

## **Biotic Factors Affecting the Abundance of Vascular Epiphytic Bromeliads Growing in Cloud Forest in Reserva Biologica Los Cedros, Ecuador**

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### **Authors' contributions**

*This work was carried out in collaboration between all authors. Author MB designed the study, wrote the protocol and interpreted the data with support from author AD. Author AM anchored the field study and author MAC provided further taxonomic expertise. Author MB gathered the initial data and performed preliminary data analysis. Authors MB and AD managed the literature searches and produced the initial draft. All authors read and approved the final manuscript*

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### **ABSTRACT**

**Aims:** In this paper we investigate whether the abundance of epiphytic bromeliads growing in cloud forest was affected by: (1) phorophyte family; (2) phorophyte size; and (3) the abundance of other epiphytes.

**Study Design:** The abundance of bromeliads was compared on 35 random trees from each of the three most abundant tree families (Burseraceae, Moraceae and Clusiaceae) present within a study site consisted of a 25 m x 25 m riverine area, situated along the Rio Los Cedros, within the Reserva Los Cedros Biological Reserve. All trees and bromeliad species within the study area had previously been identified by staff from the National Herbarium of Ecuador and this information was made available to the authors. Verification of botanical identification was further supported on-site.

**Place and Duration of Study:** A one month study at Reserva Biologica Los Cedros, near the town

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**Methodology:** For each of the 105 trees sampled we recorded the following data: total number of bromeliads, number of each of the five most abundance species of bromeliads in the study area; tree family, tree diameter at breast height (DBH), tree height, percent cover of vascular epiphytes; percent cover of non-vascular epiphytes. Data were collected non-invasively from ground level by using binoculars.

**Results:** The results showed no evidence of phorophyte specificity amongst epiphytic bromeliads. However, larger phorophytes held more bromeliads irrespective of phorophyte family and even when supporting high abundances of other vascular epiphytes.

**Conclusion:** We conclude that it is tree size and not the phorophyte species that is most important in driving high abundance and diversity in bromeliad communities. We also conclude that the bromeliad component of epiphyte communities is not affected by competition from other co-occurring epiphytes. Further research is needed to understand how species interactions within epiphyte communities drive epiphyte community assembly, dynamics and diversity.

**Keywords:** Vascular epiphyte; species interactions; *Tremarctos ornatus*; bromeliaceae; burseraceae; moraceae; clusiaceae.

## 1. INTRODUCTION

Epiphytes are of global importance as together they constitute approximately 10% of total global plant diversity [1]. Tropical epiphytes such as bromeliads are also useful indicators of forest quality and diversity, provide habitats for other species and are considered a keystone component of the forest with regards their role in ecosystem processes such as the recycling of nutrients and species interactions [2,1]. Epiphytic bromeliads have also been reported as an important component of the Andean/Spectacled Bear (*Tremarctos ornatus*) diet [3-8]. Several factors have been suggested as important determinants of abundance and diversity in bromeliad communities. Early work [9] suggested that epiphytes display phorophyte (host tree) species preference. Later work across a wide range of epiphyte taxa [10-12] also found strong associations between epiphyte species abundance and particular phorophyte species. Phorophyte species preference in epiphytes could be a reflection of the most suitable ecological conditions present on the phorophytes [13,14]. However, other researches on epiphytes also from a further wide range of taxonomic groups suggest that there is no phorophyte preference amongst epiphytes [15-17].

Previous studies have found that epiphyte species richness and abundance is positively correlated with phorophytesize [18,19,16,17,12] and one study [12] revealed that epiphyte growth was greater on phorophytes with higher overall epiphyte abundance. This suggests large degrees of mutualistic species interdependence within epiphyte communities and that

interspecific competition did not significantly adversely affect abundance or diversity of other epiphytic species. By contrast, other research [20] presents evidence to suggest interspecific competition for space between two out of four lichen species tested, and competition for light appeared relevant to all four species. A theory has been proposed to suggest that the abundance and diversity of a mature epiphyte community may be the result of facilitation mechanisms in an autogenic succession [21].

