Physical factors influencing macro-invertebrate assemblages in epiphytic bromeliads in the rainforest of Belize.

Joaquín Urrutia Panizzo

Norwegian University of Life Sciences
Department of International Environment and Development Studies, Noragric
Master Thesis 60 credits 2011

panizzo@gmail.com

Noragric
Department of International Environment and Development Studies
P.O. Box 5003
N-1432 Ås
Norway
Tel.: +47 64 96 52 00
Fax: +47 64 96 52 01
Internet: http://www.umb.no/noragric

Table of contents

– **It is the epiphytes that tell you you're in a rain forest.**

(Forsyth & Miyata)

Abstract

Epiphytic bromeliads from the genus *Aechmea* are found on many different tree species in the tropics. These bromeliads have evolved water storage tanks where they are able to host many different macro-invertebrate species. The aim of the present study was to assess if six physical variables: i) tree height, ii) tree width, iii) bromeliad weight, iv) bromeliad longest leaf length, v) bromeliad temperature and vi) bromeliad position, have an effect on macro-invertebrate assemblages in *Aechmea* bromeliads found on the canopy of the endangered Fiddlewood tree (*Vitex gaumeri*). Twenty-five *Aechmea* bromeliads from 15 Fiddlewood trees were collected, and a total of 136 morpho-species where recorded. A sample-rarefaction curve showed that new species are expected to be added with increased sampling effort. Results of backward stepwise regression examining aspects of physical variables affecting morpho-species richness showed that bromeliad weight was the only variable that yielded significant results ($P = 0.005$, $R^2 = 29.77$). Additionally, results from a non-metric multi-dimensional scaling (MDS) ordination shows that each bromeliad sampled contained very dissimilar faunal assemblages in terms of composition and abundance. Results are consistent with other studies showing that weight is a significant predictor of macro-invertebrate richness. I conclude that the importance of these plants and their associated animal communities must not be underestimated. Further research on epiphytic communities may bring increased insights on potential effects of climate change on tropical ecosystems and may prove useful for the enhancement of forest management strategies.

Resumen

Bromelias epifíticas del género *Aechmea* se encuentran en muchas especies diferentes de árboles en los trópicos. Estas bromelias han desarrollado tanques de almacenamiento de agua donde pueden alojar muchas especies diferentes de macro-invertebrados. El objetivo del presente estudio fue evaluar si seis variables físicas: i) la altura del árbol, ii) el diámetro del árbol, iii) el peso de las bromelias, iv) longitud de la hoja más larga, v) la temperatura de las bromelias y vi) la posición de las bromelias, tienen un efecto sobre conjuntos de macro-invertebrados en bromelias del género *Aechmea* que se encuentran en las copas de los árboles "ya ´ axnik" (*Vitex gaumeri;* especie en peligro de extinción). Veinticinco bromelias del género *Aechmea* fueron recolectadas de 15 árboles *Vitex*, y un total de 136 morfo-especies de macro-invertebrados fueron registradas. Una curva de rarefacción mostró que la aparición de nuevas especies de macro-invertebrados es esperada con un incremento en el muestreo. Los resultados de una regresión lineal múltiple examinando las variables físicas que afectan a la riqueza de morfo-especies mostraron que el peso de las bromelias fue la única variable que produjo resultados significativos (p= 0,005, R^2= 29.77). Además, los resultados de un escalamiento multidimensional (EMD) muestran que cada bromelia presenta agrupaciones de animales muy diferentes en términos de composición y abundancia. Los resultados son consistentes con otros estudios que muestran que el peso es un predictor significativo de la riqueza de macro-invertebrados. Mi conclusión es que la importancia de estas plantas y sus correspondientes comunidades de animales no debe ser subestimada. Estudios posteriores sobre las comunidades epifíticas pueden proveer un mejor entendimiento sobre los efectos potenciales del cambio climático en los ecosistemas tropicales y pueden ser útiles para la mejora de las estrategias de manejo forestal.

1. Introduction

1.1. *Study background*

Forest canopies have enormous importance in the overall functioning of forest ecosystems (Lowman & Moffett 1993; Pypker et al. 2005). High structural complexity, high species diversity, and pronounced fluctuations in microclimate and resource availability separate them from forest interiors (Winkler & Preleuthner 2001). However, despite their importance, canopies have until recently been largely neglected by researchers (Barker & Pinard 2001) – primarily due to the difficulty of accessing these systems.

The principal constraints to research specifically imposed by limitations in canopy access are problems associated with the choice of site or study species, achieving adequate replication, avoiding disturbance to the subject being studied, and working in a heterogeneous, three-dimensional, environment (Barker & Pinard 2001). However, several exciting and innovative canopy access tools have been designed over the past two decades that have facilitated our understanding of canopy fauna and flora (Lowman 2001).

One of the most striking features of forests in the wetter tropics is the profusion of smaller vascular plants that festoon the trees (Kelly 1985). Epiphytes are plants that live on larger plants utilizing them solely for structural purposes. Epiphytes represent 10% of the global plant species (Nieder et al. 2001) and they are almost exclusively found in tropical forests (Forsyth & Miyata 1985). Vascular epiphytes have been the subject of intense research in tropical forests; one family in particular, the Bromeliaceae, has been the subject of much research (Richardson 1999; Benzing 2000; Araújo et al. 2007; Jabiol et al. 2009) due to their particular chemical and morphological adaptations that allow them to thrive in the low light conditions of the canopy layers, and even become a hotspot for macro-invertebrate life.

