How diverse are epiphyte assemblages in plantations and secondary forests in tropical lowlands?

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Abstract

The on-going destruction of old-growth forests puts tropical forest species under great pressure because of the resulting loss of habitat. An important biotic component of these forests are vascular epiphytes, which structurally depend on trees. In human-modified landscapes potential hosts may still be present, e.g. in the form of isolated remnant trees, small groups of planted trees, in patches of secondary forests, or in plantations. For this study, we assessed the potential of timber monocultures and secondary forest patches to function as refuges for vascular epiphytes. We studied epiphyte assemblages in teak and pine plantations and secondary forest patches of unknown age along a rainfall gradient (1100 – 4200 mm) at the Pacific coast of western Panama and also in a few oil palm plantations. Invariably, rainfall had the expected positive influence on epiphyte diversity and abundance. Individual-based rarefaction curves showed that species richness was significantly lower in timber and oil palm plantations compared to secondary forest patches, which in turn hosted less species-rich epiphyte assemblages than (cultivated and wild grown) pasture trees from the same study region. Our results suggest that the value of timber and oil palm plantations as refuges for vascular epiphytes in human-modified landscapes is limited. Secondary forest patches were more promising in that regard.

Keywords: accidental epiphyte, land-use change, plantations, secondary forest, vascular epiphytes

Resumen

La destrucción continua de los bosques primarios coloca a las especies de los bosques tropicales bajo gran presión por la pérdida de hábitat. Un componente biótico importante de estos bosques son las epífitas vasculares, las cuales dependen estucturalmente de los árboles. En los paisajes modificados por el humano los hospederos potenciales pueden estar presentes todavía, por ejemplo en forma de remanentes de árboles aislados, en grupos pequeños de árboles cultivados, en bosques secundarios, o en plantaciones. Para este estudio se evaluó el potencial de los monocultivos de madera y parches de bosques secundarios como refugios de las epífitas vasculares. Se estudió el ensamblaje de las epífitas en plantaciones de teca y pino y en parches de bosque secundario de edad desconocida a lo largo de un gradiente de precipitación (1100 – 4200 mm) en la costa del Pacífico del occidente de Panamá y, adicionalmente, en algunas plantaciones de palmas aceiteras. La precipitación tuvo un efecto positivo en la diversidad y abundancia de epífitas. Las curvas de rarefacción basada en individuos mostraron que la riqueza de especies fue significativamente inferior en plantaciones de madera y palmas aceiteras en comparación a los parches de bosque secundario, los que a su vez hospedaron a menos especies que los ensamblajes de epífitas en árboles de pastos (cultivados y de crecimiento espontáneo) en la misma región de estudio. Nuestros resultados indican que las plantaciones de madera y palmas aceiteras tienen un valor limitado como refugios de epífitas vasculares en paisajes modificados por el humano. En este sentido los parches de bosques secundarios son más prometedores.

Palabras claves: bosque secundario, cambio de uso del suelo, epífitas accidentales, epífitas vasculares, plantaciones

Introduction

Globally, tree plantations are gaining economic importance. Between 2005 and 2010 the total area they covered increased by some 5 million hectares a year [1]. Structurally, tree plantations are far less complex than most natural forests, and are consequently of less ecological value. In spite of this, plantations are not necessarily "ecological deserts" and may provide habitat for a variety of native forest organisms [reviewed by 2]. Epiphytes are diverse and important elements of tropical forests, but depend mechanically on their host trees and are thus highly vulnerable when deforestation occurs [e.g. 3-6]. Continuous destruction of their natural habitat [1] leaves a fragmented matrix in which plantations may be one possible refuge. Generally, older plantations are structurally more complex than younger plantations [7] and support more diverse assemblages of forest species of diverse ecological groups [2 and references therein]. However, Kanowski et al. [7] point out that this effect correlates inversely with management intensity.

An increase in abundance and diversity with plantation age has also been observed in vascular and non-vascular epiphytes [8-11]. A number of studies have focused on epiphytes in plantations themselves and on a possible positive, cascading effect on other biota. For example, in oil palm plantations epiphytes have been shown to promote the existence of foraging birds [12, 13], and a similar effect was found in a shade coffee plantation [14]. Investigating the potential economic benefit of removing epiphytes from oil palms, Prescott et al. [15] found that their removal did not affect the productivity of the crop species.

In agroforestry systems, epiphytes have been studied in cacao and coffee plantations [16-19]. Shade coffee plantations may host considerable epiphyte diversity, although they are not suitable for all forest species [18], especially hygrophilous. Drought vulnerable species are typically missing [20]. As with oil palm plantations, increased management intensities have a negative influence on epiphyte assemblages in both coffee plantations [21, 22] and ancient

tea gardens [23]. Vascular and non-vascular epiphytes have also been studied in monoculture plantations of, for example, *Eucalyptus, Quercus, Araucaria* and *Pinus* [8, 24, 25]. These studies compared epiphyte assemblages in both native and exotic monocultures and concluded that native monocultures have a less negative effect on epiphyte diversity and, in two cases, on epiphyte abundance as well.

The present study encompasses the tropical lowlands of Panama and consists of a system of forest fragments and isolated trees that are separated by agricultural land and settlements. The only easily accessible forest fragments are secondary stands. Primary forest is almost entirely gone except on the south-western edge of the Azuero peninsula. Other potential hosts for epiphytes in this agricultural landscape are pasture trees (mainly cultivated, sometimes growing wild) and living fences [26]. In Panama teak, pine and eucalypts are commonly planted crop trees. Additionally, there are reforestation programs [e.g. PRORENA, 27] and studies of native trees [e.g. The Sardinilla Project, 28], which analyze the development of trees. So far, however, the potential additional benefit of the establishment of an epiphyte flora in these stands has largely been ignored. Studies of epiphyte assemblages in disturbed habitats typically have found decreased diversity and abundance relative to primary forest (fragments) [e.g. 3, 29, 30]. Assemblages of secondary forests were dominated by less specialized, drought-tolerant species, such as xeromorphic bromeliads [31]. Furthermore, conspecifics differed physiologically in secondary and mature forests [32, 33]. In general, the repopulation of secondary forest by epiphytes seems to be a slow process [e.g. 34, 35], likely due to dispersal limitations [e.g. 36] and inherently slow individual growth [e.g. 37, 38].

For this study, data on the epiphyte assemblages of monoculture tree plantations and secondary forest patches were collected and compared to those on pasture trees within the same region. Pasture trees of this region host surprisingly diverse assemblages [39]. If plantations grow in a matrix of such viable epiphyte assemblages, can they provide complementary refuge for epiphytes and increase connectivity? For the epiphyte assemblages on pasture trees, the rainfall gradient in the study region was the most important factor explaining species abundance and richness [39]. As plantations and secondary forest patches are colonized from their surrounding matrix, we expected rainfall to have a similarly important role.