Overall, current research on a range of epiphyte species has produced varied findings but suggests that epiphyte abundance may be affected by phorophyte family, phorophyte size and by the abundance of other epiphytes. Interestingly, although several studies have investigated epiphyte-phorophyte interactions by examining patterns across a wide range of taxonomic groups, there has been very little more narrow-taxonomic range research into epiphyte-phorophyte interactions in groups other than epiphytic orchids and what exists there is inconclusive and often contradictory [1]. In particular, no previous study has compared the effect of these variables simultaneously on the abundance of epiphytic bromeliads. In this paper we describe an investigation into the effect of these variables on five species of bromeliads growing in cloud forest in Reserva Los Cedros, northwest Ecuador.

We aimed to test the following hypotheses:

- 1) The abundance of bromeliads is affected by the family of the phorophyte tree.
- 2) The abundance of bromeliads is affected by the size of the phorophyte tree.

- 3) The abundance of bromeliads is affected by the abundance of other vascular and non-vascular epiphytes growing on the phorophyte tree.

## 2. METHODOLOGY

### 2.1 Study Area

The study area, the cloud forest of Reserva Los Cedros, is located on the western slopes of the Andes in Imbabura province, Ecuador. It forms the southern buffer zone for the Cotacachi-Cayapas Ecological Reserve, has an average annual rainfall of 3150 mm and a vegetation type that is broadly classified as very humid premontane and very humid lower montane forest (elevation 1000 m - 2700 m, temperature 16°C – 25°C) [22].

### 2.2 Study Site

The study site consisted of a 25 m x 25 m riverine area, situated along the Rio Los Cedros, within the Reserva Los Cedros Biological Reserve. All trees within the study area had previously been identified by staff from the National Herbarium in Quito (Herbario Nacional del Ecuador). The species of bromeliads present on the site had also been previously identified by staff from the National Herbarium as during a preliminary site visit, species of epiphytic bromeliad (Bromeliaceae) were obtained by opportunistic collection from fallen trees and sent to Quito for identification by staff including one co-author of this paper (Chincheró). Correct identification of bromeliads was verified in the field by another of the co-author botanical experts (Mariscal) from the National Herbarium. Despite this support, it was not possible to identify one species of *Tillandsia* to species.

### 2.3 Data Collection

The abundance of bromeliads was compared on 35 random trees from each of the three most abundant tree families (Burseraceae, Moraceae and Clusiaceae) present within the 25m x 25m study. The following data were recorded for each of the 105 trees sampled: total number of bromeliads, number of each of the five most abundance species of bromeliads in the study area (listed in Table 1); tree family, tree diameter at breast height (DBH), tree height, percent cover of vascular epiphytes; percent cover of non-vascular epiphytes. Data were collected by means of non-invasive field work whereby

identification of bromeliads was achieved from ground level with the use of binoculars. Canopy access techniques were considered but not employed during this study as we considered them to be too potentially destructive to epiphytic plant communities at this site.

### 2.4 Statistical Analysis

All statistical analysis was carried out using SPSS version 15. Kruskal Wallis tests were used to compare the abundance of bromeliads on different phorophytes. The relationship between abundance of bromeliads and (1) tree size (2) abundance of vascular epiphytes (3) abundance of non-vascular epiphytes was examined by correlation analysis using Pearson's correlations and partial correlation analysis. Tree size was considered in terms of tree trunk girth (DBH) and tree height. Data for abundance of vascular and non-vascular epiphytes were first square root transformed to linearise relationships with bromeliad abundance.

## 3. RESULTS AND DISCUSSION

### 3.1 Results

The abundance of bromeliads did not differ significantly between tree family although overall abundance was generally greatest for Clusiaceae (Table 1).

