Mongabay.com Open Access Journal - Tropical Conservation Science Vol.6 (1):283-302, 2013

Research Article

Climatic and structural factors influencing epiphytic bromeliad community assemblage along a gradient of water-limited environments in the Yucatan Peninsula, Mexico.

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Abstract

There is a lack of knowledge on the factors driving epiphytic community assemblage along water-limited environments. Epiphytic bromeliad and host communities were analyzed in a range of vegetation types, following a precipitation gradient from 500 to 1500 mm y^{-1}. Plots were set up in scrub mangrove, coastal sand dune scrub, deciduous, semi-deciduous and sub-perennial forests within the Yucatan Peninsula in Mexico. Identity and abundance of hosts and epiphytes, as well as host height and seasonal microenvironmental variables, were recorded at each vegetation type. The study found epiphytic bromeliads to be mainly located in the lower canopy strata of all but the wettest site (sub-perennial forest). Total epiphyte richness (estimated using species accumulation curves) increased with annual precipitation. Bromeliad species density decreased with vapor pressure deficit and increased with host species density. Semi-variograms and kriging analysis showed a high spatial correlation in bromeliad and host species density. The species composition, however, was unrelated to space, according to a Mantel test, but related to host species composition. The current study shows that diversity and structural integrity of the canopy may be as important as climate in the conservation of epiphytic composition in water-limited environments, where epiphytes are found in sheltered, lower canopy strata.

Keywords: Bromeliaceae, community assemblage, epiphyte, evaporative demand, host specificity.

Resumen

Hay poco conocimiento sobre los factores que guían el ensamblaje de epífitas en ambientes estacionalmente secos. Las comunidades de bromeliáceas epífitas y los hospederos fueron analizadas en diferentes tipos de vegetación siguiendo un gradiente de precipitación (500 a 1500 mm anuales). Se establecieron cuadrantes en un manglar chaparro, matorral de duna costera, selva baja caducifolia, mediana sub-caducifolia y alta sub-perennifolia de la Península de Yucatán, México. La identidad y abundancia de epífitas y hospederos, así como la altura de los hospederos y variables microambientales fueron registradas. La gran mayoría de las bromeliáceas epífitas se localizaron en el estrato bajo del dosel en todos los casos, con la única excepción del tipo de vegetación más húmedo (selva alta sub-perennifolia). La riqueza de especies de epífitas (calculada por medio de curvas de acumulación de especies) aumentó con el incremento en la precipitación media anual. La densidad de especies epífitas disminuyó al aumentar el déficit de presión de vapor y aumentó con la densidad de especies de potenciales hospederos. Se determinó mediante semi-variogramas y análisis de kriging que el espacio influía sobre la densidad de especies epifitas y hospederas así como sobre las variables ambientales. Sin embargo, de acuerdo a la prueba de Mantel, la composición de especies no mostró esta correlación espacial, y se relacionó con la composición de especies de hospederos. El presente trabajo subraya la importancia no sólo del clima sino de conservar la diversidad de hospederos y la estructura del dosel para poder conservar la riqueza de bromeliáceas epífitas en sitios secos, debido a que las especies se establecen en las partes bajas del dosel.

Palabras clave: Bromeliaceae, ensamblaje de comunidades, epifitas, demanda evaporativa, especificidad de hospederos

Received: 16 January 2013; Accepted: 9 May 2013; Published: 24 June 2013.

Cite this paper as: Cach-Pérez, M. J., Andrade, J. L, Chilpa-Galván, N., Tamayo-Chim, M., Orellana, R. and Reyes-García, C. 2013. Climatic and structural factors influencing epiphytic bromeliad community assemblage along a gradient of water-limited environments in the Yucatan Peninsula, Mexico. *Tropical Conservation Science* Vol. 6(2):283-302. Available online: www.tropicalconservationscience.org

Introduction

In a changing world where species are faced with habitat fragmentation and climate change, understanding the factors that drive plant species diversity and distribution is important for conservation and management. Of the different plant life forms, the epiphytes are one of the most vulnerable groups to both disturbance [1-2] and climate change [3-5] due to their lack of access to permanent water sources, their perennial character, and their fine tuning to seasonal precipitation [6]. Nevertheless, few studies have been published describing the current abundance and distribution of the epiphytes in seasonally dry tropical environments such as coastal dune scrubs, mangroves, and dry forests [7-9].

Over a wide range of habitats, epiphytic richness increases with precipitation, limited by the presence of frost at some of the wettest environments [10-11]. Under similar precipitation ranges, fog and dew occurrence may have a positive effect on the water status of the epiphyte, favoring establishment [6, 12-13]; while large diurnal/seasonal oscillations in temperature and humidity may have a negative effect on epiphyte establishment [14].

Epiphytes grow embedded in a matrix of host trees/shrubs/palms with a combination of architectural and phenological traits that may influence epiphyte establishment. Several studies have shown a relationship between specific host traits and epiphytic abundance [15-19]. Host richness may also define the complexity of microclimates available for colonization [20-21], promoting vertical stratification of the epiphytes along the canopy strata [22-23]. In result, epiphytes with different light and water use strategies can assemble at different canopy heights [6, 12, 24].

When comparing species richness and composition in a gradient of environments, space can also constitute an important factor, since it is related to the species dispersal capacity and to historical changes in vegetation [15, 25-26]. Ignoring space may therefore lead to incomplete ecological conclusions.

The Bromeliaceae are a neotropical family, frequently showing xeromorphism [27-28], where the epiphytic habit is highly represented [29]. *Tillandsia* is among the most drought tolerant genera, thriving in habitats with very limited precipitation [13, 30-31].

The Yucatan Peninsula in Mexico represents a neotropical environment, with a precipitation gradient from a coastal drier northwestern region (500 mm y^{-1}) to an inland wetter southern region (1600 mm y^{-1} [32]), a small elevation gradient (0-380 m.a.s.l.), and no physical barriers to migration. This gradient maintains different plant communities in the region, offering an excellent opportunity to study the assembly of epiphytic bromeliad communities in different vegetation types. Among these vegetation types are coastal sand dune scrubs, mangroves, and a progression of seasonal forests from deciduous to sub-perennial with incrementing canopy height.

We characterize and compare the epiphytic bromeliad communities associated with the changing environments and the structure of the host communities, in order to understand the factors that determine species assemblages and highlight the importance of conserving these plants in different plant communities. Our research questions were: 1) How different are species richness and composition among these different vegetation types and how do they relate to spatial separation? 2) How do the vegetation types differ structurally and climatically and how do they affect the epiphytic composition? 3) Are the species similarly stratified vertically within the canopy in these habitats and do they resemble stratification found in wet forests? 4) How are the epiphytes related to the potential hosts (trees and palms)? To our knowledge, this is the first published study to compare the species composition and factors driving this distribution (microclimate, canopy structure, host species identities) among a gradient of water limited environments, though a few studies have similar approaches for wetter forests and/or along altitudinal gradients [15, 33-34]. We established plots in coastal sand dune scrub, scrub mangrove, and deciduous, semi-deciduous and sub-perennial forests to characterize the structure and composition of the epiphytic bromeliads and host communities, and measured the seasonal microclimate in which epiphytic bromeliads were growing.

