot of a canonical correspondence analysis (CCA) for the epiphyte communities in 25 settlements in Panama. Rain and tree height were used as environmental variables, both of which showed a significant effect on community composition ($P < 0.01$). The first two axes of the CCA are depicted. The graph displays 6% of the inertia (= weighted variance) in the abundance and 72% of variance in the weighted averages and class totals of species with respect to the environmental variables. The eigenvalues of axis 1 and axis 2 are 0.47 and 0.23, respectively. Quantitative environmental variables are indicated by arrows, inverted triangles display settlement centroids and small triangles epiphyte species (names were omitted for clarity).
The large-scale land-use changes in tropical biodiversity hot spots call for more attention to the biodiversity of settlements. We tested if Mango trees were better or worse hosts compared to other trees. The largest Mango trees (size class 4, dbh > 100–237 cm) tended to host more epiphyte individuals than similarly large trees of other species, but this trend was not significant (KW: $\chi^2 = 3.4$, df = 1, $P = 0.06$). In the three smaller dbh classes, no significant differences were found either (all KW: $P \geq 0.10$). We did not find consistent differences in species numbers. Larger size classes did not differ (all KW: $P \geq 0.16$), while the second smallest Mango trees (size class 2, dbh > 38–50 cm) tended to host fewer epiphyte species than other hosts (KW: $\chi^2 = 2.99$, df = 1, $P = 0.08$).

**Discussion**

Host tree composition in towns and pastures was quite unequal. Only 23% of their host tree species found in settlements were also observed in pasture plots. The relative abundances of tree species were also significantly different in the two habitat types as indicated by the results of a correlation analysis of host tree ranks (Pearson’s product moment correlation: $P < 0.01$, $r = 0.29$).
anthropic environments (Lugo 2010). In this context, we studied a system that is typical for many other regions in Central and South America. In these rural landscapes, habitat conversion has very large effects on typical components of tropical forests such as epiphytes. However, the notion of very low epiphyte diversity in these situations remained largely untested until now.

This study, which included vascular epiphytes, hemi-epiphytes, nomadic vines and mistletoes, provides a quantitative assessment of epiphyte assemblages in settlements compared to two other habitats. In spite of considerable loss in species, we showed that epiphyte assemblages in rural settlements were nonetheless diverse. Moreover, the diversity of epiphytes per tree was similar to that in undisturbed forest, but significantly lower than in pasture trees. Differences in epiphyte diversity among settlements could mainly be explained by the amount of annual rainfall. A first analysis of the suitability of Mango trees as epiphyte host provided evidence that large/old individuals hold disproportionately large epiphyte loads.

While the three habitats differed considerably in species number and abundance, there was relatively little variation in the proportion of trees, which were used as hosts. In the pristine lowland forest plot, 83% of the trees with a dbh > 10 cm hosted epiphytes (Zotz and Schultz 2008), compared to 93% of all pasture trees and 72% of all trees in settlements. Very similar proportions have been reported for Singapore (87%, Izuddin and Webb 2015). In contrast, overall species richness and abundance were quite different among habitat types. We conclude that the negative effect of disturbance is relatively moderate. Adhikari et al. (2012) have reported similar observations for epiphytic orchids in Nepal, a result which can be generalised to other groups of organisms (e.g. arthropods – Turner and Foster 2009; spiders – Floren et al. 2011 and birds – Van Bael et al. 2013). It remains to be established, however, if the epiphyte populations in the settlements are really viable in the long term.