Methods

Study region

The study was conducted at the Pacific slope of Panama in the lowlands (< 500 m above sea level) of four provinces (Chiriquí, Veraguas, Herrera and Los Santos; Fig. 1). Annual precipitation in the region ranges from 1100 to 4200 mm, with a dry season (< 100 mm month^{-1}) of approximately three months from January to March [39] in the wetter areas. Roughly, the eastern coast of the Azuero peninsula is the driest part of the region, and rainfall increases towards the west. The mean annual temperature varies from approximately 27°C at the coast to 25°C inland [40]. In the drier part, however, the dry season lasts from December to May and the mean annual temperature is around 28°C [41]. For many decades, the main land use has been agriculture (mostly cattle breeding and the cultivation of rice or sugarcane) and small communities are scattered throughout the region. Thus, current vegetation resembles tropical dry to wet savannah. Woodlands are rare, usually small, and almost entirely secondary.
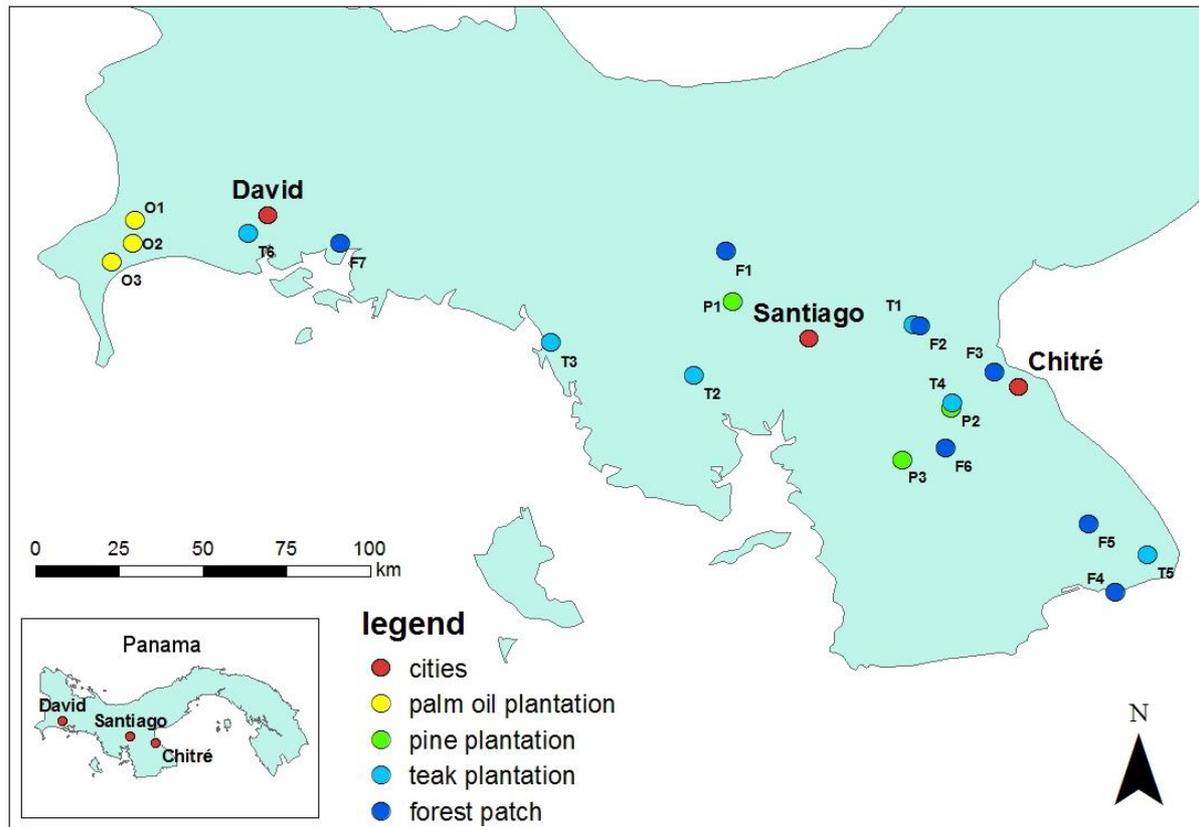
Fig. 1. The study was conducted in the lowlands along the Pacific coast of western Panama in the provinces of Chiriquí, Veraguas, Herrera and Los Santos. A rainfall gradient spans this region: the eastern coast of the peninsula of Azuero receives the least amount of rain (from Chitré to the south: about 1100 mm a^{-1}). Towards the west mean annual rainfall increases reaching 4200 mm a^{-1} in some parts.

Data sampling

We studied epiphyte assemblages in three types of plantations (teak, pine and oil palm) and secondary forest patches, which were selected along the rainfall gradient of the study region in seven secondary forest patches, six teak plantations (*Tectona grandis* L.f.), and three pine plantations (*Pinus caribaea* Morelet). The three oil palm (*Elaeis guineensis* Jacq.) plantations were located relatively close to each other (< 15 km) at the western end of the study region (see Fig. 1). In each forest patch and plantation ten trees were systematically selected (aiming for a straight line through the entire stand and an even distribution along this line) and their epiphytes registered and counted from the ground, names follow The Plant List [42]. To test if plantation trees host a subset of the species present in their direct vicinity we also examined ten non-plantation trees in close proximity (within a < 100 m radius) to the teak and pine plantations. These trees were mainly cultivated trees but there were also wild individuals on pastures surrounding the plantations. We only chose trees growing nearby and aimed for an even distribution of tested trees around the plantations.

The oil palm plantations were mostly surrounded by settlements and cultivated land. Trees were scarce and those nearby did not host any epiphyte. Thus, no data on trees outside the

oil palm plantations were recorded. We documented holoepiphytes [as defined by 43]. Individuals roughly < 25% of the maximum size (length of the longest leaf or stem) of a given species were excluded. Plant units connected by rhizomes were defined as 'stand' after Sanford [44]. Voucher specimens were deposited in the Herbarium of the University of Panama (PMA). In the few cases where there was a high abundance of epiphytes, individual numbers were quantified in a 90° sector of each tree crown and later extrapolated to the entire crown. The remaining crown was searched for additional species.

Ground-based censuses are known to yield incomplete results [45], but given that the epiphyte flora in the lowlands is not as diverse as in the cloud forest studied by Flores-Palacios and García-Franco and that trees could be searched from all sides, it was expected that sampling from the ground with binoculars would introduce only a small error. Binoculars were used for better observation of the upper crown parts. The GPS coordinates of trees were taken and their location marked in a sketch map. The diameter at breast height (dbh) of each tree was measured. This tree size parameter was compared between plantation types and forests using the non-parametrical Kruskal-Wallis rank sum test (KW) and the post hoc Nemenyi-Damico-Wolfe-Dunn test (NDWD). Additionally, we roughly measured the area of the plantations and forest patches studied using Google Earth version 7.1.5.1557 (accessed: 11 January 2016). Areas did not differ significantly between plantation types and forests (KW: $Chi^2 = 1.5$, df = 3, P = 0.7).

We also censused epiphyte assemblages on pasture trees in order to compare the epiphyte diversity of the plantations and secondary forest patches to another habitat type prevalent in the study region. The first census of these assemblages was done in 2005 [for details see 39]. For this study, we repeated the census on 13 of the original pasture plots. Briefly, in each 1-ha plot 10-11 isolated trees had originally been inspected for epiphytes. When reconducting the census in 2012 some trees had been lost and the number of trees ranged from six to ten per site. The trees growing on the pastures were a mixture of cultivated and wild individuals, although a few trees could have been remnants of the original forest. Only the pasture plot closest to each plantation or forest patch was included in this analysis. The mean distance of plantations or secondary forest patches to the next pasture plot was approximately 9 km.