Methods

Field sites

Five sites were selected representing different vegetation types: coastal sand dune scrub, scrub mangrove, deciduous, semi-deciduous and sub-perennial forests. As is common throughout the world, all of these environments have suffered some degree of human disturbance; four of these sites are located within nature reserves, three of which are also archeological sites (Fig. 1).

The coastal sand dune scrub, located at San Benito (21°19'N; 89°26'W) has 2 m.a.s.l. of elevation and mean precipitation of 500 mm y^{-1}. Vegetation is dominated by palms, shrubs and succulents. The high vegetation density at the site suggests a fairly conserved state, even though it is localized in patches due to urbanization.

The scrub mangrove was located at the Celestún Biosphere Reserve (20°51'N; 90°22' W), a protected area of 81,432 ha at 3 m of elevation and with mean precipitation of 675 mm y^{-1} [35]. This vegetation is largely dominated by *Rhizophora mangle* L. (red mangrove), with individuals of *Avicennia germinans* (L.) L. (black mangrove) also present, both short in stature due to reduced water currents causing local hyper-salinity.

The deciduous forest was characterized at the Dzibilchaltún National Park, a secondary forest regenerating in a 538 ha protected area (21º05'N; 89º 35'W), with an elevation of 10 m.a.s.l. and 900 mm y^{-1} of precipitation. The forest is dominated by trees mainly of the Fabaceae family (legumes) [36-37].

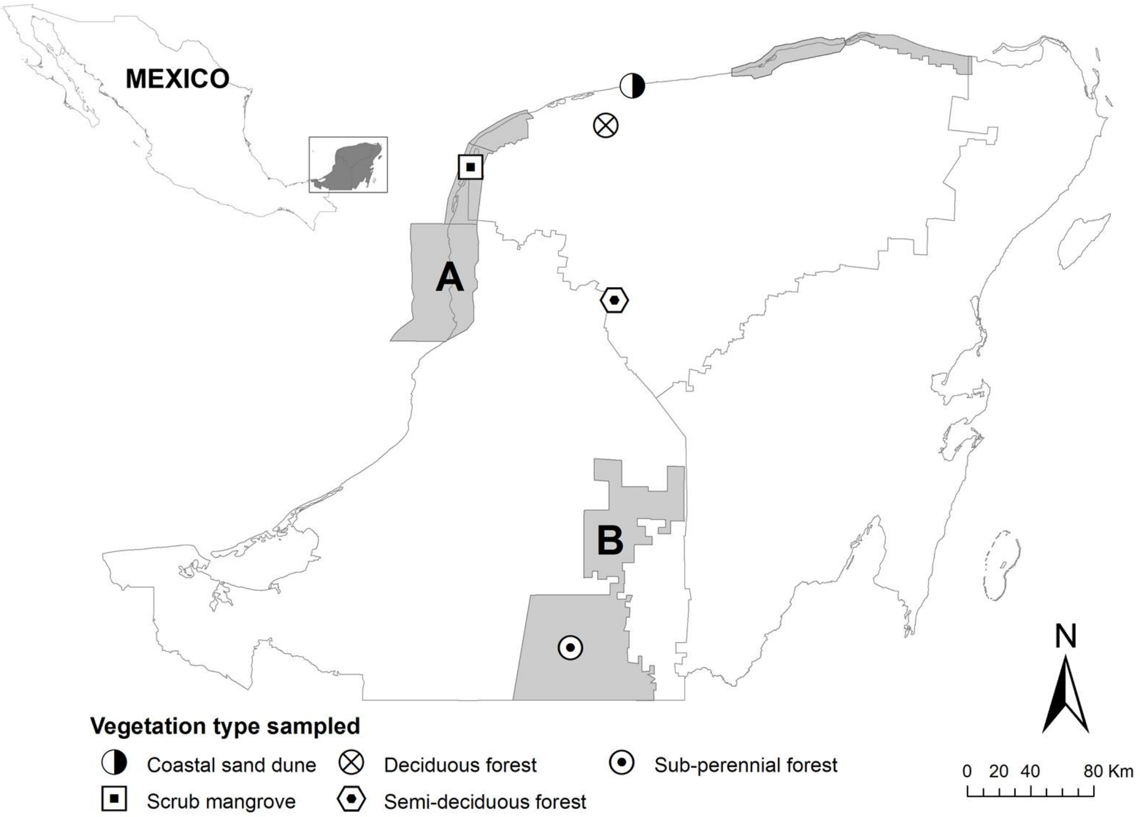

Fig. 1. Map of study sites in the Yucatan Peninsula, Mexico. The grey areas are the main Nature Reserves of the region. A.- Biosphere Reserve Ría Celestún along with the Estate Reserve El Palmar and Biosphere Reserve Los Petenes, and B.- Biosphere Reserve Calakmul; two small protected areas are located under the points that represent the deciduous forest (Dzibilchaltún National Park) and the semi-deciduous forest (Biocultural Reserve Kaxil-Kiuic).

The semi-deciduous forest was characterized at the Kaxil Kiuic Biocultural Reserve (20°05'N; 89°32'W), which extends for 1650 ha at 79 m of elevation. Mean annual precipitation is 1150 mm. The forest is dominated by species of the families Fabaceae, Meliaceae y Malvaceae [38].

The sub-perennial forest was characterized at the Calakmul Nature Reserve (18° 06'N; 89° 48'W), a conserved forest of 713,185 ha. Elevation is 230-380 m.a.s.l. and mean precipitation 1500 mm y^{-1}. We focused on the southern end of the reserve, where a sub-perennial forest with high fog and dew formation is localized (at 250 m of elevation). The forest is dominated by trees, mainly of the families: Meliaceae, Moraceae and Sapindaceae [39].

Field measurements

Permanent plots measuring 10 x 10 m were established in the five study sites. Within each plot, all potential hosts were counted, identified and tagged; these included trees, arborous cacti and palms. The minimum diameter at breast height (DBH) measured in the forests was 4 cm, and the large majority of epiphytes were found in hosts over this size. Because in the coastal sand dune scrub and scrub mangrove many trees and palms have a DBH < 4 cm, all trees and palms were measured. At these two sites diameters were sampled just below the start of the first branch because the trees and palms did not reach breast height.

Epiphytic bromeliads were counted and identified; binoculars were used where canopy height was above 2 m. Juvenile bromeliads with no defined adult morphology (measuring approximately <8 cm in longitude) were annotated but not included in the final numbers presented in the results because these are difficult to identify to a species level, are more difficult to spot in the upper canopy, and can be a very unstable component due to high death rates.