These quantitative results have to be interpreted with caution in the case of the forest habitat. Our sampling design allowed unambiguous quantitative comparisons of the epiphyte assemblages in rural settlements and pastures. For forest trees, on the other hand, our argument suffers from the fact that we could not obtain data for epiphytes from a forest in our study area and that the data stem from a single small plot. The study region has been altered to its actual, almost forest-free state for more than a century (Heckadon-Moreno 2009) and no previous records of epiphyte assemblages exist. However, the chosen forest site is relatively close to our study region and belongs to the same forest type as the potential vegetation. Thus, our estimates for epiphyte species and individuals per tree should be valid, but regional species numbers for forest trees (Figure 2) are bound to be underestimates. It should be noted that both tree species composition and relative abundances were quite different in the different habitats. Thus, we cannot completely rule out that the detected differences in epiphyte assemblages were not only related to habitat, but also to host tree identity. On the other hand, Wagner et al. (2015) have shown that vascular epiphytes are largely unrestricted in their host ranges, which suggests that a host bias should be of lesser importance compared to an effect of habitat.

As expected, differences in epiphyte diversity in the settlements could be related to the rainfall gradient that characterised the study region. Poltz and Zotz (2011) had already found this strong correlation of epiphyte diversity and rainfall for epiphyte assemblages on pasture trees within the same area. Although Wolf (2005) found epiphyte assemblages from sites at distances up to 10 km to be more similar in their composition, our comparison of assemblages in settlements and neighbouring pasture plots (distance < 6 km) resulted in no correlation of distance and composition. However, the question if vascular epiphytes are dispersal limited is far from being resolved. Dispersal limitation for vascular epiphytes has been repeatedly inferred from observational studies (Zotz et al. 1999; Werner and Gradstein 2008) and experimental studies have also supported the notion (Ackerman et al. 1996; Cascante-Marín et al. 2009). Conversely, a rather limited role of dispersal limitation in vascular epiphytes can be deduced from the results of two studies in modified landscapes in Ecuador (Köster et al. 2009; Werner and Gradstein 2009). In line with the latter, our results also support the notion that, at least in fragmented landscapes, dispersal limitation is less prevalent.

Drought tolerance in epiphytes is expected to be more important in fragmented landscape compared to intact forest. Its importance was inferred from the recorded number of individuals with CAM. Within the subset of settlements with comparable precipitation to the forest plot, 40% of the species (almost 51% of the individuals) were using this water-saving type of metabolism. This was considerably more than the 20% CAM species (4% of individuals) in the forest used for comparison (Zotz 2004). Our observation in human settlements is fully compatible with earlier reports of increasing abundances of xerophytic Bromeliaceae in other secondary habitats (e.g. Dunn 2000; Barthlott et al. 2001), as is the assumed loss of hygrophilous species (Werner and Gradstein 2009).

Bromeliaceae were also prominent in the pasture plots (HJR Einzmann, unpubl. data), where almost 45% of the trees hosted Bromeliaceae compared to 30% in the settlements. Differences were even more pronounced in terms of abundance. On average, a pasture tree hosted almost six times more individuals than a tree in settlements. This agrees with findings from isolated oak trees in Mexico, on which the biomass of drought-tolerant Tillandsia species was significantly increased in comparison to forest oak trees (Flores-Palacios and García-Franco 2004).

Epiphytes depend on suitable hosts (Wagner et al. 2015), so humans can potentially impact epiphytes by planting and promoting particular tree species. A case in point is M. indica, a species which is frequently planted throughout the tropics, but its suitability as a host for epiphytes is contested. Schimper (1888) was probably
the first to comment on this species with ambivalent remarks regarding its suitability. This ambivalence has continued in later publications as Johansson (1974) found Mango trees to be poor hosts, while Nir (1988) observed a considerable number of orchid species on Mango. In our study, many Mango trees were entirely free of epiphytes, others heavily loaded. One explanation for such a bimodal colonisation pattern might be that their dense, evergreen foliage is a strong barrier for propagules (Schimper 1888). However, once colonisation has occurred as a chance event, plants can thrive because conditions inside the crown are conducive to epiphyte growth. Indeed, the largest Mango trees tended to host more epiphyte individuals than all other studied trees, but in smaller size classes no difference was observed. Thus, our data support the notion described above that dispersal is limited by dense foliage but this is overcome with increasing time of exposure. Yet, one has to keep in mind that tree size and age are by no means comparable between species, so that different growth rates of trees may cause different epiphyte loads at comparable tree sizes (see Wagner et al. 2015 and references therein). Therefore, a simple comparison of epiphyte assemblages from Mango trees and other hosts of similar size is not necessarily indicative of host quality, but may be related to the time available for colonisation.