Multivariate analysis
We tested whether the composition of epiphyte assemblages in plantations and secondary forests was related to rainfall, tree size and area via a canonical correspondence analysis (CCA) using Canoco 4.5 [46]. The identity of each study site was incorporated into the analysis as a qualitative explanatory variable by creating dummy variables. Rainfall, tree size and area were included as environmental variables and their effect assessed using a Monte Carlo permutation test with manual forward selection (9999 runs). The analyses were run with log-transformed abundance data so as to reduce the weight of very abundant species. Scaling of data was symmetric between inter-species and inter-sample distances. Biplot scaling was used.

Comparing species richness
In human-modified landscapes plantations and secondary forest patches may be refuge habitats for epiphytes as are isolated pasture trees [39]. To compare the species richness of plantations and forest patches to that found on pasture trees, we used individual-based rarefaction curves, which correct for differences in the numbers of individuals in a sample

[47]. As all epiphytes from the included trees of the different habitats were subjected to the rarefaction procedure, the resulting curves show average species numbers per habitat type. The significance of the observed differences in species richness (P < 0.05) can be assessed by visually comparing rarefaction curves and their 95% confidence intervals.

Rainfall gradient
Data on annual rainfall at the respective sites were obtained from the electricity supplier ETESA (Empresa de Transmisión Eléctrica. S.A.), which provides mean monthly rainfall data from some 300 rain gauges distributed throughout Panama. The mean annual rainfall was calculated for each site from the nearest rain gauge (distance < 4 ± 3 km mean ± standard deviation, years of measurements range from 12 to 61). To test if epiphyte diversity correlated with annual rainfall we calculated the Shannon index for each plantation and forest patch – for epiphyte assemblages on pastures this was shown already by Poltz and Zotz [39]. We then conducted linear regressions.

Data Analysis
Unless otherwise indicated, statistical analyses were conducted with R [48] with the add-on libraries vegan 2.2-1 [49] and coin [50].

Results
We documented 57 epiphyte species (7136 individuals) in 155 of the 279 studied trees in plantations and secondary forest patches. In the secondary forest patches we found 46 (3439 individuals) species (Appendix 1). In teak plantations 19 species (361 individuals) were registered. In the oil palm plantations species richness was low with just 5 species (plus one accidental epiphyte species), but abundance was high with a total of 1529 individuals. By far the most prevalent species was *Nephrolepis biserrata*, a facultatively epiphytic fern, which accounted for approximately 80% of all individuals in the oil palm plantations. Also noteworthy was the epiphytic occurrence of the terrestrial orchid *Oeceoclades maculata* (Lindl.), which is a native to Africa that has naturalized in South and Central America. Finally, the pine plantations were almost free of epiphytes with only two species with one individual each. Native trees in the vicinity of the teak and pine plantations hosted more species (35 and 16 respectively), as well as more individuals (1492 and 313) than the plantation trees. In the pasture plots we inspected 113 trees that hosted a total of 60 epiphytic species (over 18,000 individuals).

Tree size
The trees of the different systems differed in size, and such differences could be a confounding factor behind variation in epiphyte species number and abundance between plantation trees and their direct neighbors. The mean dbh of native trees outside teak plantations was twice as much as that of teak trees (NDWD: P < 0.001; Table 1), whereas the dbh of native trees outside pine plantations did not differ from that of pines (NDWD: P = 0.8). Trees of secondary forests had larger dbh than teak and pine trees (NDWD: P < 0.001).

Multivariate analysis
Of the three environmental variables included in the analysis differences in annual rainfall explained about 60% of the variation in the multivariate analysis and dbh explained 24%, but area explained only 15% of the variation. Rain was strongly and inversely correlated with the first axis (r = -0.9; Fig. 2), thus the scatter along the first axis mainly reflects the rainfall

gradient, with the driest sites at the right end of this axis. Tree size (dbh) correlated strongly with the second axis (r = 0.7).

Table 1. Tree diameter at breast height (dbh, mean ± standard deviation) of the plantations, trees outside plantations and secondary forest patches. Numbers in brackets are the respective numbers of inspected sites/trees. Different letters indicate significant differences (Nemenyi-Damico-Wolfe-Dunn test: P < 0.05). Please note that due to the remaining old leaf bases on palms a comparison would be pointless.

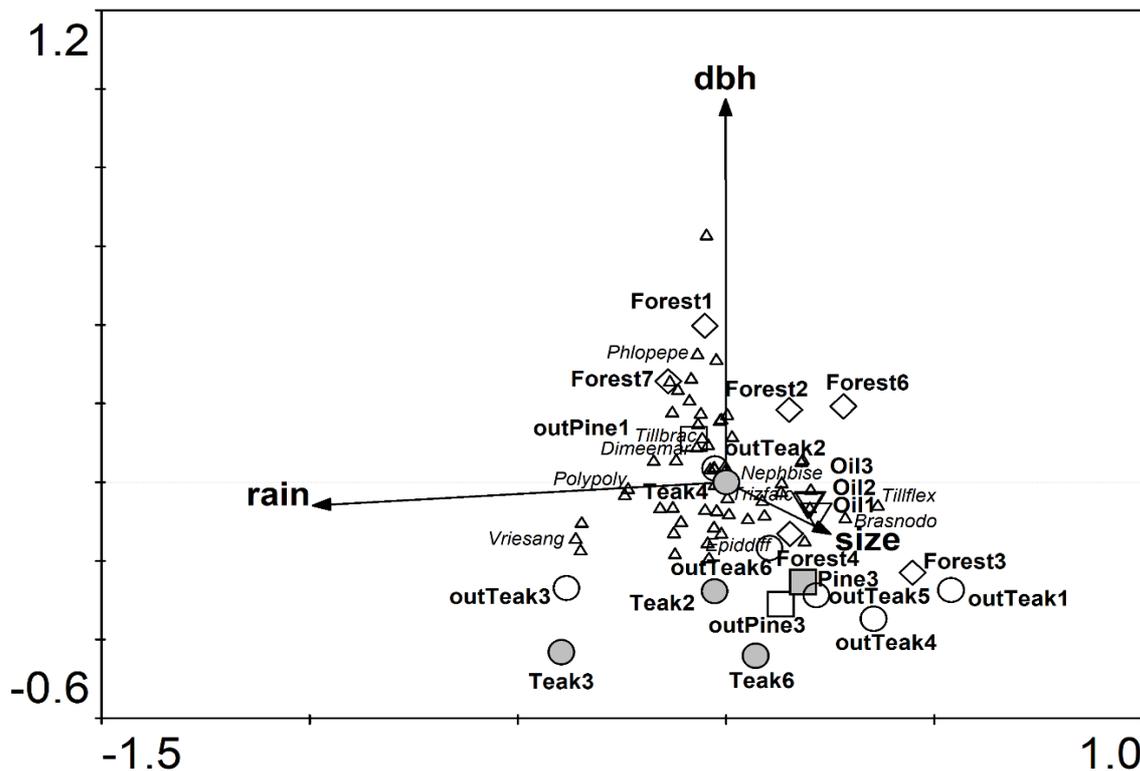|	dbh (cm)
Teak (6/61)	28.3 ± 7.8 [a]
outside Teak (6/58)	78.1 ± 37.2 [b]
Pine (3/30)	27.9 ± 7.2 [c]
outside Pine (3/30)	36.5 ± 19.8 [c]
Forest (7/70)	76.8 ± 63.4 [b]
Pasture (13/113)	75.7 ± 54.1 [b]