Height of the canopy strata where the epiphytes were found was recorded using a 15 m calibrated pole (Crain 90182, Crain Enterprises, USA) or in the tallest trees of the sub-perennial forest, using a clinometer (Silva Surveymaster, Silva, Sweden). Botanical vouchers for hosts were deposited at the herbarium of the Centro de Investigación Científica de Yucatán (CICY). The bromeliad species have been extensively studied in the area by the taxonomist Dr. Ivón Ramírez; the species in our plots were identified following her illustrated book [40], and at the most diverse site of Calakmul the taxonomist Dr. Juan Pablo Pinzón assisted the field study. The species can be verified by local specimens sampled at each location deposited at the CICY herbarium.

The number of plots varied according to site, due to both logistic limitations (accessibility to remote or inundated sites), scale (coastal scrub with small and densely packed trees vs. larger, more scattered trees in the forests), and biodiversity of potential hosts (from one dominant tree species in the scrub mangrove to more than 27 tree species in the sub-perennial forest) of the ecosystem. Three plots were sampled at the coastal sand dune scrub (a total of 101 bromeliads counted) and the scrub mangrove (113 bromeliads counted), 11 plots at the deciduous forest (364 bromeliads counted), 13 plots at the semi-deciduous forest (88 bromeliads counted) and six plots at the sub-perennial forest (599 bromeliads counted). Species accumulation curves indicated that the sampling effort was sufficient, as in most cases the percent of species sampled was above 70%, above which number the asymptotic estimation of species richness becomes stable [41]; exceptions were the sampled hosts in the sub-perennial forest and the epiphytes at the semi-deciduous forest. The predicted epiphytic richness values also are similar to those listed in a previous taxonomic study [40].

Microclimate

Simultaneously in at least in two plots, we characterized the photon flux density (PFD), temperature and relative humidity during the wet, early dry and dry seasons in the strata with the highest number of epiphytic bromeliads within each vegetation type (between 1.5 and 4.5 m, depending on the vegetation type). We used sensors (quantum sensors S-LIA-M003 and temperature and humidity sensors S-THB-002) connected to a data logger (HOBO micro station H21-002, station and sensors form Onset, Bourne, MA, USA). Measurements were made during at least four consecutive days; seasons were characterized once per site between July 2009 and May 2011. Vapor pressure deficit (VPD) was calculated based on air temperature and relative humidity measurements.

Models and Statistical Analyses

We used a sample-based protocol (using plots as units) to develop a species accumulation curve using EstimateS software (Version 9,[42]) which randomizes sample order 100 times to obtain a mean species accumulation curve. The curves were fitted using the exponential model [43], which is best when sampling small areas and well known groups, for all the sites except Calakmul, which was a large and more diverse area, and for which we used the Clench model [43]. The models were fitted by the quasi-Newton method provided by the package Statistica 8 (Statsoft, Inc. 1984-2007, USA). To estimate the proportion of species sampled (P_{ss}) we used the formula [41]:

$$P_{ss} = \frac{S_{obs}}{\frac{a}{b}} \qquad (1)$$

Where *a/b* represents the asymptote of the curve calculated by the exponential or Clench models, and is also the number of predicted species richness. P_{ss} was multiplied by 100 to express as a percentage.

An analysis of variance (ANOVA; α=0.05) was used to test differences in the height at which the bromeliad species were found and the differences in species density among the habitats. An ANOVA of repeated measures was performed to assess differences in seasonal microclimate data among strata. For both ANOVAs, data were tested for normality and homocedasticity and converted using the square root function in the case of epiphytic height to normalize. A Tukey post hoc test was performed. Statistica 8 software was used in all cases.

Simple linear regressions were fitted in order to relate species density and richness with VPD or precipitation. Bromeliad species density was also related through simple linear regressions to plot maximum canopy height and environmental variables (minimum VPD, mean annual precipitation) and potential host species density to epiphyte species density. For all regressions, SPSS software (SPSS Inc., Chicago, USA) was used. We explored space correlation of bromeliad species density introducing UTM coordinates of each plot into the package GS+ (V.5.1, Gamma Design Software, Michigan U.S.A) and running a semi-variance analysis that showed spatial correlation (spherical model, R^2= 0.23). We then used semi-variograms and Kriging analysis to address both the spatial relationship among the plots and the linear relationship between bromeliad species density and the explanatory variables (host species density, precipitation, VPD, canopy height) [26]. The regression kriging estimator of the explanatory variables $Z_{rk}(x)$ is defined as the sum of regression estimate $Z_r(x)$ obtained as a linear function of each explanatory variable with bromeliad species density, and the kriged estimate of spatially correlated residual values $\varepsilon_{OK}(x)$, using the equation:

$$Z(x) = Z_r(x) + \varepsilon_{OK}(x) \tag{2}$$

Regression kriging estimates were obtained using simple linear regressions between bromeliad species density and each of the explanatory variables. Variables were formally tested for normality and homocedasticity. Residuals of these regressions were obtained by the SPSS software; estimates of residuals at unobserved locations were obtained from the ordinary kriging using GS+ and applied to the variogram.

We tested whether the bromeliad species identity and abundance were correlated with those of the hosts (comparison of vegetation assemblages, β diversity) and whether both epiphyte and phorophyte communities were correlated to the distance between the sites. To test this we used the Relate test in the software PRIMER 6 (Plymouth Routines In Multivariate Ecological Research), which is analogous to a Mantel Test, using Spearman's rank correlation coefficient rho (ρ), where identical matrices would yield a maximum ρ value of 1 with 999 permutations on the kinship matrix [44]. To normalize the data, a fourth root transformation was applied.

Assembly patterns of epiphytic bromeliads and hosts species were also explored by Detrended Correspondence Analysis (DCA, [45]) in CANOCO version 4.51 [46] using species abundance data. For host analysis, we excluded the scrub mangrove, being unable to calculate abundance of the dominating host (*Rhizophora mangle*) because of the high frequency of re-rooting, which made it very difficult to distinguish different individuals.

Results

Microenvironmental canopy conditions of all five vegetation types were highly contrasting between the wet and dry seasons, with VPD and PFD also showing variation among sites (Table 1). The highest seasonal fluctuations within one site were observed in the deciduous forest, which had the highest daily PFD (18.5 ± 0.76 mol m^{-2} d^{-1}) and the highest maximum VPD (7.83 ± 0.39 KPa) during the dry season. The highest minimum VPD (VPD_{min}) values were registered at the coastal sand dune scrub and the semi-deciduous forest (0.43 ± 0.06 and 0.44 ± 0.01 KPa, respectively). All five vegetation types, even the wettest forest (sub-perennial), exhibited high VPD values (maximum and minimum) at least during the late dry season.

