Abstract: Ongoing destruction of tropical forests makes isolated pasture trees potentially important for the persistence of original forest dwellers such as many vascular epiphytes. We studied epiphyte assemblages on 100 isolated trees at ten pasture sites in southwest Panama along an elevational gradient ranging from 140 to 1240 m a.s.l. We analysed epiphyte species composition (richness, similarity) and registered climate and host trait variables of potential influence on their occurrence. We found a total of 5876 epiphyte individuals belonging to 148 species. Epiphyte abundance, species richness and diversity all varied about 4-fold among the 10 sites, with a high similarity of epiphyte assemblages among sites. Two sites at 870 and 1050 m a.s.l. did not fit into the overall elevational trend of increased abundance, species richness and diversity. However, all three measures were significantly correlated with humidity as the independent variable. This highlights that a gradient in humidity, and not elevation as such, is responsible for the typical elevational changes in epiphyte assemblages, so that special local conditions may lead to deviations from expected patterns. Our documentation of current elevational diversity patterns also provides a baseline for the study of long-term changes in epiphyte assemblages in anthropogenically modified landscapes.

Keywords: diversity; humidity; local climate; modified landscape; pastures; temperature

1. Introduction

Despite their important role as the habitat of at least half of the global terrestrial biodiversity, tropical forests keep decreasing in cover due to human activities [1,2]. As human populations grow, there is an increasing need for land to provide food, living space and other resources, which currently represents the principal threat to tropical biodiversity [3–5]. Resolving the conflict between environmental conservation and economic globalisation represents a big challenge [6]. In the tropics, land use change rather than climate change or invasive species is the most important cause of decreasing biodiversity [7]. Knowledge of the current status of tropical biodiversity in modified landscapes will allow us to establish management plans for conservation and sustainable development beyond primary forests [8].

In many pristine tropical forests, vascular epiphytes are one of the most species-rich plant groups, with major impacts on nutrient and hydrological cycles in the ecosystem [9–11]. Epiphyte diversity can be impressive, e.g., a single tree may harbour almost 200 vascular epiphyte species [12]. However, epiphyte richness in human-modified landscapes is usually substantially reduced (see [13,14]). In the case of pastures, isolated trees kept to offer shade for livestock can provide connectivity and allow gene flow among epiphyte populations in pastures and surrounding forest patches [15–17].

Knowledge of the structure and dynamics of vascular epiphyte assemblages on isolated trees is still relatively limited. Traditionally, studies with epiphytes were mainly
undertaken in relatively pristine forests and, to a lesser degree, in secondary forests (e.g., [18–22]). More recently, isolated trees in pastures have been included in a number of studies that compared vascular epiphyte assemblages in primary forests, fragmented forests and isolated pasture trees [13,23–27].

Epiphyte communities and their relationship with large-scale environmental gradients has been studied for decades mainly in forests [28] and, lately, in isolated pasture trees in the lowlands (e.g., [11,13,17]). The elevational gradients and the “mid-elevation bulge” of vascular epiphytes are well known. However, diversity changes in vascular epiphyte assemblages in pastures along an elevational gradient in a single region have not been documented. Epiphytes do not show an exceptional elevational pattern: many groups of organisms show an increase in richness from the lowlands until a maximum is reached at intermediate elevations [29]. Maxima of vascular epiphyte diversity are typically reached at c. 1400–1600 m, e.g., Küper, Kreft, Nieder, Köster and Barthlott ([20], at 1500 m a.s.l., in a range from 0 to 3200 m a.s.l. in Ecuador), Krömer, Gradstein and Acebey [19], Krömer, Kessler, Gradstein and Acebey ([10], at 1500 m a.s.l., from 350 to 4000 m a.s.l. in northern Bolivia) and Hietz and Hietz-Seifert ([30], at 1400 m a.s.l., from 720 to 2370 m a.s.l. in Mexico).

The current study focused on epiphyte assemblages on isolated pasture trees along such an elevational gradient in western Panama to test whether elevational trends were comparable to those documented in previous studies in forest settings (see [19–21,28,30]). Since the studied elevational gradient ended at c. 1200 m, we expected a steep and continuous increase in species numbers with elevation. We also describe the variation of β-diversity in the elevational gradient and the effects of some important biotic and abiotic variables that typically have a direct effect on epiphyte assemblages [14,23]. Since epiphyte communities on isolated pasture trees tend to have low β-diversity [24], we expected the same, simple pattern along the gradient. Further, we expected clear relationships between changes in local climate and changes in epiphyte assemblages.