Larger trees, particularly taller trees, were found to support significantly more bromeliads than smaller trees but simple correlation analysis did not detect this effect for any individual species of bromeliad (Table 2, Fig. 1, Fig. 2). Larger trees were found to have significantly lower overall percentage covers of other vascular and non-vascular epiphytes ( $r = -.30$ ,  $P = .002$  for the correlation between tree height and abundance of vascular epiphytes;  $r = -.37$ ,  $P < .001$  for the correlation between tree height and abundance of non-vascular epiphytes). This suggested the possibility of a confounding effect whereby large trees provided more habitat and so less competition for space. However, removing this possibility by controlling for the abundance of other epiphytes in a partial correlation analysis produced essentially same overall result as that from the simple bi-variate correlation; the only difference found was that the most abundant single species of bromeliad, *G. jaramilloi*, was now found to grow significantly more abundantly on taller trees (Table 2).

Tree size as a product of height and DBH [23] revealed that larger trees supported a

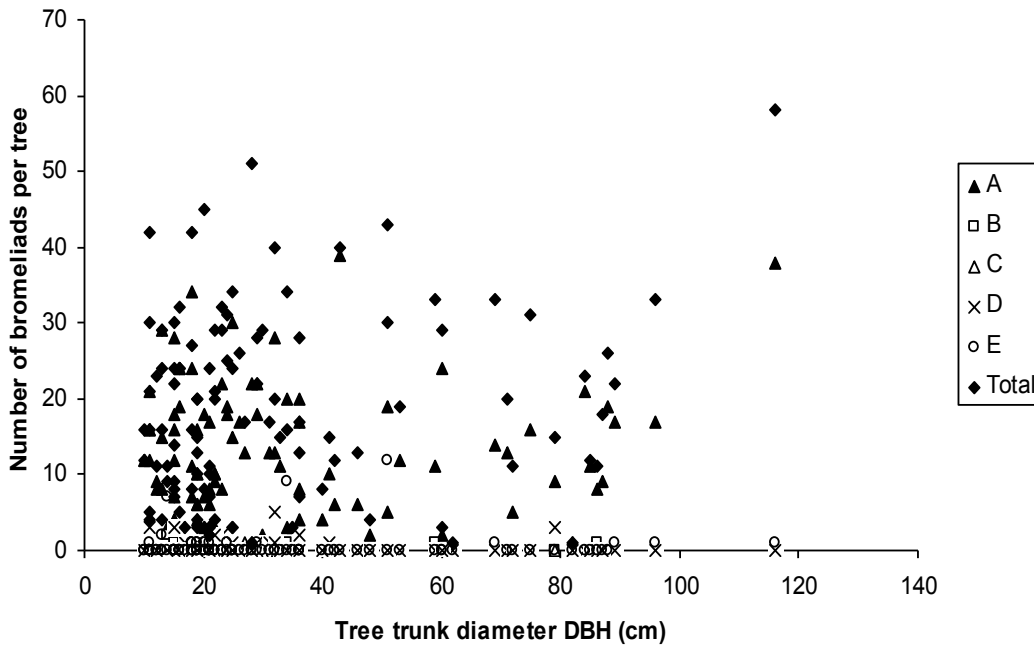
significantly greater abundance of bromeliads overall even when controlling for the abundance of other vascular and non-vascular epiphytes (partial correlation analysis  $r = .273$ ,  $P = .004$  for vascular epiphytes;  $r = .230$ ,  $P = .018$  for non-vascular epiphytes). However, no significant relationship was detected between overall tree size and the abundance of any individual species of bromeliad.

The overall abundance of bromeliads has a quadratic relationship with abundance of other vascular epiphytes; bromeliad abundance was

greatest at intermediate abundances of other species (Fig. 3). A significant linear relationship was found between the abundance of bromeliads and abundance of other vascular epiphytes when the latter were square root transformed (Table 3). This was true even when controlling for any confounding effects of tree size. Again, at an individual species level this effect was detected only for the most abundant single species of bromeliad, *G. jaramilloi* (Table 3). The abundance of non-vascular epiphytes was found to have no significant effect on the abundance of bromeliads (Table 3).