For both host (mainly trees and palms) and bromeliad epiphytic species, there was an overall high percentage of sampled species in the census, and a good fit (R^2>0.96) of the species accumulation curves, making it valid to compare total predicted richness values among vegetation types (Table 2). Both hosts and epiphytes showed a positive relationship between predicted species richness and precipitation (R^2=0.76 and 0.83, respectively), with this regression not being significant for species density (but see analyses below). In contrast, host and epiphyte species density was negatively related to VPD_{min} (R^2=0.19 and 0.64, respectively), a variable that showed no significant relation to total richness.

Table 1. Seasonal photon flux density (PFD, mol $m^{-2}d^{-1}$), maximum and minimum vapor pressure deficit (VPD_{max} and VPD_{min}, Kpa) of each of the five vegetation types. Data was collected from the strata where epiphytic bromeliads were most abundant within each site, and are presented as mean ± SE. Different letters denote statistical differences between seasons for each vegetation type. Abbreviations: CSD= coastal sand dune; SM = scrub mangrove; DF = deciduous forest; SMDF = semi-deciduous forest and SPF = sub-perennial forest.

Site	**PFD**			**VPD_{max}**			**VPD_{min}**		
	Wet	Early dry	Dry	Wet	Early dry	Dry	Wet	Early dry	Dry
CSD	8 ± 0.57^{a}	2.23 ± 0.08^{b}	7.28 ± 0.21^{a}	2.37 ± 0.18^{b}	2.21 ± 0.18^{b}	6.62 ± 0.39^{a}	0.19 ± 0.01^{b}	0.33 ± 0.02^{a}	0.43 ± 0.06^{a}
SM	6.74 ± 0.65^{a}	1.83 ± 0.06^{b}	8.23 ± 0.11^{a}	3.72 ± 0.23^{b}	2.08 ± 0.19^{c}	4.82 ± 0.22^{a}	0.23 ± 0.01^{b}	0.27 ± 0.01^{b}	0.39 ± 0.01^{a}
DF	4.24 ± 0.15^{b}	6.02 ± 0.06^{b}	18.5 ± 0.76^{a}	4.07 ± 0.12^{b}	1.06 ± 0.11^{c}	7.83 ± 0.39^{a}	0.25 ± 0.02^{b}	0.22 ± 0.01^{b}	0.31 ± 0.01^{a}
SMDF	4.59 ± 1.25^{a}	0.86 ± 0.003^{b}	7.59 ± 0.25^{a}	2.14 ± 0.21^{a}	0.55 ± 0.002^{b}	1.83 ± 0.27^{a}	0.25 ± 0.01^{b}	0.21 ± 0.01^{b}	0.44 ± 0.01^{a}
SPF	4.59 ± 1.26^{b}	0.66 ± 0.03^{c}	7.59 ± 0.25^{a}	2.24 ± 0.27^{b}	1.25 ± 0.05^{b}	5.36 ± 0.44^{a}	0.05 ± 0.02^{c}	0.18 ± 0.01^{b}	0.23 ± 0.01^{a}

In total, 15 species of epiphytic bromeliads were surveyed, belonging to three genera (Table 2b). Only five were strictly tank species, which have a water reservoir formed by the leaf bases, (*Aechmea bracteata* (Sw.) Griseb., *Catopsis nutans* L., *Tillandsia dasyliriifolia* Baker, *Tillandsia elongata* Kunth var. subimbrincata (Baker) L. B. Sm. and *Tillandsia utriculata* L. and the remaining 10 were atmospheric species, which lack a water reservoir. In the sub-perennial forest that receives the highest annual precipitation of the vegetation types surveyed, we found the greatests number of bromeliad species, though the semi-deciduous forest was predicted to show a similar diversity. Among the species found in the wettest forest are *Tillandsia juncea* (Ruiz y Pav.) Poir. vel sp. aff., *Tillandsia polystachia* (L.) L. and *Tillandsia variabilis Schltdl*. The lowest richness was found in the scrub mangrove, located on one of the driest sites of the Yucatan Peninsula, and having two species, *T. dasyliriifolia* and *Tillandsia yucatana* Baker.

The most widespread epiphytic bromeliads (present in three vegetation types) were *A. bracteata*, *Tillandsia balbisiana* Schult. f., *Tillandsia brachycaulos* Schltdl., *Tillandsia schiedeana* Steud., and *T. yucatana* (Fig. 3). *T. brachycaulos, Tillandsia fasciculata* Sw. and *T. yucatana* were the most abundant species in the region, while *C. nutans* and *T. elongata* were the least abundant, with a distribution restricted to one vegetation type (Fig. 2).

Table 2. Host and epiphytic bromeliad species density and richness in relation to precipitation (Pp) and minimum vapor pressure deficit (VPD). Species density (number of species per plot) is presented as means ± standard error, values showing the same letter are not statistically different. Predicted richness values in each vegetation type were obtained from species accumulation curves, actual observed species are shown in parenthesis, all curves had an R^2>0.96 and percent of total species that were sampled are shown. Significant R^2 are shown for the simple regressions of VPD or precipitation vs. species density or predicted richness; symbols in parenthesis denote positive (+) or negative (-) interactions, n.s. is not significant at P>0.05. Abbreviations: CSD= coastal sand dune; SM = scrub mangrove; DF = deciduous forest; SMDF = semi-deciduous forest and SPF = sub-perennial forest. *No curve could be fitted for the scrub mangrove because all plots had identical epiphytic species composition.

	Vegetation type					**R^2 regressions**	
	CSD	**SM**	**DF**	**SMDF**	**SPF**	**VPD**	**Pp**
a) Hosts							
Species density	10 ± 3.1^{a}	1.3 ± 0.6^{c}	7.5 ± 2.3^{ab}	5.4 ± 1.9^{b}	8.3 ± 4.4^{ab}	(-)0.19	n.s.
Predicted richness	20(15)	2(2)	32(30)	35(31)	58(27)	n.s.	(+)0.76
Species sampled (%)	84	99	95	89	48		
b) Epiphytic bromeliads							
Species density	3.7 ± 0.6^{b}	1.3 ± 0.6^{c}	3.1 ± 1.5^{bc}	1.4 ± 0.9^{bc}	5 ± 1^{a}	(-)0.64	n.s.
Predicted richness	4(4)	2*	9(8)	16(5)	16(10)	n.s.	(+)0.83
Species sampled (%)	99	--	90	32	76		

Similar vertical segregation was observed in all the species and sites, with all of the species grouping at medium or low canopy height and absent at the top canopy (Fig. 2). The maximum canopy height was very variable at each site, being 2.7 m in the coastal sand dune scrub, 1.7 m in the scrub mangrove, 9.3 m in the deciduous forest, 12.8 m in the semi-deciduous forest and 18.3 m in the sub-perennial forest. Consistent with the maximum canopy height, 63.5% of the individuals in the coastal sand dune scrub and 88.2% in the scrub mangrove were found between 0.5 – 1.5 m height; 75.3% and 66% of the epiphytic bromeliads were found between 1.5 – 5 m and 2 – 6 m in the deciduous forest and semi-deciduous forest, respectively; finally, in the sub-perennial forest 58.6% were located between 2 and 10 m. The sub-perennial forest, the tallest and most complex environment, also exhibited more species-specific segregation along the vertical gradient than the rest of the environments.