Conclusions
Trees in human settlements in rural Panama hosted a remarkable number of epiphytes, both in terms of species and abundance. Successful species were mainly those that were able to survive in relatively drought-prone conditions. The original species composition of the study region is unknown but comparing our data set with the epiphyte assemblage of a nearby lowland forest indicates a loss of hygrophilous species and an increase in abundance of drought-resistant species. Taken together, our results are in line with the findings of several previous reports from both tropical low and highlands. Although epiphytes at large are negatively affected, it is well established by now that some groups, e.g. some bromeliads, benefit from human disturbance of native vegetation. Human settlements are able to support trees with epiphyte assemblages similarly diverse as those found in pristine forest. However, they cannot draw from a similarly large species pool nor do abundances reach the levels on trees in less disturbed habitats.

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Supplemental data
Supplemental data for this article can be accessed here.

Notes on contributors
Helena Einzmann wrote her Master’s thesis on epiphyte assemblages as a function to their host tree phenology. She is currently a Ph.D. student, focusing on epiphyte assemblages in human-modified landscapes to assess their dynamic in fragmented habitats. Lisa Döcke worked in this project during her undergraduate studies, before writing her Bachelor’s thesis on the green hawker (Aeshna viridis) in 2014. Gerhard Zott, Professor of Ecology at the University of Oldenburg and Research Associate of the Smithsonian Tropical Research Institute, has been studying the ecology of vascular epiphytes for more than 25 years. Research questions range from functional anatomy to global biogeography of this group.

References
Ackerman JD, Sahat A, Zimmerman JK. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. Oecologia 106:192–198.
Adhikari YP, Fischer A, Fischer HS. 2012. Micro-site conditions of epiphytic orchids in a human impact gradient in Kathmandu valley, Nepal. Journal of Mountain Science 9:331–342.
Andersson MS, Gradstein SR. 2005. Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in western Ecuador. Biodiversity and Conservation 14:1101–1120.
Instituto Geográfico Nacional “Tommy Guardia”. 1988. Atlas Nacional de la República de Panamá. Panamá City: Instituto Geográfico Nacional “Tommy Guardia”.
Barthlott W, Schmit-Neuerburg V, Nieder J, Engwald S. 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecology 152:145–156.
Bhatt A, Gairola S, Govender Y, Bajinath H, Ramdhani S. 2015. Epiphyte diversity on host trees in an urban environment, eThekwini Municipal Area, South Africa. New Zealand Journal of Botany 53:24–37.
Boelter CR, Zartman CE, Fonseca CR. 2011. Exotic tree monocultures play a limited role in the conservation of Atlantic Forest epiphytes. Biodiversity and Conservation 20:1255–1272.
Carvajal-Hernández CI, Krömmer T, Vázquez-Torres M. 2014. Riqueza y composición florística de peritobiontes en bosque mesófilo de montaña y ambientes asociados en el centro de Veracruz, México. Revista Mexicana de Biodiversidad 85:491–501.
Cascante-Marin A, von Mejlenfeldt N, de Leeuw HMH, Wolf JHD, Oostermeijer JGB, den Nijs JCM. 2009. Dispersal limitation in epiphytic bromeliad communities in a Costa Rican fragmented montane landscape. Journal of Tropical Ecology 25:63–73.
Crayn DM, Winter K, Smith JAC. 2004. Multiple origins of crassulacean acid metabolism and the epiphytic habit in the Neotropical family Bromeliaceae. Proceedings of the
National Academy of Sciences of the United States of America 101:3703–3708.