Fig. 2. Triplot of a canonical correspondence analysis (CCA) for the epiphyte assemblages in secondary forest patches (diamond), teak and pine plantations (filled circle and square), their respective surrounding trees (empty circle and square) and three oil palm plantations (inverted triangle) in western Panama. Note that sites that did not host epiphytes do not appear in this graphic. The first two axes of the CCA are depicted. The graph displays 8% of the inertia (= weighted variance) in the abundances and 85% of variance in the weighted averages and class totals of species with respect to the environmental variables. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.77 and 0.43, respectively. Rain (annual rainfall), tree dbh and area of the forest patch or plantation (size) were used as environmental variables. Quantitative environmental variables are indicated by arrows, for sites only the respective centroids are depicted and small triangles show epiphyte species (for reasons of clarity only the ten most abundant species are named and the names are abbreviated to the first four letters of the genus plus the first four letters of the epithet).

Comparing species richness

Rarefaction curves (Fig. 3) indicate that the expected species numbers of plantations were invariably lower than those in the pastures, all the plantations and the patches of secondary forest. The pine plantations were almost devoid of epiphytes. Trees outside teak plantations hosted consistently more epiphytes than did the plantations of this exotic tree species (Appendix 1 and Fig. 3). The species richness of epiphytes on trees outside teak plantations was not significantly different from that of secondary forest patches (Fig. 3).
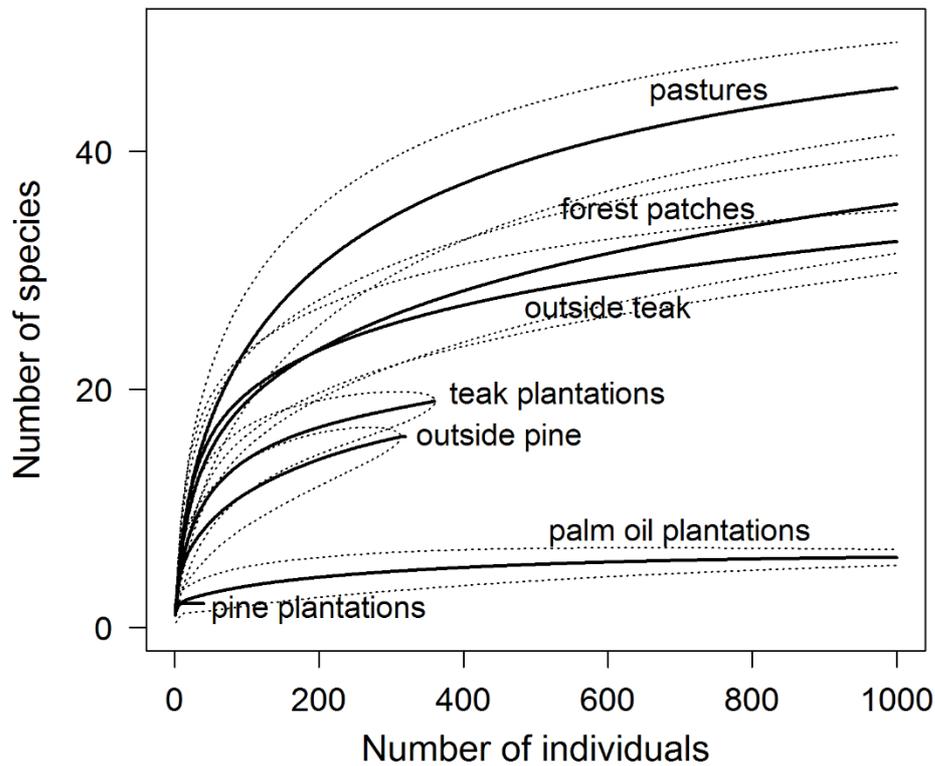
Fig. 3. Individual-based rarefaction curves for epiphytes growing on isolated trees in pastures, on trees in teak and pine plantations and trees outside the plantations, oil palm plantations and secondary forest patches. Dashed lines indicate 95% confidence intervals.
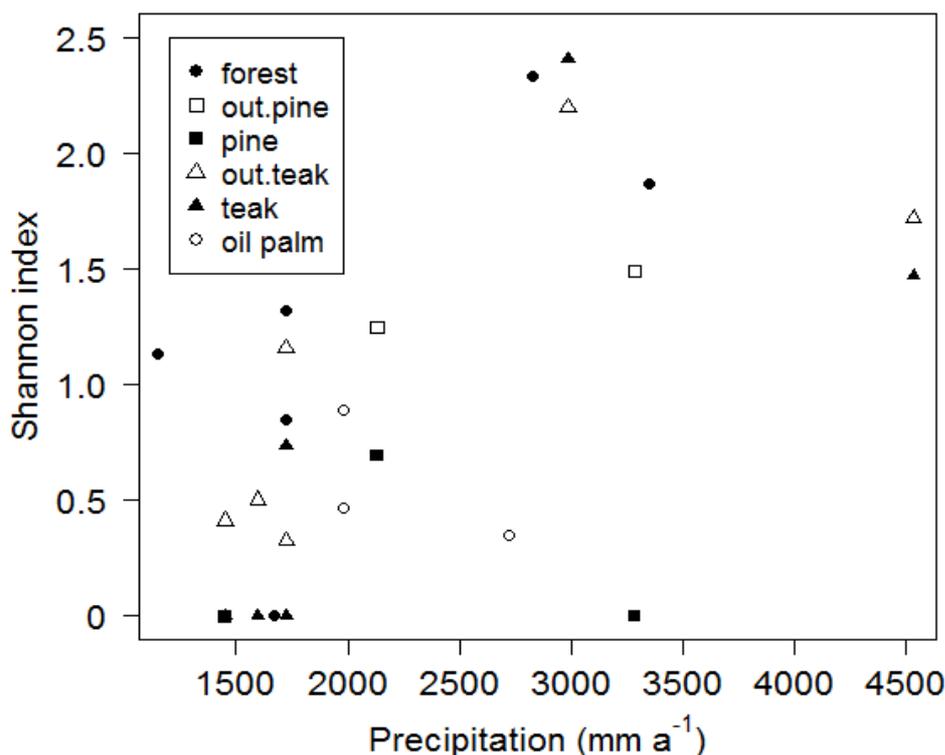
Fig. 4. Diversity of epiphyte assemblages in the studied habitat types in relation to annual precipitation. Seven secondary forest patches, six teak, three pine plantations and three oil palm plantations were studied. Symbols (forest, out.pine, pine and teak) overlap in the lower left corner.