The variable host species density was weakly related to bromeliad species density (R^2=0.11, P<0.05), while precipitation and canopy height were not related to bromeliad species density (Fig. 3). Yet the kriging analysis of the residuals of those regressions suggested that the regressions could be significant (R^2=0.5 in all cases) when the spatial autocorrelation was taken into account. The semi-variograms suggest that 75-95% of the variance in the residuals is spatially correlated at a distance of 198-268 km, 100 km below the maximum distance between plots of all vegetation types, indicating negligible space effect in those sites farther apart (Table

3). In contrast, VPD_{min} was not spatially correlated and was the best variable to explain bromeliad species density, having a negative effect.

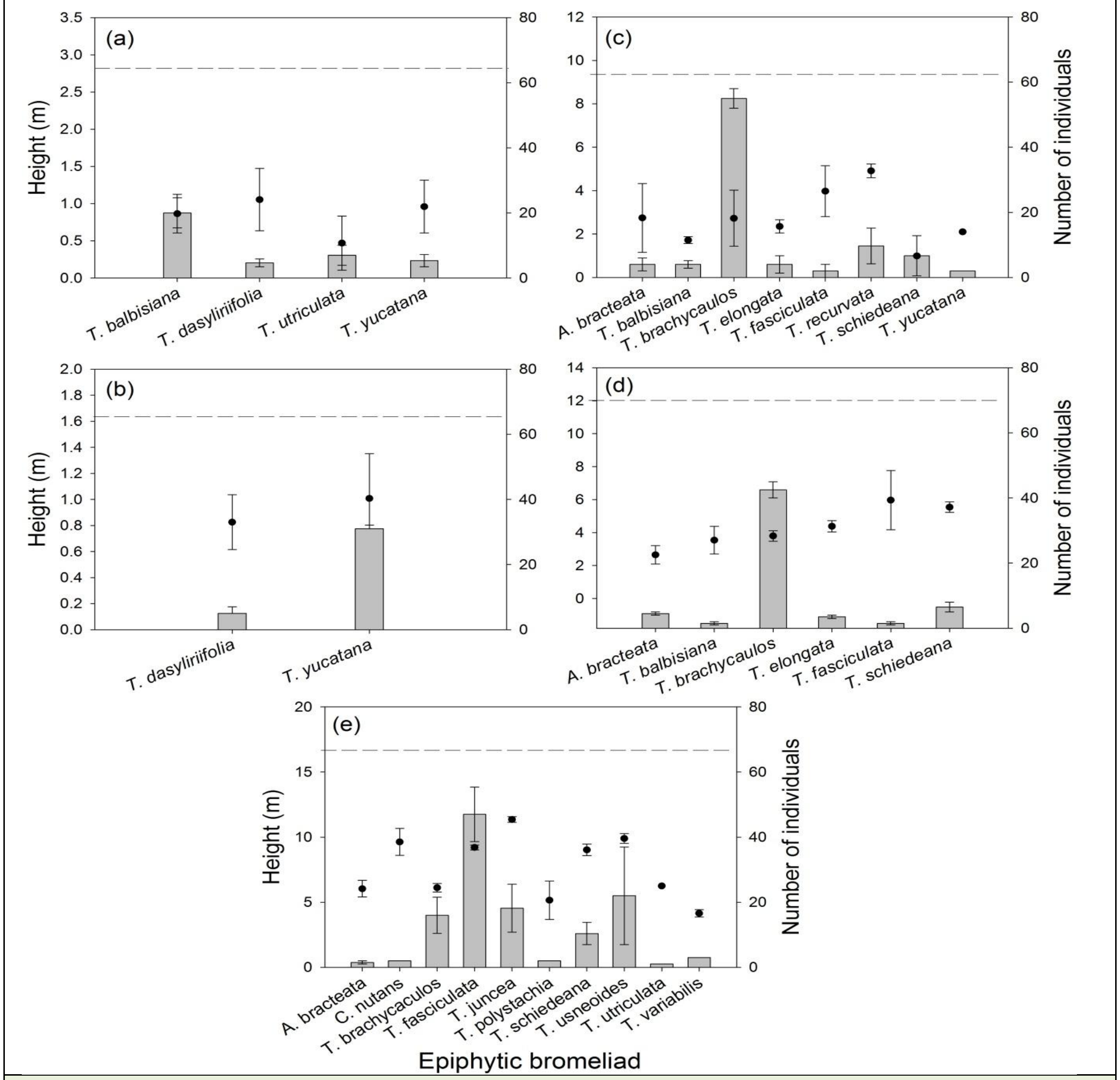

Fig. 2. Distribution (circles) and number of individuals (bars) of epiphytic bromeliads along the vertical profile of five vegetation types of the Yucatan Peninsula. Means per plot ± standard error are shown. (a) Coastal sand dune scrub; (b) scrub mangrove; (c) deciduous forest; (d) semi-deciduous forest; (e) sub-perennial forest. Data of distributions are means ± SD; dotted lines represent the maximal canopy height recorded. For clarity in the vertical distribution, different scales are shown for each graph.

DCA diagrams (Fig. 4) showed how the epiphytic bromeliads and hosts species in plots assembled or grouped by vegetation types and how the species exchanged between them. The assemblage of the epiphytic bromeliads along the first axis follows the pattern of mean annual precipitation on each vegetation type along the gradient present in the Yucatan Peninsula, from the coastal sand dune scrub to sub-perennial forest (Fig. 4a). Both epiphytic and host species identity and abundance overlapped in the plots of the semi-deciduous and deciduous forest. Host composition is very characteristic in the coastal sand dune scrub and sub-perennial forest (Fig. 4b). Even though in the DCA, epiphytic and host assemblages appeared to have different patterns, the two groups were highly correlated in the Mantel test (rho=0.72, P=0.01, Table 4). Neither host nor epiphyte composition showed a correlation with space (distance between plots, Table 4).