**Table 1. Mean number of number of bromeliad species per host tree**

Bromeliad species	Host tree family			Kruskal wallis test	
	Burseraceae	Moraceae	Clusiaceae	H	P
<i>Guzmania jaramilloi</i>	10.56	10.18	14.52	5.62	0.060
<i>Guzmania testudinis</i>	0.09	0.08	0.09	0.45	0.797
<i>Pitcairnia ferrellingramiae</i>	0.00	0.05	0.06	1.99	0.372
<i>Pitcairnia nigra</i>	0.23	0.41	0.36	2.05	0.370
<i>Tillandsia sp.</i>	0.97	0.18	0.09	2.94	0.230
ALL	19.41	15.44	21.52	4.69	0.096



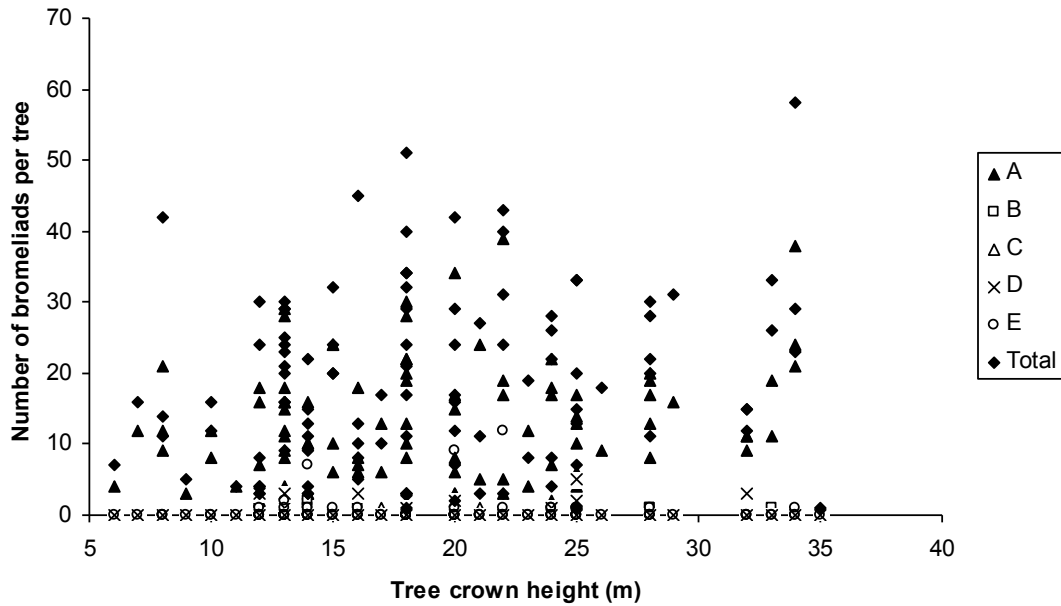
**Fig. 1. The relationship between tree trunk diameter (DBH) and the abundance of bromeliads.**  
 Key A = *Guzmania jaramilloi*; B= *Guzmania testudinis*; C= *Pitcairnia ferrellingramiae*;  
 D= *Pitcairnia nigra*; E= *Tillandsia sp*

**Table 2. Correlation values between bromeliad abundance and phorophyte DBH and canopy height. Values are given for bivariate person correlations and for partial correlations controlling for the abundance other epiphytes**