Rainfall gradient

Although none of the studied habitats showed a significant increase of epiphyte diversity with annual rainfall (Fig. 4), there was the expected trend towards higher diversity with higher rainfall for epiphytes in secondary forest patches (linear regression (lr): $F_{(1,5)}$ = 5.27, P = 0.07), in teak plantations (lr: $F_{(1,4)}$ = 4.3, P = 0.1), and in trees outside teak plantations (lr: $F_{(1,4)}$ = 5.5, P = 0.08; Fig. 4).

Discussion

This study documents the vascular epiphyte assemblages of three different types of tree plantations and several secondary forest patches along the western Pacific coast of Panama. In general, epiphyte diversity and abundance were low compared to natural lowland forest [51], and even compared to pasture trees. Although epiphyte assemblages in secondary forest patches met our expectations of being significantly more diverse than those in plantations, we made the surprising observation that the most diverse epiphyte assemblages in this landscape were found in pasture trees.

In order to take local conditions into account we compared the epiphyte assemblages of teak and pine plantations with those of trees in close proximity and, likewise, we included only those pasture trees that were closest to plantations and forest patches. In direct comparison, teak and pine plantations hosted considerably fewer epiphytes than the trees surrounding them (Fig. 3). In a comparative study in Mexico, pine plantations hosted a similarly low richness of epiphytic ferns compared to secondary humid montane forests [52]. In the case of the teak plantations, this difference is probably partly due to tree size, although there is very little information on the suitability of teak as a host for epiphytes [53]. Here, native trees outside the plantations had a significantly larger mean dbh than plantation trees (78 vs. 28 cm). It is well established that the dbh of the host correlates positively with epiphyte species and individual numbers, in part because older trees have a larger dbh, thus there has been more time for colonization by epiphytes and also more substrate that can be colonized [e.g. 54]. However, low epiphyte loads on plantation trees cannot simply be explained by tree size.

The size difference between the pines we studied and native trees outside the plantations was not very large, but the latter hosted substantially more epiphytes (Fig. 3): pines are typically characterized as poor hosts, one possible reason being phenolic or resinous substance in the bark [e.g. 55, 56, but see 57 for an exception]. Another aspect that has been linked to less successful epiphyte establishment in plantations are management practices such as the application of fertilizers or chemicals, manual removal of epiphytes, or thinning, but also the presence or absence of shade trees [7, 10, 58, 59]. We did not systematically assess management practices in our study sites, but conversations with some of the plantation managers indicate that the only regular treatment is thinning, i.e. the cutting of entire trees to open more space for the remaining ones. This is performed for the first time a few years after the establishment of the plantation, and repeated at least twice before the final harvest. At many sites the undergrowth is also cut on a regular basis. Some sites have experienced fires in the undergrowth that spread from surrounding sugarcane plantations.

The most important aspect in regard to the suitability of trees for epiphytes is rotation time. In this region, plantations are often harvested within 20 years. This makes them primarily sinks for propagules, because most epiphytes are slow-growing and first reproduction may take up

to a decade [37]. The comparatively young age of the plantation trees was reflected in their smaller size compared to trees outside plantations and to secondary forest patches. The epiphyte individuals observed in the teak (and pine) plantations were mostly relatively small; we hardly found any reproducing individuals. In contrast to the low diversity observed in the teak and pine plantations, high diversity in cacao or coffee plantations was documented where there were structurally diverse, large shade trees [18, 21, 60]. This difference is due to the fact that the majority of epiphytes in cacao or coffee plantations do not grow on the crop itself. Teak and pine plantations almost entirely lack such structural diversity. Furthermore, shade trees in cacao or traditional coffee plantations are unlikely to be cut down all at once, but rather single trees might be harvested, for example in order to buffer low market prices for coffee [60]. While this creates a more stable system than timber monocultures with short rotation times, epiphyte assemblages may be negatively affected due to systematic epiphyte removal from the shade trees [61].

While it is obvious that the accumulation of organic material in leaf bases makes oil palms unique hosts compared to the other studied plantations trees, few epiphyte species benefit [see also 62]. We did not encounter any trees that hosted epiphytes in close proximity to the oil palm plantations. This might be another, alternative explanation for the low diversity hosted by the palms. However, a few epiphyte species did successfully colonize the palms. For palms dbh is not a good age indicator as it changes little over time. Furthermore, with the remaining leaf bases a comparison between the dbh of oil palm and teak and pine plantations is pointless. Their relatively small height (4.9 ± 1.0 m, n = 30) suggests that the oil palm plantations were still quite young, which should be kept in mind when comparing them to the other habitat types.

The low value of oil palm plantations for biodiversity, not only epiphyte diversity, has been emphasized before [63]. Wilcove *et al.* [63] evaluated the impact of logging and the agricultural conversion of primary or logged forests on biodiversity in Southeast Asia, concluding that the conversion to plantation crops resulted in a massive loss of biodiversity. It has been suggested that the conversion of pre-existing cropland, such as rubber plantations to oil palm plantations, is preferable to the conversion of primary and secondary forests [64]. In the system studied here, the conversion of agricultural land (pasture with native trees) to a monoculture plantation would cause a greater loss of local epiphyte diversity and abundance than the conversion of secondary forest patches.

Secondary forest patches hosted more epiphytes than plantations did. In fact, the 70 trees studied in forest patches hosted almost as many individuals as the 194 trees and 30 palms examined in all the other systems combined. Surprisingly, the assemblages in the secondary forest patches were still less diverse than those of the pastures. This finding is difficult to generalize because the term "secondary forest" describes a highly heterogeneous set of vegetation entities [e.g. 65, 66]. In Singapore, plant diversity in secondary forests appeared to increase only very slowly and more than 60% of the epiphyte species of the native flora were lost [67]. Fifteen year old fallows in Bolivia hosted 60% – 70% fewer epiphyte species than neighboring natural forest [4]. In contrast, the comparison of the epiphyte assemblages of secondary forests in Central Panama ranging in age from 35 to 115 years showed a relatively quick recovery of diversity but a rather slow recovery of abundance levels [34]. How fast epiphyte diversity is restored in secondary forests will strongly depend on seed availability and connectedness to seed sources. The results of a study in Costa Rica indicate that the

restoration of the species diversity and composition of several bromeliad assemblages was highly idiosyncratic [68], and it is likely that chance has a great influence on the formation of epiphyte assemblages [69]. There is no data on the original epiphyte flora of the region from the time before its conversion from forest to the current state. That forest patches are less diverse than epiphyte assemblages on pasture trees clearly indicates a net loss, but we are unable to quantify how this would compare to the natural state.

As expected, rainfall had a strong influence on epiphyte assemblages [see also 39, 70, 71, 72], which was reflected in the multivariate analysis. We also found clear positive trends of epiphyte diversity with increased rainfall, although the trends were marginal and not statistically significant. For example, teak plantations showed higher diversity in more humid areas, which arguably reflects the higher diversity of epiphytes present in the areas surrounding these plantations. As a rule, epiphyte diversity strongly responds to moisture availability [73], which has also been documented in a fragmented, modified landscape with a strong rainfall gradient [39].