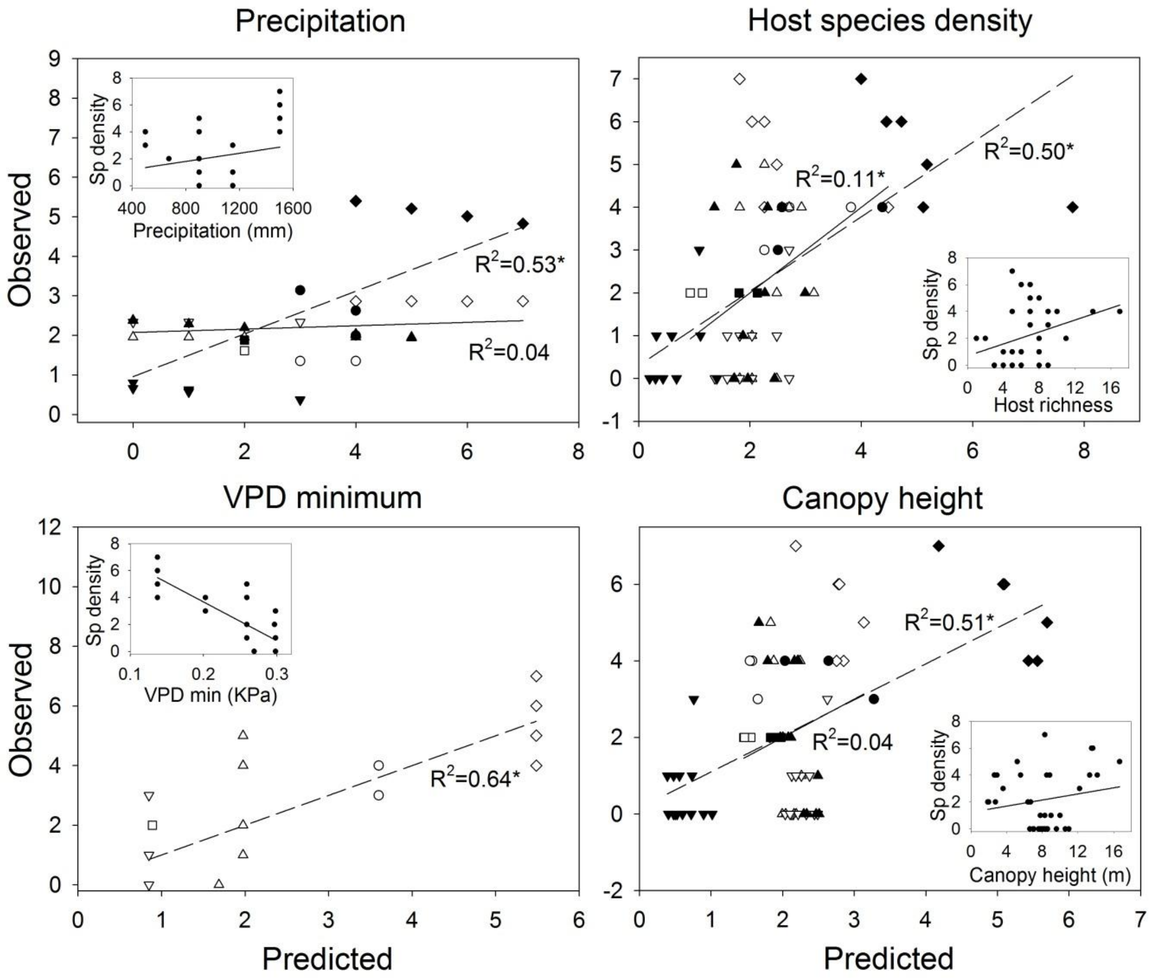

Fig. 3. Results of cross validation analysis used to compare the performance of regression and regression kriging analysis for mean annual precipitation, host species density, minimum vapor pressure deficit and canopy height. Continuous line for regressions of observed vs predicted values (open symbols) and broken fit line for regressions of observed vs predicted using kriging (closed symbols), VPD showed no spatial correlation. Circles= coastal sand dune; squares= scrub mangrove; upward triangle= deciduous forest; downward triangle= semi-deciduous forest and diamonds= sub-perennial forest. Smaller graphs show the relationship of the raw data of bromeliad species density and the explanatory variables.

The families of hosts with the highest number of epiphytic bromeliads (in all five vegetation types) were Moraceae, Ulmaceae and Fabaceae (Fig. 5). The host family with the greatest number of individuals in the coastal sand dune scrub was Arecaceae (palms); however, the greatest number of epiphytic bromeliads were located on individuals of the less abundant family Euphorbiaceae (Euphorbiaceae had 8.5 times fewer individual trees than Arecaceae, but 4.5 times more individual epiphytic bromeliads). Similarly, in the deciduous forest and semi-deciduous forest, we registered the highest epiphytic bromeliad abundance in the Ulmaceae and Erythroxylaceae families, respectively, which were not the most abundant families. In contrast, in the sub-perennial forest, the greatest number of epiphytic bromeliads were found in the two most abundant host families (Moraceae and Sapindaceae).

Table 3. Parameters and statistics of semi-variogram models fitted for precipitation, host species density (Host sp dens), minimum vapor pressure deficit (VPD_{min}) and maximum canopy height.

Variables	Model	Nugget variance	Total variance	Range (m)	Relative structural variance (%)	R^2
Precipitation	Spherical	1.83	7.32	198700	75	0.46
Host sp dens	Spherical	0.32	7.22	268200	95.6	0.43
VPD_{min}	Linear	1.23	1.23	337703	0	0.02
Canopy Height	Spherical	1.67	7.56	233700	77.9	0.53

Discussion

There was a common pool of epiphytic bromeliad species shared among the coastal sand dune scrub, scrub mangrove, deciduous forest, semi-deciduous forest and sub-perennial forest, with 60% of the species shared by at least two vegetation types. Most of the species belonged to the highly drought-tolerant genus *Tillandsia* [6, 28-29], with one species of the genus *Aechmea* that was widely spread and one species of the genus *Catopsis* that was limited only to the wettest site, the sub-perennial forest. Most of the species specific to just one site were found in the mesic sub-perennial forest.

Table 4. Mantel test of correlation between the composition of bromeliad and potential host communities and space (distance between plots). Correlations are shown using Spearman's rho (ρ).

	Spearman's *rho*	P
Bromeliad species vs phorophyte species	0.72	0.01
Bromeliad species vs space	-.34	0.99
Phorophytes species vs space	-.78	0.99

All five vegetation types showed highly variable microenvironments, with an intense five-month drought when light and VPD conditions were commonly harsh, though values oscillate among the sites (Table 1). Goode & Allen [14] found low germination in the epiphytic bromeliad *Aechmea bracteata* under highly changing microenvironmental conditions, which would reduce establishment in most of the sites included in this study. To counteract the changing environment, most epiphytic bromeliads grew in the less variable, medium and lower canopy strata (Fig. 3), where our microclimatic data showed low light values compared to the upper canopy. These more protected lower canopy microenvironments may allow the establishment of drought-resistant epiphytes; in all but the wettest site, the upper stratum of the canopy is less populated. This contrasts with wet forests or even dry forests with high dew and fog formation, which may have several species that are confined to the upper canopy [17, 24, 34].