2. Materials and Methods

This study was conducted in southwest Panama, Gualaca district (between 8°32′27.36″ N, 82°32′27.36″ W from the lowlands at 140 m a.s.l. and 8°41′27.42″ N, 82°13′47.27″ W at 1240 m a.s.l, near the Cordillera Central). We studied 100 trees distributed in 10 1-ha pasture plots at elevation intervals from 70 to 190 m (Figure 1). According to Tosi Jr [31], the surrounding vegetation type represented patches of tropical lowland forest in the lower regions and pristine montane forest in the highlands. There is a dry season between January and April that governs lowland and highland pastures [17,32]. The pasture trees at 1240 m a.s.l. were mostly remnants of the cleared forest in close proximity to the Fortuna Forest Reserve, whereas most other trees along the gradient were planted, common pasture trees or had established spontaneously after clearance. Most of the pastures were established more than 60 years ago (personal communication of local farmers). Typical tree species were *Tabebuia rosea* (Bertol.) DC. (Bignoniaceae), *Byrsonima crassifolia* (L.) Kunth (Malpighiaceae) and *Guazuma ulmifolia* Lam. (Malvaceae). Within each pasture plot, we randomly selected ten trees with a diameter at breast height (DBH) ≥ 10 cm [following 17] and their geographical coordinates were recorded with a GPS. We recorded the DBH of each host tree. We monitored air temperature and relative humidity at each elevation with Hobo U23 Pro V2 data loggers (Onset Computer Corporation, MA, USA). The devices were installed in one haphazardly chosen tree per site at its first inner branches at approximately 3 m height. Data were logged every 30 min for 186 days (August 2017 to February 2018) and loggers were checked for consistent readings before and after the measurement campaign. We quantified tree density in each 1-ha pasture plot and noted the surrounding forest cover (expressed as area percentage) in a radius of 100 m of the plots using the measuring tools of Google Earth Pro 7.1.7.2606 software and satellite images from 2018. Surrounding forest cover area was studied because it represents a potential source pool of epiphytes for neighbouring pastures.
software and satellite images from 2018. Surrounding forest cover area was studied because it represents a potential source pool of epiphytes for neighbouring pastures.

Figure 1. Study area in Gualaca district in southwest Panama. Ten plots were established along the elevational gradient from 100 to 1240 m a.s.l. In each plot, ten trees were selected, and their epiphyte assemblages were studied.

We recorded all vascular epiphytes in the selected trees. Following Poltz and Zotz [17], small seedlings were excluded because of (1) difficulties in species determination and because of (2) their high mortality rates. When growing close together, individual epiphytes cannot always be distinguished from neighbours. In these cases, we defined individuals following Sanford [33] as a “stand”, i.e., a cluster of individuals or stems belonging to the same species separated from other clusters. In our analyses, we only considered true epiphytes as defined by Zotz [34], but hemi-epiphytes, mistletoes and vines were noted to contribute to a general distributional database. Tall trees were accessed with single-rope climbing techniques [35].

Species identification of vascular epiphytes was mostly conducted in the field. When this was not possible, fertile and sterile individuals were sampled and processed in the Herbario de la Universidad Autónoma de Chiriquí (UCH). To identify species, we used several keys of vascular epiphytes from Panama, Costa Rica and Mesoamerica [36–39]. Some problematic specimens were sent to specialists for identification. In many cases, reproductive structures were lacking and we had to name morphospecies. Scientific names were standardised according to The Plant List [40]. Vouchers are deposited in the Chiriquí Herbarium, UCH.

A profile of the local climate was produced from temperature and relative humidity data. We calculated site averages of both variables. Differences among sites in regard to climate and surrounding forest cover were assessed with regression analyses and Pearson correlation tests.