Bromeliad species	Pearson correlations		Partial correlations controlling for vascular epiphyte abundance		Partial correlations controlling for non-vascular epiphyte abundance	
	DBH	Canopy height	DBH	Canopy height	DBH	Canopy height
<i>Guzmania jaramilloi</i>	r= 0.13 P=0.170	r= 0.19 P=0.054	r= 0.20 P=0.053	<b>r= 0.27 P=0.004</b>	r= 0.17 P=0.086	<b>r= 0.23 P=0.018</b>
<i>Guzmania testudinis</i>	r=-0.02 P=0.816	r=-0.03 P=0.774	r=-0.05 P=0.580	r=-0.08 P=0.431	r=-0.01 P=0.952	r=-0.00 P=0.977
<i>Pitcairnia ferrellingramiae</i>	r=-0.08 P=0.415	r= 0.00 P=0.991	r=-0.07 P=0.500	r= 0.02 P=0.804	r=-0.10 P=0.320	r=-0.01 P=0.887
<i>Pitcairnia nigra</i>	r=-0.05 P=0.573	r=-0.04 P=0.706	r=-0.04 P=0.651	r=-0.06 P=0.562	r=-0.02 P=0.840	r=-0.08 P=0.397
<i>Tillandsia sp.</i>	r= 0.04 P=0.648	r= 0.02 P=0.829	r= 0.06 P=0.531	r= 0.05 P=0.636	r= 0.07 P=0.452	r= 0.05 P=0.599
ALL	r= 0.18 P=0.062	<b>r= 0.20 P=0.041</b>	<b>r= 0.24 P=0.012</b>	<b>r= 0.30 P=0.002</b>	<b>r= 0.20 P=0.040</b>	<b>r= 0.22 P=0.023</b>

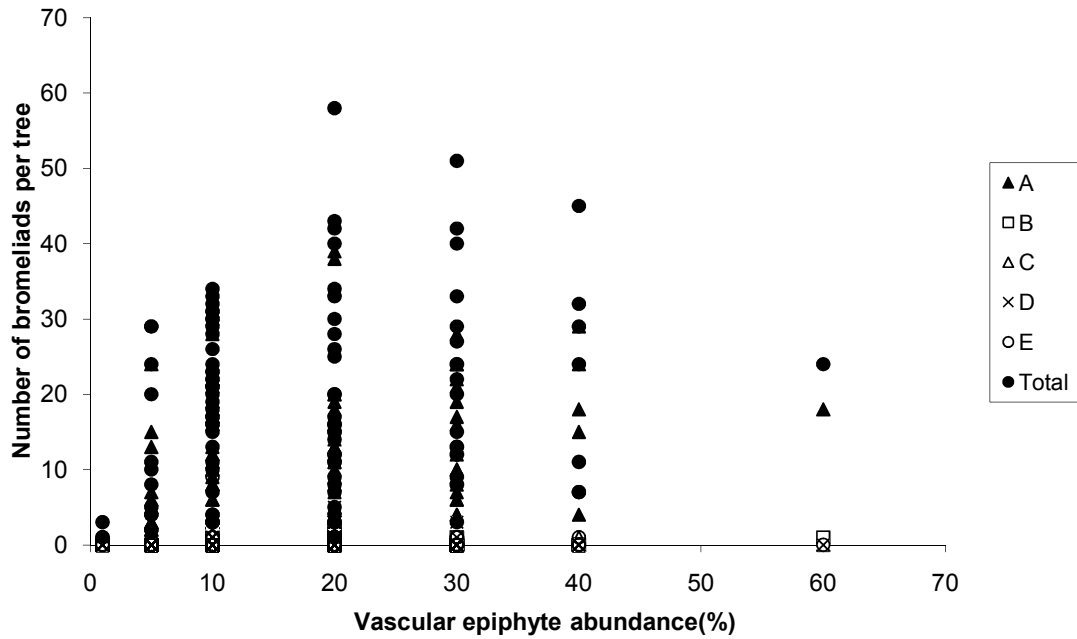
**Table 3. Correlation values between bromeliad abundance and the abundance of other vascular and non-vascular epiphytes. Values are given for bivariate Pearson correlations and for partial correlations controlling for phorophyte DBH and height**