Datos Climáticos Históricos [Internet]. Panamá: Empresa de Transmisión Eléctrica S.A.; [citado 2015 Oct 30]. Available from: http://www.hidromet.com.pa/clima_historicos.php?sen sor=2/
de Ramos E. 2004. Población de la república por sexo, según provincia, distrito y corregimiento: Censos de 1990 y 2000. Panamá: Instituto Nacional de Estadística y Censo. p. 1–16. [citado 2014 Dec 11]. Available from: http://www islacioneria. gob.pa/INEC/Avance/Avance.aspx?ID_CATEGORIA=5&id CIFI RAS=21&id DIOMA=1

Dray S, Dufour AB. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Dunn RR. 2000. Bromeliad communities in isolated trees and three successional stages of an Andean cloud forest in Ecuador. Selbyana 21:137–143.

Einzmann HJR, Beytschlag J, Hofhansl F, Wanek W, Zotr G. 2015. Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. AoB Plants 7:pl0073.

Etats AT. 2010. Diversity of vascular epiphytes along disturbance gradient in Yayu Forest, Southwest Oromia, Ethiopia. Addis A中國a: Addis Ababa University.

FAO. 2010. Global forest resources assessment 2010 - main report. FAO Forestry Paper 163. Rome: FAO.

FAO. 2014. State of the world’s forests 2014 ( SOFO)– enhancing the socioeconomic benefits from forests. Rome: Food and Agriculture Organization of the United Nations (FAO).

Floren A, Mueller T, Deleemann-Reinholt C, Linsenmair KE. 2011. Effects of forest fragmentation on canopy spider communities in SE-Asian rain forests. Ecotopica 17:15–26.

Flores-Palacios A, García-Franco JG. 201. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. Selbyana 22:181–191.

Flores-Palacios A, García-Franco JG. 2004. Effect of isolation on the structure and nutrient content of oak epiphyte communities. Plant Ecology 173:259–269.

Fox J, Weisberg S. 2011. An R companion to applied regression. Thousand Oaks (CA): Sage.

Goslee SC, Urban DL. 2007. The ecosist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22:1–19.

Grolli NJ, Grossen GR. 1996. Null models in ecology. Washington (DC): Smithsonian Institution Press.

Haro-Carrón X, Lozada T, Navarrete H, Koning GHJ. 2009. Conservation of vascular epiphyte diversity in shade cacao plantations in the Chocó region of Ecuador. Biotropica 41:520–529.

Heckadon-Moreno S. 2009. De selvas a potreros. 1st ed. Panamá: Exedra Books.

Hietz P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. Conservation Biology 19:391–399.

Hietz P, Hietz-Seifert U. 1995. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. Journal of Vegetation Science 6:719–728.

Hietz-Seifert U, Hietz P, Guevara S. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biological Conservation 75:103–111.

Hothorn T, Hornik K, van de Wiel MA, Zeileis A. 2006. A lego system for conditional inference. The American Statistician 60:257–263.

Hylland R. 2009. No increase in colonization rate of boreal bryophytes close to propagule sources. Ecology 90:160–169.

Izuddin M, Webb EL. 2015. The influence of tree architecture, forest remnants, and dispersal syndrome on roadside epiphyte diversity in a highly urbanized tropical environment. Biodiversity and Conservation 24:2063–2077.

Jim CY. 2014. Ecology and conservation of strangler figs in urban wall habitats. Urban Ecosystems 17:405–426.

Johansson D. 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeografica Suecia 59:136–267.

Johansson V, Rantisu T, Snall T. 2012. Epiphyte metapopulation dynamics are explained by species traits, connectivity, and patch dynamics. Ecology 93:235–241.

Jost L, Chao A, Chazdon RL. 2011. Compositional similarity and β (beta) diversity. In: Magurran AE, McGill BJ, editors. Biological diversity - frontiers in measurement and assessment. New York: Oxford University Press Inc. p. 66–84.