Implications for conservation

Monoculture tree plantations in the study area present a sink for epiphyte propagules rather than having much value as a refuge habitat in this fragmented landscape. This is partly due to the fact that some species such as pines are poor hosts, and partly because short plantation harvest rotations hamper the development of richer assemblages of epiphytes, which in turn could act as source populations for the surrounding fragmented landscape. However, we did find mature epiphyte individuals in plantations, which may increase connectivity in the landscape. The secondary forest patches were more promising as refuges, although they hosted less diverse epiphyte assemblages than did isolated pasture trees.

Acknowledgments

References

[1] FAO. 2010. Global forest resources assessment 2010 - Main report, In: *FAO Forestry Paper*. Food and Agriculture Organization of the United Nations, Rome.

[2] Brockerhoff, E. G., Jactel, H., Parrotta, J. A., Quine, C. P., and Sayer, J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation*, 17: 925-951.

[3] Barthlott, W., Schmit-Neuerburg, V., Nieder, J., and 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.

[4] Krömer, T. and Gradstein, S. R. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana*, 24: 190-195.

[5] Werner, F. A., Homeier, J., and Gradstein, S. R. 2005. Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. *Ecotropica*, 11: 21-40.

[6] Köster, N., Friedrich, K., Nieder, J., and Barthlott, W. 2009. Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conservation Biology*, 23: 911-919.

[7] Kanowski, J., Catterall, C. P., Wardell-Johnson, G. W., Proctor, H., and Reis, T. 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management*, 183: 265-280.

[8] Boelter, C. R., Zartman, C. E., and Fonseca, C. R. 2011. Exotic tree monocultures play a limited role in the conservation of Atlantic Forest epiphytes. *Biodiversity and Conservation*, 20: 1255-1272.

[9] Merwin, M. C., Rentmeester, S. A., and Nadkarni, N. M. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica*, 35: 37-47.

[10] Andersson, M. S. and Gradstein, S. R. 2005. Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in western Ecuador. *Biodiversity and Conservation*, 14: 1101-1120.

[11] Coote, L., Smith, G. F., Kelly, D. L., O'Donoghue, S., Dowding, P., Iremonger, S., and Mitchell, F. J. G. 2008. Epiphytes of Sitka spruce (*Picea sitchensis*) plantations in Ireland and the effects of open spaces. *Biodiversity and Conservation*, 17: 953-968.

[12] Azhar, B., Lindenmayer, D. B., Wood, J., Fischer, J., Manning, A., McElhinny, C., and Zakaria, M. 2013. The influence of agricultural system, stand structural complexity and landscape context on foraging birds in oil palm landscapes. *Ibis*, 155: 297-312.

[13] Koh, L. P. 2008. Can oil palm plantations be made more hospitable for forest butterflies and birds? *Journal of Applied Ecology*, 45: 1002-1009.

[14] Cruz-Angón, A. and Greenberg, R. 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. *Journal of Applied Ecology*, 42: 150-159.

[15] Prescott, G. W., Edwards, D. P., and Foster, W. A. 2015. Retaining biodiversity in intensive farmland: epiphyte removal in oil palm plantations does not affect yield. *Ecology and Evolution*, 5: 1944-1954.

[16] Sporn, S. G., Bos, M. M., and Gradstein, S. R. 2007. Is productivity of cacao impeded by epiphytes? An experimental approach. *Agriculture Ecosystems & Environment*, 122: 490-493.

[17] Haro-Carrión, X., Lozada, T., Navarrete, H., and Koning, G. H. J. 2009. Conservation of vascular epiphyte diversity in shade cacao plantations in the Chocó region of Ecuador. *Biotropica*, 41: 520-529.

[18] Hietz, P. 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. *Conservation Biology*, 19: 391-399.

[19] Mehltreter, K. 2008. Helechos. In: *Agroecosistemas Cafetaleros de Veracruz: Biodiversidad, Manejo y Conservacion*. Manson, R. H., Hernández-Ortiz, V., Gallina, S., and Mehltreter, K., (Eds.), pp. 83-93. INECOL, Xalapa.

[20] Krömer, T., García-Franco, J. G., and Toledo-Aceves, T. 2014. Epífitas vasculares como bioindicadores de la calidad forestal: impacto antrópico sobre su diversidad y composición. In: *Bioindicadores: guardianes de nuestro futuro ambiental.* González-Zuarth, C. A., Vallarino, A., Pérez-Jimenez, J. C., and Low-Pfeng, A. M., (Eds.), pp. 605-623. Instituto Nacional de Ecología y Cambio Climático (INECC) – El Colegio de la Frontera Sur (ECOSUR), México, D. F. y Campeche.

[21] Mondragón, D., Santos-Moreno, A., and Damon, A. 2009. Epiphyte diversity on coffee bushes: A management question? *Journal of Sustainable Agriculture*, 33: 703-715.

[22] Moorhead, L. C., Philpott, S. M., and Bichier, P. 2010. Epiphyte biodiversity in the coffee agricultural matrix: canopy stratification and distance from forest fragments. *Conservation Biology*, 24: 737-746.

[23] Qi, D.-H., Guo, H.-J., and Sheng, C.-Y. 2013. Assessment of plant species diversity of ancient tea garden communities in Yunnan, Southwest of China. *Agroforestry Systems*, 87: 465-474.

[24] Ardila R., A. I., Moncada, B., and Lücking, R. 2015. Epiphyte homogenization and de-diversification on alien *Eucalyptus* versus native *Quercus* forest in the Colombian Andes: a case study using lirellate Graphidaceae lichens. *Biodiversity and Conservation*, 24: 1239–1252.

[25] Calviño-Cancela, M., López de Silanes, M. E., Rubido-Bará, M., and Uribarri, J. 2013. The potential role of tree plantations in providing habitat for lichen epiphytes. *Forest Ecology and Management*, 291: 386-395.

[26] Budowski, G. 1987. Living fences in tropical America, a widespread agroforestry practice. In: *Agroforestry: Realities, possibilities and potentials*. Gholz, H. L., (Ed.), pp. 169-178. Martinus Nijhoff Publishers, Netherlands, Dordrecht.

[27] PRORENA. *Proyecto de reforestación con especies nativas*. http://prorena.research.yale.edu//home.htm accessed 2 August 2011.

[28] Potvin, C. 2011. *The Sardinilla Project*. http://biology.mcgill.ca/faculty/potvin/sardinilla_obj.html accessed 25 August 2011.

[29] Pincheira-Ulbrich, J., Rau, J. R., and Smith-Ramirez, C. 2012. Vascular epiphytes and climbing plants diversity in an agroforestal landscape in southern Chile: a comparison among native forest fragments. *Boletin De La Sociedad Argentina De Botanica*, 47: 411-426.

[30] Köster, N., Nieder, J., and Barthlott, W. 2011. Effect of host tree traits on epiphyte diversity in natural and anthropogenic habitats in Ecuador. *Biotropica*, 43: 685-694.