Bromeliad species	Pearson correlations		Partial correlations controlling for tree DBH		Partial correlations controlling for tree height	
	Vascular epiphytes	Non-vasc. epiphytes	Vascular epiphytes	Non-vasc. epiphytes	Vascular epiphytes	Non-vasc. epiphytes
<i>Guzmania jaramilloi</i>	<b>r= 0.24 P=0.014</b>	r= 0.07 P=0.481	<b>r= 0.31 P=0.001</b>	r= 0.15 P=0.121	<b>r= 0.27 P=0.005</b>	r= 0.12 P=0.209
<i>Guzmania testudinis</i>	r= 0.16 P=0.111	r=-0.08 P=0.398	r= 0.17 P=0.081	r=-0.08 P=0.428	r= 0.16 P=0.096	r=-0.08 P=0.417
<i>Pitcairnia ferrellingramiae</i>	r=-0.08 P=0.434	r=-0.03 P=0.700	r=-0.08 P=0.414	r=-0.04 P=0.690	r=-0.06 P=0.525	r=-0.07 P=0.480
<i>Pitcairnia nigra</i>	r=-0.06 P=0.536	r=-0.11 P=0.272	r=-0.07 P=0.448	r=-0.13 P=0.183	r=-0.05 P=0.605	r=-0.09 P=0.337
<i>Tillandsia sp.</i>	r= 0.08 P=0.417	r= 0.07 P=0.463	r= 0.09 P=0.359	r= 0.09 P=0.382	r= 0.09 P=0.356	r= 0.09 P=0.344
ALL	<b>r= 0.26 P=0.008</b>	r= 0.02 P=0.836	<b>r= 0.33 P=0.001</b>	r= 0.10 P=0.293	<b>r= 0.30 P=0.002</b>	r= 0.10 P=0.364



**Fig. 2. The relationship between tree crown height from the ground and the abundance of bromeliads**

Key A = *Guzmania jaramilloi*; B= *Guzmania testudinis*; C= *Pitcairnia ferrellingramiae*; D= *Pitcairnia nigra*; E= *Tillandsia sp*



**Fig. 3. The relationship between the abundance of other vascular epiphytes and the abundance of bromeliads.**

Key A = *Guzmania jaramilloi*; B= *Guzmania testudinis*; C= *Pitcairnia ferrellingramiae*; D= *Pitcairnia nigra*; E= *Tillandsia sp*

### 3.2 Discussion

Current research on a range of epiphyte species has produced varied findings but suggests that the abundance of particular epiphytes may be affected by phorophyte family, phorophyte size and by the abundance of other epiphytes [12]. Overall we found that tree size is the crucial determinant of abundance of bromeliads, not tree identity, and that irrespective of tree size, the abundance of bromeliads is greatest when there is a high abundance of other vascular epiphytes. In terms of the effect of tree size, our findings contradict with the overall findings of other research [9,10] who report evidence of phorophyte specificity in epiphytes such as orchids, bryophytes and lichens. A study on the epiphytic bromeliad, *Tillandsia usneoides*, and the epiphytic fern, *Polypodium polypodioides* concluded that they were clearly associated with specific phorophytes [12]. Strong patterns of phorophyte preference have also been reported amongst the bromeliads *Guzmania monostachya* and *Werauhia (Verauchia) gladioliflora* in Costa Rica [24]. However, this research was conducted in a very different forest type (forest plantations), rendering direct comparison difficult.

Our results showing no phorophyte specificity agree with those of previous researches [15,16,17]. In comparing results of this study with those of other studies, we acknowledge that previous studies have identified phorophytes to species level whilst we examined the effects at the level of tree family and that factors such as growth rate, mortality and structural stability are likely to vary between different species of the same family and even different populations of species [25]. Having said this, we think it is possible to draw some comparisons with other studies. Although not statistically significant, our research found that, overall, trees of the family Clusiaceae hosted the greater abundance of epiphytic bromeliads and that Moraceae hosted the lowest. Research on a number of species within these families have found that Clusiaceae were characterised by their slow to intermediate growth rates [26] whilst Moraceae were characterised by their comparatively rapid growth rates [27]. Members of the group found to host intermediate abundance of epiphytic bromeliads in our study, the Burseraceae, have been reported as having smooth bark [16], fragrant resin [28], long life span and comparative slow growth rates [27]. Finally, trees with high growth rates and short life spans such as *Cecropia obtusifolia* Bertol. have been observed to have a