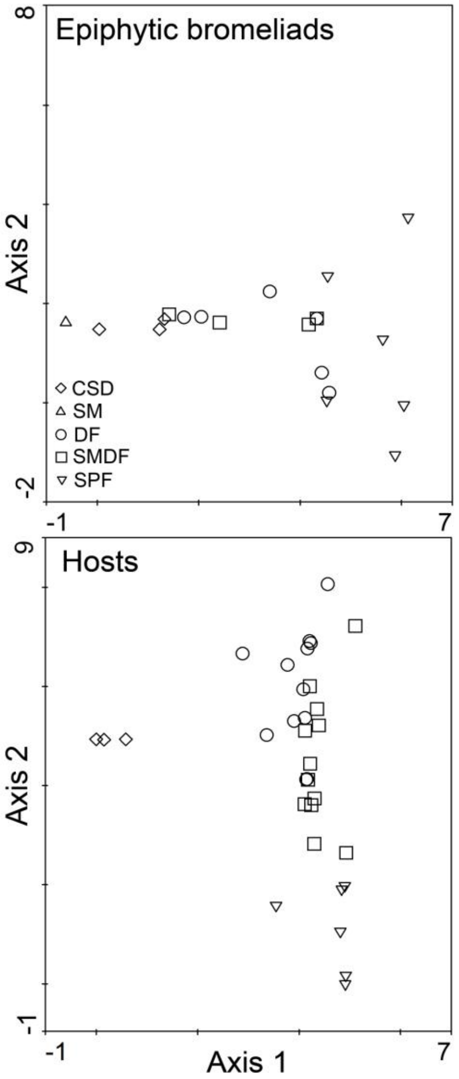

Fig. 4. Detrended Correspondence Analysis of epiphytic bromeliads and hosts Analysis based on abundance data for both epiphytic bromeliads (total inertia 3.575) and hosts (total inertia 9.288). Abbreviations: CSD= coastal sand dune; SM = scrub mangrove; DF = deciduous forest; SMDF = semi-deciduous forest and SPF = sub-perennial forest. Eigenvalues = 0.900 and 0.230 for axis 1 and 2 respectively for epiphytic bromeliads; 0.984 and 0.787 for hosts. For the epiphytic bromeliads graph, plots with no epiphytic bromeliads are not shown and some symbols overlap due to very similar species composition (mangrove plots).

In agreement with previous published studies [10-11], as precipitation increased, so did the number of total species richness (both for epiphytes and hosts, Table 2). Contrastingly, when the data were analyzed as species richness per plot, species density, the patchy local distribution of the bromeliads and, to a lesser extent, hosts showed a different pattern, with higher species abundance in plots with lower VPD_{min} (Table 2), even when the values used for the regression were the same for all the plots within one vegetation type. Water being the most limiting factor in these dry environments [47], annual precipitation may ultimately allow a higher number of species, while at drier sites the species pool is reduced to only those that can tolerate higher stress [48]. It would be expected that the same pattern observed for total richness would be present in species density, which represents richness at a smaller scale. VPD_{min} is particularly important to the epiphytic bromeliads because all the *Tillandsia* and *Aechmea* species surveyed in our study show crassulacean acid metabolism, and thus open stomata primarily at night, when minimum VPD values are registered. Changes in the nighttime evaporative demand, which can be measured through VPD, will determine water loss in the epiphytes [49-50], and can be important for survival since water in epiphytes is only obtained in pulses and must be conserved in between pulses [47]. Low VPD may also be related to greater frequency of dew and/or fog events, an important water source in epiphytes [6, 12-13].

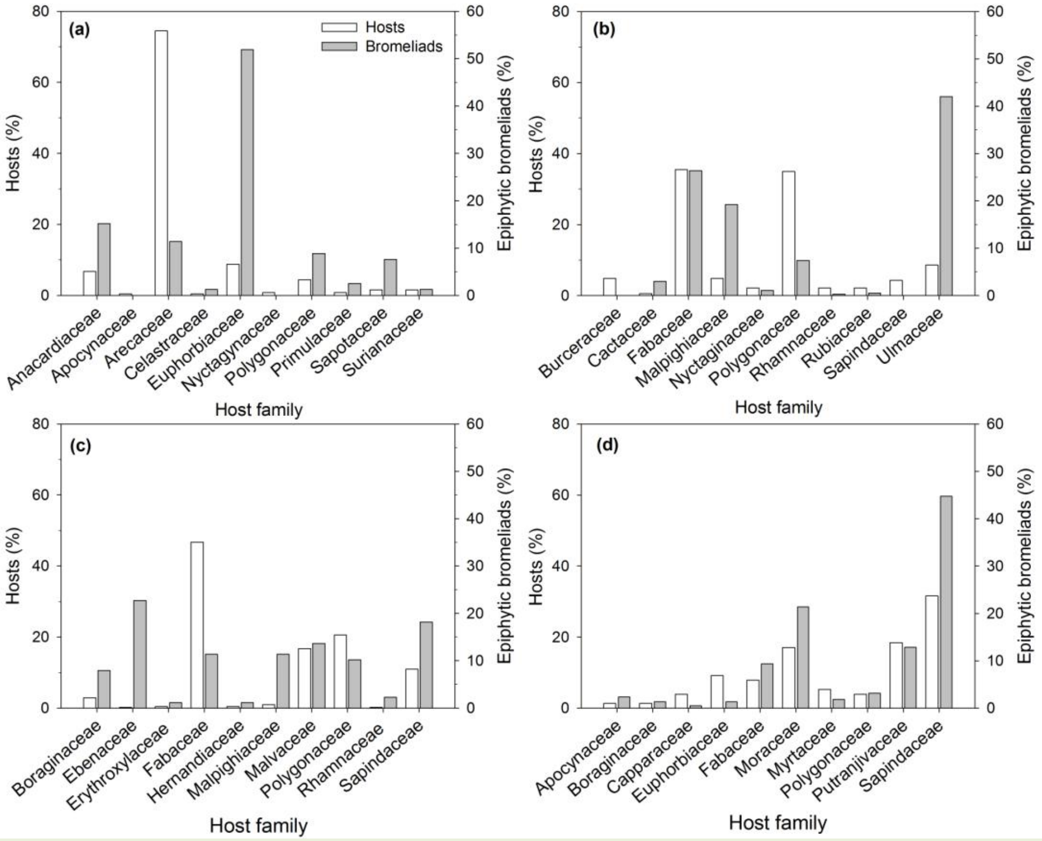

Fig. 5. Hosts families with the highest number of individuals and epiphytic bromeliads in four vegetation types. (a) coastal sand dune; (b) deciduous forest; (c) semi-deciduous forest; (d) sub-perennial forest.

The discrepancy between the correlations in VPD_{min} and precipitation in relation to species density or richness suggests that at sites with higher VPD, and thus higher evaporative demand, species show a more patchy distribution, as local microenvironmental differences may influence the probability of establishment. Chilpa-Galván and collaborators [51] found that in the deciduous forest of Dzibilchaltún, epiphytes congregate near a permanent water source (exposed underground lake) that influences the mesoenvironment by lowering nighttime VPD, and are absent from plots farther from the water. In contrast, at sites with low VPD, species may be more evenly distributed and will be present in most of the plots sampled, increasing species density; this would be more determinant for the epiphytes, as shown by a larger R^2 (Table 2).