Judith C, Schneider JV, Schmidt M, Ortega R, Gaviria J, Zizka G. 2013. Using high-resolution remote sensing data for habitat suitability models of Bromeliaceae in the city of Mérida, Venezuela. Landscape and Urban Planning 120:107–118.

Kartzenkel TR, Trapnell DW, Shefferson RP. 2013. Critical importance of large native trees for conservation of a rare Neotropical epiphyte. Journal of Ecology 101:1429–1438.

Köster N, Friedrich K, Nieder J, Bartholtott W. 2009. Conservation of epiphyte diversity in an Andean landscape transformed by human land use. Conservation Biology 23:911–919.

Larrea ML, Werner FA. 2010. Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. Forest Ecology and Management 260:1950–1955.

Lindemayer DB, Laurance WF, Franklin JF. 2012. Global decline in large old trees. Science 338:1305–1306.

Lölé S, Snall T, Rydin H. 2006. Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. Journal of Ecology 94:856–868.

Lugo AE. 2010. Let’s not forget the biodiversity of the cities. Biotropica 42:576–577.

Moorhead LC, Philpott SM, Bichier P. 2010. Epiphyte biodiversity in the coffee agricultural matrix: canopy stratification and distance from forest fragments. Conservation Biology 24:737–746.

Nir MA. 1988. The survivors: orchids on a Puerto Rican coffee finca. American Orchid Society Bulletin 57:989–995.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2015. Vegan: community ecology package [Internet]. R package version 2.2-1. [citado 2015 Nov 5]. Available from: http://CRAN.R-project.org/package=vegan

Oliveira Alves ME, Brun C, Sulzbach Dal Forno R, Essi L. 2014. A survey of vascular epiphyte species of the urban area of Palmeira das Missões, RS, Brazil. Ciência e Natura 36:268–276.

Paton S. 2014. 2014 meteorological summary for the San Lorenzo-Fort Sherman Canopy Crane [Internet]. Smithsonian Tropical Research Institute; [citado 2015 Oct 30]. Available from: http://biogeodb.stri.si.edu/physical_mon itoring/research/sherman/summary

Poltz K, Zotr G. 2011. Vascular epiphytes on isolated pasture trees along a rainfall gradient in the lowlands of Panama. Biotropica 43:165–172.

R Core Team. 2013. R: a language and environment for statistical computing. 3.0.2 ed. Vienna (Austria): R Foundation for Statistical Computing.

Sanford WW. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. Journal of Ecology 56:697–705.

Schimper AFW. 1888. Die epiphytische Vegetation Amerikas. Jena: Verlag von Gustav Fischer.

Silvera K, Santiago LS, Cushman JC, Winter K. 2010. The incidence of crassulacean acid metabolism in Orchidaceae...
derived from carbon isotope ratios: a checklist of the flora of Panama and Costa Rica. Botanical Journal of the Linnean Society 163:194–222.
Smith JAC, Winter K. 1996. Taxonomic distribution of crassulacean acid metabolism. In: Winter K, Smith JAC, editors. Crassulacean acid metabolism biochemistry, ecophysiology and evolution. Berlin: Springer. p. 427–436.
Snäll T, Ehrén J, Rydin H. 2005. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. Ecology 86:106–115.
ter Braak CJF, Smilauer P. 1997–2002. Canoco for windows. 4.5 ed. Wageningen (The Netherlands): Biometris - Plant Research International.
ter Steege H, Cornelissen JHC. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21:331–339.
The Plant List. 2013. Version 1.1. Published on the Internet; [cited 2015 Sept 15]. Available from: http://www.theplantlist.org/
Turner EC, Foster WA. 2009. The impact of forest conversion to oil palm on arthropod abundance and biomass in Sabah, Malaysia. Journal of Tropical Ecology 25:23–30.
Turner IM, Tan HTW, Tee YC, Ibrahim AB, Chew PT, Corlett RT. 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. Conservation Biology 8:705–712.
Van Bael SA, Zambrano R, Hall JS. 2013. Bird communities in forested and human-modified landscapes of Central Panama: a baseline survey for a native species reforestation treatment. International Journal of Biodiversity Science, Ecosystem Services & Management 9:1–9.
Venables WN, Ripley BD. 2002. Modern applied statistics with S. 4th ed. New York: Springer.
Wagner K, Mendieta-Leiva G, Zotz G. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. AoB Plants 7:plu092.
Werner FA, Gradstein SR. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. Biodiversity and Conservation 17:3195–3207.
Werner FA, Gradstein SR. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science 20:59–68.
Wester S, Zotz G. 2010. Growth and survival of Tillandsia flexuosa on electrical cables in Panama. Journal of Tropical Ecology 26:123–126.
Wolf JHD. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212:367–393.
Woods CL, Cardelús CL, DeWalt SJ. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.
Zotz G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? Oecologia 138:184–192.
Zotz G. 2013a. The systematic distribution of vascular epiphytes – a critical update. Botanical Journal of the Linnean Society 171:453–481.
Zotz G. 2013b. Hemiepiphyte: a confusing term and its history. Annals of Botany 111:1015–1020.
Zotz G, Bader MY. 2009. Epiphytic plants in a changing world - global change effects on vascular and non-vascular epi-