low abundance of epiphytes in Veracruz, Mexico [29]; the authors attributed this in part to low wood density and to hollow trunks and branches resulting in reduced phorophyte-epiphyte stability.

The positive relationship found in our study between phorophyte size and the abundance of epiphytic bromeliads, supports previous studies of epiphytic bromeliads and other groups of epiphytes. For example findings from one study [30] suggest that trunk diameter is indicative of approximate tree age and that larger, older trees host larger numbers of vascular epiphytes while other research reports that: phorophytes with larger trunk diameters were found to host larger numbers of epiphytic orchids [31]; epiphyte bromeliad abundance was positively related to phorophyte surface area [24] and that epiphytic bromeliads in secondary and mature, premontane forests in Costa Rica occurred more frequently on larger phorophytes [23]. One study [15] also report that vascular epiphytes in Tintal, Mexico, tended towards phorophytes of larger diameters, with the exception of most *Tillandsia* species which appeared to be biased towards smaller phorophytes. Our results did not find this negative relationship for the specific species of *Tillandsia* analysed here. Several hypotheses can be suggested for why there may be a causal relationship for our finding of a greater abundance of epiphytes on larger trees. For example, larger trees are often older trees may have a greater diversity of microsites for epiphyte colonization [31] (due to, for example, hollows caused by physiological changes and cumulative exposure to disease and injury). Also older trees can have higher diversity of epiphytes as they have been available for longer for epiphytes to complete their life cycles [31] and can contribute important habitat patches in epiphyte meta-population dynamics, particularly where epiphyte dispersal rates are limited [32].

Our finding that bromeliad abundance was unaffected by the abundance of non-vascular epiphytes contrasts with other research [33] that concludes that the presence of non-vascular epiphytes help to facilitate the establishment of epiphytic bromeliads. The mechanism behind the facilitation effect is considered to be that non-vascular epiphytes retain higher levels of nutrients and humidity than bare phorophyte surfaces [21,33]. In general, such studies have found that early colonisers, such as mosses and lichens, facilitate the formation of a layer of organic matter which serves as a more effective

substrate for vascular epiphytes than bare bark. These colonisers provide a substrate for water retention, mineral accumulation and physical 'anchoring' for mid-late successional communities such as epiphytic bromeliads. However, it should be noted that detailed research involving direct experimental manipulation of plant communities [34] supports the hypothesis that differences in seed dispersal and stochastic events also play major roles in determining epiphyte community assembly.

Overall, our results support previous work that finds little evidence to suggest direct competition in epiphyte communities [30]. However, the quadratic curve relationship between bromeliad abundance and vascular epiphyte abundance may indicate that the bromeliads studied have only moderate competitive strengths and are mid-successional species. Our finding that the abundance of bromeliads increases with increased abundance of other vascular epiphytes, at least at low and medium abundances, supports other research findings [21] which suggest that the abundance and diversity of a mature epiphyte community may be a result of a facilitation in an autogenic succession, where the establishment of vascular epiphytes further provides suitable habitat for a other vascular epiphyte species.

#### 4. CONCLUSION

In conclusion our results indicate that larger trees have more bromeliad abundance and diversity per unit of tree trunk surface area in all three tree families studied irrespective the abundance of other vascular and non-vascular epiphytes growing on the phorophyte tree. We recommend that further research is needed to understand how species interactions within epiphyte communities drive epiphyte community assembly, dynamics and diversity.

#### COMPETING INTERESTS

Authors have declared that no competing interests exist.

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