To compare epiphyte richness per elevation and evaluate sampling effort, we used epiphyte richness (α-diversity) per tree at each site and estimated the richness per elevation...
with the Chao 1 richness estimator [41]. Further, we produced species accumulation curves of the trees sampled in every pasture by randomising the trees with 100 permutations. We also calculated the abundance, richness and diversity per tree (here as the Shannon–Wiener index) as the average per elevation (β-diversity). With these data, changes in diversity components along the elevational gradient were assessed with regression analyses and Pearson correlation tests. Additionally, we tested if local climate variables that may influence epiphyte assemblages were correlated with the elevational gradient (relative air humidity and temperature). Furthermore, to test whether differences among host trees could influence epiphyte assemblages along the elevational gradient, we performed Kruskal–Wallis tests (KW) on tree size (DBH) and also tree density between the pasture plots. Finally, the relationship between tree size and epiphyte richness was analysed with a Pearson correlation test with the aim to find a positive correlation on the trees hosting epiphytes. Diversity types (α, β, γ) are also graphically defined in Figure S1.

To analyse variation in vascular epiphyte assemblage composition along the elevational gradient (β-diversity), we used a general multiple assemblage abundance-based overlap measure \( C_q^N \) [42,43], in which we produced similarity profiles at the tree scale for every pasture [43,44]. This analysis allows comparisons of communities by transforming the occurrence and abundance data to Hill numbers, which facilitates the use of numerous diversity parameters. The resulting graph relates similarity as a function of the sensitivity parameter “q” (x-axis). Values on the y-axis range from 0 to 1, indicating how similar the studied assemblages are, with 0 being completely distinct and 1 identical. When \( q = 0 \), similarity is calculated as the Sørensen index, which takes into account all species from the database and abundance is irrelevant; when \( q = 1 \), similarity is calculated as the Horn overlap index that weighs species proportionally to their frequency; and when \( q = 2 \), the measure is based on the Morisita–Horn index that weighs abundant species more than rare species [45]. For clarity, only data of five plots, but spanning the entire elevational range, were considered.

The composition of epiphyte assemblages on every studied tree along the gradient was analysed with non-metric multidimensional scaling (NMDS) using Euclidean distance. The stress value for NMDS was 0.16. To test differences within epiphyte assemblages at each elevation and according to local relative humidity, a permutational analysis of variance (PERMANOVA) was conducted. All tests were run with R v.3.3.2 software [46], where the package “vegan” [47] was used to calculate species accumulative curves, similarity profiles, NMDS and PERMANOVA and the package “vegetarian” was used to elaborate similarity profiles [48].

3. Results

3.1. Climatic Variables and Vegetation along the Elevational Gradient

The average temperature decreased by 0.6 °C with each increase of 100 m in elevation (Figure 2A, \( R^2 = 0.99 \), Pearson correlation test, \( t = −25.58, df = 8, p = 0.01 \)). Increases in relative humidity were not as tightly coupled with elevation but still significantly related (Figure 2B, \( R^2 = 0.57 \), Pearson correlation test, \( t = 3.25, df = 8, p = 0.01 \)). Surrounding forest cover increased more than 5-fold within the studied elevational range (\( R^2 = 0.76 \), Pearson correlation test, \( t = 4.98, df = 8, p = 0.01 \)), i.e., the proportion of modified vegetation strongly decreased towards the mountain range (Figure 2C). Tree density varied from 12 to 37 tree ha\(^{-1}\) in the pastures but did not vary with elevation (KW = 9, df = 9, \( p > 0.05 \), Table 1). Tree size did not vary with elevation either (KW = 15.89, df = 9, \( p > 0.05 \)).
3.2. Taxonomic Composition of Vascular Epiphyte Assemblages

We registered 6027 structurally dependent plants, representing 167 species. Approximately 97% of all the individuals and 89% of the species were true epiphytes, representing 148 species and 5876 individuals, distributed in 49 genera and 13 families (Table S1). Hemi-epiphytes, mistletoes and vines made up 2% of the plants and 11% of the species.

Orchidaceae was the most important family accounting for more than 50% (75 taxa) of the epiphyte species and 49% (2905) of the individuals, Polypodiaceae represented 17% of the species (841/14% individuals) and Bromeliaceae represented 16% of the species (1809/31% individuals). These three families were abundant over the entire gradient. *Tillandsia fasciculata* was the single most abundant species, with 569 individuals at eight sites.
Other common species were *Vriesea sanguinolenta* (563 individuals), *Polypodium polypodioides* (387 individuals), *Catopsis nutans* (360 individuals) and *Epidendrum difforme* sensu lato (348 individuals), which were all found at nine sites.