Werner FA, Gradstein SR. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. Biodiversity and Conservation 17:3195–3207.
Werner FA, Gradstein SR. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science 20:59–68.
Wester S, Zotz G. 2010. Growth and survival of Tillandsia flexuosa on electrical cables in Panama. Journal of Tropical Ecology 26:123–126.
Wolf JHD. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212:367–393.
Woods CL, Cardelús CL, DeWalt SJ. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.
Zotz G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? Oecologia 138:184–192.
Zotz G. 2013a. The systematic distribution of vascular epiphytes – a critical update. Botanical Journal of the Linnean Society 171:453–481.
Zotz G. 2013b. Hemiepiphyte: a confusing term and its history. Annals of Botany 111:1015–1020.
Zotz G, Bader MY. 2009. Epiphytic plants in a changing world - global change effects on vascular and non-vascular epi-

Werner FA, Gradstein SR. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. Biodiversity and Conservation 17:3195–3207.
Werner FA, Gradstein SR. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science 20:59–68.
Wester S, Zotz G. 2010. Growth and survival of Tillandsia flexuosa on electrical cables in Panama. Journal of Tropical Ecology 26:123–126.
Wolf JHD. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212:367–393.
Woods CL, Cardelús CL, DeWalt SJ. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.
Zotz G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? Oecologia 138:184–192.
Zotz G. 2013a. The systematic distribution of vascular epiphytes – a critical update. Botanical Journal of the Linnean Society 171:453–481.
Zotz G. 2013b. Hemiepiphyte: a confusing term and its history. Annals of Botany 111:1015–1020.
Zotz G, Bader MY. 2009. Epiphytic plants in a changing world - global change effects on vascular and non-vascular epi-

Werner FA, Gradstein SR. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. Biodiversity and Conservation 17:3195–3207.
Werner FA, Gradstein SR. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. Journal of Vegetation Science 20:59–68.
Wester S, Zotz G. 2010. Growth and survival of Tillandsia flexuosa on electrical cables in Panama. Journal of Tropical Ecology 26:123–126.
Wolf JHD. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212:367–393.
Woods CL, Cardelús CL, DeWalt SJ. 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. Journal of Ecology 103:421–430.
Zotz G. 2004. How prevalent is crassulacean acid metabolism among vascular epiphytes? Oecologia 138:184–192.
Zotz G. 2013a. The systematic distribution of vascular epiphytes – a critical update. Botanical Journal of the Linnean Society 171:453–481.
Zotz G. 2013b. Hemiepiphyte: a confusing term and its history. Annals of Botany 111:1015–1020.
Zotz G, Bader MY. 2009. Epiphytic plants in a changing world - global change effects on vascular and non-vascular epi-