[31] Köster, N., Kreft, H., Nieder, J., and Barthlott, W. 2013. Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics. *Journal of Biogeography*, 40: 963-976.

[32] Goode, L., Erhardt, E., Santiago, L. S., and Allen, M. 2010. Carbon stable isotopic composition of soluble sugars in *Tillandsia* epiphytes varies in response to shifts in habitat. *Oecologia*, 163: 583-590.

[33] Susan-Tepetlan, T. M., Velazquez-Rosas, N., and Krömer, T. 2015. Changes in functional traits of vascular epiphytes of cloud forest and secondary vegetation in central Veracruz, Mexico. *Botanical Sciences*, 93: 153-163.

[34] Woods, C. L. and DeWalt, S. J. 2013. The conservation value of secondary forests for vascular epiphytes in central Panama. *Biotropica*, 45: 119-127.

[35] Martin, P. A., Newton, A. C., and Bullock, J. M. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proceedings of the Royal Society B-Biological Sciences*, 281: 1-8.

[36] Nadkarni, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica*, 32: 358-363.

[37] Schmidt, G. and Zotz, G. 2002. Inherently slow growth in two Caribbean epiphytic species: a demographic approach. *Journal of Vegetation Science*, 13: 527-534.

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

[39] Poltz, K. and Zotz, G. 2011. Vascular epiphytes on isolated pasture trees along a rainfall gradient in the lowlands of Panama. *Biotropica*, 43: 165-172.

[40] Anonymus. 1988. *Atlas nacional de la República de Panamá*, Instituto Geográfico Nacional ''Tommy Guardia'', Panamá.

[41] Heckadon-Moreno, S. 2009. *De selvas a potreros*. Exedra Books, Panamá.

[42] The Plant List. 2013. http://www.theplantlist.org/ accessed 19 January 2016.

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

[44] Sanford, W. W. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. *Journal of Ecology*, 56: 697-705.

[45] Flores-Palacios, A. and García-Franco, J. G. 2001. Sampling methods for vascular epiphytes: their effectiveness in recording species richness and frequency. *Selbyana*, 22: 181-191.

[46] ter Braak, C. J. F. and Smilauer, P. 1997-2002. *Canoco for Windows*. Biometris - Plant Research International, Wageningen, The Netherlands.

[47] Gotelli, N. J. and Graves, G. R. 1996. *Null models in Ecology*. Smithsonian Institution Press, Washington, D.C.

[48] R Core Team. 2013. *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

[49] Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. 2015. vegan: *Community Ecology Package*. R package version 2.2-1. http://CRAN.R-project.org/package=vegan accessed 6 January 2016.

[50] Hothorn, T., Hornik, K., van de Wiel, M. A., and Zeileis, A. 2006. A Lego system for conditional inference. *The American Statistician*, 60: 257-263.

[51] Zotz, G. and Schultz, S. 2008. The vascular epiphytes of a lowland forest in Panama - species composition and spatial structure. *Plant Ecology*, 195: 131-141.

[52] Carvajal-Hernández, C. I., Krömer, T., and Vázquez-Torres, M. 2014. Riqueza y composición florística de pteridobiontes en bosque mesófilo de montaña y ambientes asociados en el centro de Veracruz, México. *Revista Mexicana de Biodiversidad*, 85: 491-501.

[53] Biswas, S. and Chandra, S. 1992. An observation on Teak (*Tectona grandis* Linn. f.) as a phorophyte. *Indian Forester*, 118: 871.

[54] Laube, S. and Zotz, G. 2007. A metapopulation approach to the analysis of long term changes in the epiphyte vegetation on the host tree *Annona glabra. Journal of Vegetation Science*, 18: 613-624.

[55] Wolf, J. H. D. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. *Forest Ecology and Management*, 212: 367-393.

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

[57] Jiménez Bautista, L., Damon, A., Ochoa-Gaona, S., and Clark Tapia, R. 2014. Impact of silvicultural methods on vascular epiphytes (ferns, bromeliads and orchids) in a temperate forest in Oaxaca, Mexico. *Forest Ecology and Management*, 329: 10-20.

[58] De Beenhouwer, M., Aerts, R., and Honnay, O. 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. *Agriculture Ecosystems & Environment*, 175: 1-7.

[59] Deheuvels, O., Rousseau, G. X., Soto Quiroga, G., Decker Franco, M., Cerda, R., Vilchez Mendoza, S. J., and Somarriba, E. 2014. Biodiversity is affected by changes in management intensity of cocoa-based agroforests. *Agroforestry Systems*, 88: 1081-1099.

[60] Perfecto, I., Rice, R. A., Greenberg, R., and VanderVoort, M. E. 1996. Shade coffee: a disappearing refuge for biodiversity. *Bioscience*, 46: 598-608.

[61] Toledo-Aceves, T., Garcia-Franco, J. G., Hernandez-Rojas, A., and MacMillan, K. 2012. Recolonization of vascular epiphytes in a shaded coffee agroecosystem. *Applied Vegetation Science*, 15: 99-107.

[62] Aguirre, A., Guevara, R., García, M., and Lopez, J. C. 2010. Fate of epiphytes on phorophytes with different architectural characteristics along the perturbation gradient of *Sabal mexicana* forests in Veracruz, Mexico. *Journal of Vegetation Science*, 21: 6-15.

[63] Wilcove, D. S., Giam, X., Edwards, D. P., Fisher, B., and Koh, L. P. 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends in Ecology & Evolution*, 28: 531-540.

[64] Koh, L. P. and Wilcove, D. S. 2008. Is oil palm agriculture really destroying tropical biodiversity? *Conservation Letters*, 1: 60-64.

[65] Brown, S. and Lugo, A. E. 1990. Tropical secondary forests. *Journal of Tropical Ecology*, 6: 1-32.

[66] Corlett, R. T. 1994. What is secondary forest? *Journal of Tropical Ecology*, 10: 445-447.

[67] Turner, I. M., Tan, H. T. W., Wee, Y. C., Ibrahim, A. B., Chew, P. T., and Corlett, R. T. 1994. A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. *Conservation Biology*, 8: 705-712.

[68] Cascante-Marín, A., Wolf, J. H. D., Oostermeijer, J. G. B., den Nijs, J. C. M., Sanahuja, O., and Duran-Apuy, A. 2006. Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. *Basic and Applied Ecology*, 7: 520-532.

[69] Cascante-Marín, A., Wolf, J. H. D., Oostermeijer, J. G. B., and Den Nijs, J. C. M. 2008. Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica. *Biotropica*, 40: 441-448.

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

[71] Wolf, J. H. D. and Flamenco-S, A. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, 30: 1689-1707.

[72] Kreft, H., Köster, N., Küper, W., Nieder, J., and Barthlott, W. 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. *Journal of Biogeography*, 31: 1463-1476.

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

Appendices

Appendix 1. Species abundances in the plantations, on trees surrounding the plantations, in the forest patches and on pasture trees. Numbers in brackets are the respective numbers of inspected sites/trees. *accidental epiphyte / terrestrial orchid.