### 3.3. α-Diversity along the Elevational Gradient

Regarding the sampling effort, the observed species represented between 45 and 95% of the estimated richness per site (Table 1). Species richness at 1240 m a.s.l. was substantially higher than at all other elevations (Figure 3). Not surprisingly, we found richness per tree was correlated with tree size ($R^2 = 0.11$, $t = 3.59$, df = 98, $p = 0.01$). However, neither epiphyte abundance (Pearson correlation $R^2 = 0.05$, $t = 0.60$, df = 8, $p > 0.05$), richness ($R^2 = 0.17$, $t = 1.42$, df = 8, $p > 0.05$) nor diversity per host ($R^2 = 0.10$, $t = 0.95$, df = 8, $p > 0.05$) correlated significantly with elevation along the entire gradient (Figure 4).

![Figure 3](image_url)

**Figure 3.** Species accumulation curves of epiphyte assemblages on host trees from pasture sites distributed along an elevational gradient in Gualaca district, Panama. Data show the mean ± the standard deviation of species in every pasture.

![Figure 4](image_url)

**Figure 4.** Variation in the average of (A) abundance, (B) richness and (C) diversity (as the Shannon index) of epiphyte assemblages in pasture trees ($n = 10$ per plot) along the elevational gradient in Gualaca district. Dotted lines represent linear regressions including all plots. Solid lines represent the correlation without the plots at 870 and 1050 m a.s.l. (highlighted with red symbols). Coefficients of determination and probability values are given in each plot.
This unexpected finding was driven by the low values of the two study sites at 870 and 1050 m a.s.l. Noteworthy is that relative humidity was very low at these two sites given the elevation (Figure 2B). Excluding these two plots from the analysis yielded significant increases with elevation in all three assemblage attributes (Figure 4). These significant relationships were strongly influenced, but not entirely driven by, the site with the highest values in all three measures at 1240 m. Including only the seven lowest plots in a third analysis still yielded a significant relationship for diversity ($R^2 = 0.57$, $p < 0.05$) and a trend for abundance ($R^2 = 0.39$, $p = 0.13$). Alternatively, when relating abundance, richness and diversity to relative humidity, all three relationships were highly significant (Pearson correlation, abundance, $t = 2.45$, df = 8, $p = 0.04$; richness, $t = 3.85$, df = 8, $p = 0.01$; diversity, $t = 3.78$, df = 8, $p = 0.01$, Figure 5).

![Figure 5](image_url)

**Figure 5.** Variation in the average of (A) abundance, (B) richness and (C) diversity (as the Shannon index) of epiphyte assemblages in pasture trees ($n = 10$ per plot) as a function of relative humidity along an elevational gradient in Gualaca district. Pastures at 870 and 1050 m a.s.l. are highlighted with red symbols. Coefficients of determination and $p$-values of regression analyses are given in each plot.

### 3.4. β-Diversity along the Elevational Gradient

The among-tree similarity of the epiphyte assemblages ranged between 65 and 85% ($q = 0$; Figure 6). Among-tree similarity in regard to the most common species ($q = 1$) ranged between 45 and 75% along the gradient, while variation regarding very abundant species was largest with 15–70% ($q = 2$). In brief, among-tree similarity of epiphyte assemblages varied little between elevations considering species richness ($q = 0$), but considering common and also abundant species ($q = 1$ and $q = 2$, Figure 6), the structure of epiphyte assemblages varied strongly between the different elevations.
Figure 6. Multiple-assemblage similarity profile of epiphyte assemblages growing along the elevational gradient in Gualaca district. The graph illustrates the compositional differences in the epiphyte assemblages from different elevations using similarity indices that differ in their sensitivity to relative species abundance. The x-axis shows the orders of q (sensitivity parameter) and the y-axis shows the values of mean similarity, from 0 = assemblages being completely distinct to 1.0 = assemblages being identical.

3.5. Ordination Analyses

Consistent with the relatively high similarity of epiphyte assemblages among elevations, the NMDS indicated a substantial overlap of epiphyte assemblages along the gradient (Figure 7), which was further supported by the results of the PERMANOVA regarding the elevation (F = 6.69, R² = 0.06, p = 0.01) and the local relative humidity (F = 4.20, R² = 0.04, p = 0.01).