Host species density was also positively related to epiphytic bromeliad species density with an $R^2=0.11$ (Fig.3). When the effect of space was also introduced using semi-variograms and kriging, a high autocorrelation was found between the residuals of the regression of host vs bromeliad species density, increasing the variance explained to an $R^2=0.53$. The relative structural variance, or the variance explained by space, was very high, 95% (Table 3). The effect of space in species distribution may relate to dispersion events, to a correlation with changing environmental conditions along a space continuum that both hosts and epiphytes respond to, and/or to the spatial distribution of an additional influence factor not registered in this study [25]. Precipitation and canopy height were not significantly related to bromeliad species density, but the regression became significant when the effect of space was introduced (regression using kriging expected values, Fig. 3). The correlation with space is frequent in vegetation assemblages [26], but is also relevant in our study area, as the gradient of precipitation follows a geographical continuum from the northern to the southern part of the Yucatan Peninsula, thus correlating space with forest types as a response to climate [32]. VPD_{min} did not show a spatial correlation (Table 3), as those sites with lower VPD_{min}, the sub-perennial forest and the coastal sand dune, are located in the geographical extremes of the precipitation gradient.

The effect of space, however, was not significant when β diversity (host and epiphytic species composition) was analyzed (Table 4). This was also found in a previous study with holo- and hemi-epiphytes from Colombia [15], though the study had plots of the same vegetation type that were farther apart than plots of different vegetation types, and thus had a different experimental design from the current study. In our study, the lack of correlation with space may be due to a high level of shared species among the vegetation types, since to different extents, they share the same limiting or stress factor: a prolonged dry season. The lack of spatial correlation may also be an effect of limited plot repetitions, since the correlation rho was high, even though the P value was not significant. As β diversity tests are more complex, these may require a higher number of repetitions than α diversity analyses that yielded significant results (Kriging analyses).

Even though the DCA suggested different assembly patterns of the epiphyte and potential host communities, the Mantel test indicated a strong association between the two communities. The DCA analysis reinforced the association between precipitation and bromeliad species identity and abundance, as the plots within each community clumped together, and different communities segregated among them in accord with the precipitation gradient (axis 1, Fig. 4), with the exception of the deciduous and semi-deciduous forests, which showed overlapping composition. In contrast, assembly of potential host tree species did not follow the precipitation gradient (along axis 1 or 2, Fig. 4). An important aspect to consider is that there is a gradient of tree sizes. The greater the amount of rainfall in the area, the greater the size of the tree and therefore more likely space colonization by epiphytic bromeliads.

The association between host and epiphyte communities suggested by the Mantel test may indicate different processes: 1) both communities respond to similar environmental stresses and thus form similar vegetation units, independent from each other; 2) spatial effects are responsible for the assemblages; 3) epiphytes associate to specific hosts. Benavides and collaborators [15] had investigated this question previously in swamps, floodplains and upland landscapes. Because their design was different, they could study independently the effect of space and landscape units, which cannot be done with our current design (since our mangrove plots are closer to each other than to plots in other forest types and this is the case for all the vegetation types). They found the assemblages to be space independent and also through partial Mantel tests determined that host composition was more relevant than landscape units. The authors also cited published examples of epiphytic host preference (i.e. [7, 18-19]) to sustain their hypothesis of host association as the main effect on epiphyte community assemblage. We would still argue that neither study can untangle the simultaneous effect of the environment on both communities.

Can the microenvironmental differences between hosts be more important than mesoenvironmental differences between vegetation types/landscape units? A study carried out within a deciduous forest measured larger mesoenvironmental effects among plots than the microenvironmental differences created by the hosts' canopies [51], though this effect may not necessarily be extrapolated to other environments. Some important factors such as VPD and salinity in the case of the coastal environments may also significantly affect both hosts and epiphytes more than host identity. Our data do suggest host preference within the same vegetation type, as epiphyte abundance on hosts (expressed in families) were generally highly disproportional to host frequency (either positive or negative host effects), even though this association was not always consistent when the same set of species were present in different vegetation types (Fig. 5). Different interactions that may link hosts and epiphytes remain to be further explored, such as the reported ant-bromeliad-tree symbiosis [7] and the effect that these can have on epiphyte community assemblage.

We conclude that all studied vegetation types shared in different degrees a prolonged dry season with challenging environmental conditions and a limited pool of species. The epiphytic assemblages along the precipitation gradient were associated at different scales with different biotic and abiotic factors; total species richness was associated with annual precipitation, while species density (richness per plot) was associated with VPD_{min} and potential host species density. Space (distance between the plots) also determined the variation in precipitation, canopy height and host species density, and influenced bromeliad species density throughout most of the gradient. Bromeliad species composition, however, did not show a relation to space, but was strongly related to host species composition, either due to a true association or to similar effects of environmental changes on both types of communities.

Implications for conservation

Mangroves, coastal sand dune scrubs, and seasonal forests may not be as diverse as mesic forests, but they do contain epiphytic species with high drought tolerance and excess light resistance, which are valuable for understanding stress tolerance mechanisms. As longer and more intense dry seasons and higher temperatures are expected to be more frequent with climate change in the Yucatan Peninsula [32] and in many tropical areas, it is important to understand the effects of these factors on forest structure and tree and epiphyte diversity. We observed that all the sites showed many shared species, possibly due to the small pool of species able to resist the dry conditions. Epiphyte composition was influenced by host composition and species density as much as by environmental conditions, making host diversity conservation a relevant factor for epiphyte conservation. The epiphytes were limited to the lower canopy strata in the four driest sites, indicating the importance of high canopy cover to buffer the great variability in climatic conditions. Thus it may be crucial to preserve canopy structure intact in order to maintain the local composition of epiphytic species.

Acknowledgements

We thank Angelica K. Moreno, Agatha Rosado, Celene Espadas, Claudia González, Isaac Castillo, Edilia de la Rosa, Evert Path, Filogonio May, Karen Solís, Guadalupe Carrillo, Luis Simá, Robert Us, José Luis Tapia and Juan Pablo Pinzón for field assistance and Jose Luis Hernández-Stefanoni and Tijl Essens for assistance in the use of statistical analyses as well as Dzibilchaltún National Park-INAH, and the Biosphere Reserves of Kaxil-Kiuic, Celestún and Calakmul. We thank an anonymous reviewer and Editor Alejandro Estrada for significantly improving this manuscript. This work was partially supported by Fondo Sectorial SEP-CONACYT 80181, SEMARNAT-CONACYT 107916 and UC MEXUS 2008-CL08-01. Manuel J. Cach-Pérez was recipient of a PhD fellowship from Consejo Nacional de Ciencia y Tecnología, México (CONACYT-204451).

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