Taxon	Teak (6/61)	outside Teak (6/58)	Pine (3/30)	outside Pine (3/30)	Oil (3/30)	Forest (7/70)	Pasture (13/113)
ARACEAE							
Anthurium obtusum (Engl.) Grayum	0	0	0	0	0	0	24
Anthurium schlechtendalii Kunth	0	42	0	0	0	4	24
ASPLENIACEAE							
Asplenium sulcatum Lam.	0	0	0	0	20	0	1
BROMELIACEAE							
Aechmea mexicana Baker	0	0	0	0	0	0	562
Catopsis nutans (Sw.) Griseb.	0	44	0	0	0	1	166
Guzmania monostachia (L.) Rusby ex Mez	0	0	0	0	0	0	201
Tillandsia balbisiana Schult. & Schult.f.	4	65	0	0	0	28	1821
Tillandsia brachycaulos Schltdl.	1	191	0	0	0	275	213
Tillandsia caput-medusae E.Morren	4	3	0	0	0	9	80
Tillandsia elongata Kunth	4	162	0	0	0	0	1281
Tillandsia fasciculata Sw.	24	79	0	3	0	77	2445
Tillandsia festucoides Brongn. ex Mez	6	14	0	0	0	89	1
Tillandsia flexuosa Sw.	0	9	1	11	0	249	954
Tillandsia juncea (Ruiz & Pav.) Poir.	0	0	0	0	0	4	159
Vriesea sanguinolenta Cogn. & Marchal	103	194	0	0	0	3	1612
CACTACEAE							
Epiphyllum phyllanthus (L.) Haw.	0	1	0	0	0	9	28
Hylocereus costaricensis (F.A.C.Weber) Britton & Rose	1	14	0	0	0	45	43
GESNERIACEAE							
Codonanthe crassifolia (H.Focke) C.V.Morton	0	0	0	0	0	0	113
NEPHROLEPIDACEAE							

Taxon	Teak (6/61)	outside Teak (6/58)	Pine (3/30)	outside Pine (3/30)	Oil (3/30)	Forest (7/70)	Pasture (13/113)
Nephrolepis biserrata (Sw.) Schott	0	0	0	0	1191	0	0
Nephrolepis pendula (Raddi) J. Sm.	0	0	0	0	0	0	1
ORCHIDACEAE							
Aspasia epidendroides Lindl.	0	1	0	0	0	4	261
Brassavola nodosa (L.) Lindl.	3	159	0	0	0	258	621
Bulbophyllum pachyrachis (A.Rich.) Griseb.	0	0	0	0	0	0	7
Camaridium ochroleucum Lindl.	0	2	0	88	0	151	225
Catasetum viridiflavum Hook.	2	15	1	0	5	2	69
Cattleya cf *patinii* Cogn.	1	5	0	2	0	67	48
Caularthron bilamellatum (Rchb.f.) R.E.Schult.	0	40	0	2	0	15	36
Dichaea panamensis Lindl.	0	0	0	0	0	1	0
Dimerandra emarginata (G.Mey.) Hoehne	0	1	0	51	0	724	3440
Encyclia cordigera (Kunth) Dressler	8	9	0	50	0	1	228
Encyclia sp1	0	0	0	0	0	99	1
Encyclia stellata (Lindl.) Schltr.	12	3	0	4	0	0	468
Epidendrum difforme Jacq.	102	45	0	78	0	26	1416
Epidendrum nocturnum Jacq.	0	1	0	0	0	0	0
Epidendrum sculptum Rchb.f.	0	0	0	0	0	0	70
Epidendrum strobiliferum Rchb.f.	0	1	0	0	0	1	33
Gongora quinquenervis Ruiz & Pav.	0	0	0	0	0	1	0
Heterotaxis sessilis (Sw.) F.Barros	0	60	0	1	0	0	0
Lockhartia micrantha Rchb.f.	0	0	0	0	0	7	0
*Oeceoclades maculata (Lindl.) Lindl.	0	0	0	0	2	0	0
Oncidium sp	0	0	0	0	0	0	2
Oncidium stipitatum Lindl.	0	1	0	0	0	0	2

Taxon	Teak (6/61)	outside Teak (6/58)	Pine (3/30)	outside Pine (3/30)	Oil (3/30)	Forest (7/70)	Pasture (13/113)
Orchidaceae sp3	1	0	0	0	0	0	0
Orchidaceae sp4	0	0	0	0	0	0	2
Phloeophila peperomioides (Ames) Garay	0	0	0	0	0	713	500
Pleurothallis sp1	0	0	0	0	0	0	3
Polystachya foliosa (Hook.) Rchb.f.	17	1	0	1	0	4	54
Prosthechea chacaoensis (Rchb.f.) W.E.Higgins	0	0	0	1	0	213	40
Scaphyglottis behrii (Rchb.f.) Benth. & Hook.f. ex Hemsl.	0	0	0	0	0	2	47
Scaphyglottis bidentata (Lindl.) Dressler	0	0	0	0	0	11	52
Scaphyglottis longicaulis S.Watson	0	0	0	0	0	4	0
Scaphyglottis sp	0	0	0	0	0	4	0
Sobralia bletiae Rchb.f.	0	0	0	0	0	0	4
Sobralia decora Bateman	0	0	0	8	0	2	0
Stelis sp	0	0	0	0	0	21	1
Trichosalpinx ciliaris (Lindl.) Luer	0	0	0	0	0	1	12
Trigonidium egertonianum Bateman ex Lindl.	0	0	0	0	0	0	27
Trizeuxis falcata Lindl.	9	3	0	1	306	0	116
PIPERACEAE							
Peperomia obtusifolia (L.) A.Dietr.	0	0	0	0	0	0	7
Peperomia cf *macrostachya* (Vahl) A.Dietr.	0	0	0	0	0	3	0
Peperomia rotundifolia (L.) Kunth	0	96	0	0	0	134	203
POLYPODIACEAE							
Campyloneurum phyllitidis (L.) C. Presl	0	0	0	0	0	0	18
Microgramma percussa (Cav.) de la Sota	37	65	0	0	0	20	39
Niphidium crassifolium (L.) Lellinger	0	0	0	0	0	0	3
Pecluma pectinata (L.) M.G. Price	0	0	0	0	0	0	66
Pleopeltis astrolepis (Liebm.) E. Fourn.	0	0	0	2	0	0	35

Taxon	Teak (6/61)	outside Teak (6/58)	Pine (3/30)	outside Pine (3/30)	Oil (3/30)	Forest (7/70)	Pasture (13/113)
Polypodium attenuatum R. Br.	0	0	0	0	0	12	0
Polypodium furfuraceum Schltdl. & Cham.	0	9	0	10	0	32	233
Polypodium polypodioides (L.) Watt	22	132	0	0	0	103	41
Polypodium sp1	0	0	0	0	0	1	0
Polypodium sp2	0	0	0	0	5	0	0
Polypodium triseriale Sw.	0	0	0	0	0	0	21
Serpocaulon maritimum (Hieron.) A.R. Sm.	0	4	0	0	0	1	159
PTERIDACEAE							
Ananthacorus angustifolius (Sw.) Underw. & Maxon	0	18	0	0	0	7	79
Vittaria lineata (L.) Sm.	0	3	0	0	0	0	45