Figure 7. Non-metric multidimensional scaling (NMDS) ordination analyses of epiphyte assemblages on trees along the elevational gradient in Gualaca district, Panama (n = 100). Stress value for NMDS is 0.16.

4. Discussion

As epiphytes lack access to soil, they respond more than other life forms such as trees or terrestrial herbs to variation in humidity [28]. Thus, the typically observed increase in
epiphyte abundance and species richness with elevation up to a maximum at intermediate elevations [19–21,28,30] is usually explained by an increase in water availability. Surprisingly, our results did not fulfil the expectation of a steady increase because neither epiphyte richness, abundance nor diversity showed significant trends (Figure 4). However, when these parameters were correlated directly with the hypothesised driver, i.e., with local relative humidity, a significant relationship emerged (Figure 5). This suggests that the two sites at 870 and 1050 m are drier than expected for their elevation and that this deviation causes the unexpected result. Since any elevational trend in diversity is not due to elevation as such, but rather due to spatial constraints (e.g., [49]) or co-varying abiotic factors such as temperature or moisture availability (Figure 2, [50,51]), our results actually lend support to the general mechanistic explanation for differences in epiphyte community structure.

Together with local climate, variables such as tree density, surrounding forest coverage, time since original disturbance and presence of nearby human settlements all represent local factors that can modify general patterns. For example, we found that isolated trees at 1240 m a.s.l. were remnants of the primary forest with much forest in the vicinity (Figure 3), which provides a straightforward explanation for the high $\alpha$-diversity, while most trees at lower elevations established after clearance and the remaining forest as source areas are scarce. A high degree of local variability in epiphyte communities related to a varying number of remnant trees and newly established ones was also reported for pastures in lowland Panama [11].

Tree density did not differ much among sites, similar to observations in pastures in the lowlands of Panama [17]. Previous studies emphasised the role of the spacing of isolated trees for the connectivity and genetic restoration of isolated plant populations [15]. Maintaining or even increasing tree density may be an important factor for the long-term persistence of vascular epiphyte assemblages in pastures. Further, the positive correlation of epiphyte abundance and host DBH found in this study supports the general notion that large and old trees are of disproportionate importance for epiphytes [15,23].

As expected, assemblages varied little in species composition (Figures 6 and 7), although there was variation in assemblage structure (i.e., a change in the most abundant species) along the elevational gradient. Moreover, the overlap of epiphyte assemblages in the NMDS and PERMANOVA analyses supports the notion of small differences among elevations or by comparing them with their local relative humidity. Despite that, similarity profiles suggest that heterogeneity in the structure of epiphyte assemblages was mainly caused by changes in the most abundant species at the highest elevation where humidity is highest (Figure 6). Werner, Homeier and Gradstein [27] also reported a high species richness on isolated remnant trees in Ecuador, which was still substantially reduced compared to a forest habitat.

Noteworthy is that all long-term studies (e.g., [17,27,52]) suggest that epiphyte assemblages are currently not saturated (for a theoretical treatise, see [53]). Even on isolated trees in pastures, epiphytes tend to increase in abundance and species numbers over time: Einzmann and Zotz [54] reported a 3-fold increase in abundance over just eight years. Our study provides the basis to test whether such increases are really a universal phenomenon by repeating the census on the same pasture trees in a few years.

5. Conclusions

We documented the occurrence of vascular epiphytes in pasture trees along an elevational gradient in western Panama. Surprisingly, diversity was not significantly correlated with elevation, but variations in abundance, species richness and diversity were significantly related to differences in relative humidity. The proximity of surrounding forest and land use history influenced the number of potential species that can reach isolated trees. Both introduce a high level of local idiosyncrasy. We emphasise that the value of this study is not restricted to the analysis of the status quo but also lends itself as a starting point for the investigation of long-term changes in epiphyte assemblages in this human-modified landscape.
Supplementary Materials: The following are available online at https://www.mdpi.com/1424-2818/13/2/49/s1: Figure S1: Analytical design. Alpha (α-) diversity represents the number of species in each individual tree. At each elevation, beta (β-) diversity represents the turnover between trees and gamma (γ-) represents the total diversity of a plot. We calculated the average diversity at the tree scale (τ-diversity) to perform regression analyses (n = 10) and we compared the β-diversity of each plot. Table S1: Epiphyte abundance and composition in isolated pasture trees along an elevational gradient in southwest Panama.

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