The Bromeliaceae family comprise >2600 species and 56 genera in a great variety of habitats, from granite outcrops, coastal dune fields, tropical rainforests and high altitude cloud forests (Balke et al. 2008). Epiphytic bromeliads account for more than half of the species in 26 genera (Benzing 2000). In order to even out moisture availability in the same way that soil does, some epiphytes have turned into water-storage tanks. Tank bromeliads have evolved into a clumplike shape, with long, robust leaves that funnel toward a central stem (Figure 2A). Where these long leaves converge, their bases merge to form a water tank. Some bromeliad tanks may store as much as 8 litres of water (Forsyth & Miyata 1985). Such a pitcher-like water reservoir is called a Phytotelm (plural Phytotelmata), from the greek *phyton* + *telm*= plant + pond (Maguire 1971).

The greatest abundance and diversity of tank bromeliads can be found in the wet tropics. Epiphytic bromeliads provide shelter, water, resources, and nutrients for a broad range of macro-invertebrate organisms (Richardson 1999). The importance of canopy dwelling flora as a sink of water to the rainforest ecosystem has been recognized by Hölscher (2004).

In fact, several studies have shown that a rich variety of life can be found in epiphytic bromeliads (Richardson 1999; Araújo et al. 2007; Jabiol et al. 2009). Some organisms may only spend a portion of their life inside a bromeliad and some may just venture in them to look for food or shelter. Yet others, such as the Jamaican bromeliad crab *Metopaulias depressus* studied by Diesel (1992), spend their entire life cycle inside an epiphyte´s phytotelm.

However, in an extensive review of epiphyte physiological ecology, Zotz & Hietz (2001) concluded that our understanding of epiphyte biology is highly biased. Firstly there is a taxonomical bias, with most research on epiphyte physiology focusing on very few groups, particularly bromeliads, the genus *Clausia* and, to a lesser extent, orchids. Secondly, plants occurring at extreme sites in the periphery of the forest canopy were much more likely to be studied than those in the more mesic mid- and understory. The authors also stress the significance of studying the importance of physical abiotic factors affecting epiphytes.

Many studies have focused on the relationships between epiphytic bromeliads and macro-invertebrate communities (Richardson 1999; Armbruster et al. 2002; Araújo et al. 2007; Balke et al. 2008; Jabiol et al 2009; Serramo et al. 2009). Most of these studies sample plants regardless of its host tree with only a few relating the sampled bromeliads to a specific tree species (Zotz 1997; Araújo et al. 2007). Additionally, height gradients are often ignored, with the majority of studies collecting samples from a height gradient that spans from ground level to a "hands reach" height (Richardson 1999; Armbruster et al. 2002; Araújo et al. 2007; Jabiol et al 2009; Serramo et al. 2009). Furthermore, the most common abiotic factors considered to influence macro-invertebrate assemblage composition are mostly restricted to the effects of water content (Jabiol et al 2009; Serramo et al. 2009) and bromeliad size (Richardson 1999; Araújo et al. 2007).

Just a few published studies have taken into account physical factors such as bromeliad height from the ground as an influence on macro-invertebrate assemblages (Armbruster et al. 2002). This is problematic, since distribution patterns of vascular epiphytes can vary in at least two ways. Horizontally they can differ in terms of host species and forest types, and vertically they vary from the tree base to the top of the canopy (ter Steege & Cornelissen 1989). Thus, the number and type of organisms that inhabit, or come in contact with, these plants may also be affected by their physical distribution.

1.2. *Study aim*

In the current study I try to redress some of the shortfalls outlined above. The aim of the current study was to access the entire height gradients in the canopy to sample epiphytic bromeliads of the genus *Aechmea* associated with a single tree species – the endangered Fiddlewood tree (*Vitex gaumeri)*. Specifically I aimed to describe the fauna associated with these bromeliads and to determine if macro-invertebrate species richness was significantly affected by the following physical variables: i) tree height, ii) tree width, iii) bromeliad weight, iv) bromeliad longest leaf length, v) bromeliad temperature and vi) bromeliad position.

2. Study species

The genus *Aechmea* in the bromeliad family contains >255 species (Luther 2008). Many plants in this genus are epiphytes; some *Aechmea* species are epiphytes of ant-nest gardens (Smith et al. 2004). Epiphytic bromeliads from the genus *Aechmea* live on several different tree species in the neotropical forest of Belize. However, the aim of this study is focused on determining the species richness of macro-invertebrate fauna found in the bromeliads living on Fiddlewood trees (*Vitex gaumeri*). The Fiddlewood, also known as Walking lady has a habitat restricted to southern México, Belize, Guatemala and Honduras. As of 1998, The Fiddlewood tree has been listed as an endangered species by the IUCN red list of threatened species (2010). *Vitex gaumeri* is one of the most abundant trees in the tropical forests of the Yucatan peninsula where it has been exploited by humans since the Mayan era, and still remains one of the most logged trees in the region (Rico-Gray et al. 1991; Gutiérrez-Granados et al. 2011).

3. Materials and methods

3.1. Study site

The present study was carried out at Las Cuevas Research Station (Figure 1), a research facility located in the Chiquibul forest reserve in Belize (16Q 293419 1848510). The Chiquibul forest of Belize lies within La Selva Maya, a unique geographic region containing the largest remaining intact tropical rainforest in Central America. The reserve is approximately 1,775 km^2 and situated roughly 500masl. The Las Cuevas Research Station is the only permanent settlement in the forest. Rainfall averages about 1,500mm per year, with the rainy season from June to January (Kelly 2003). The vegetation is comprised by a mosaic of deciduous semi-evergreen, deciduous seasonal forest, and stands of pine (*Pinus sp.)* in the northern sector (Wright et al. 1959).

Fig. 1. Location of Las Cuevas Research Station in Belize, Central America

3.2. Sampling

By restricting the sampling of *Aechmea* bromeliads to a single tree species, I expect to eliminate tree species as a variable affecting the presence or absence of macro-invertebrate species inhabiting the bromeliads. Identification of Fiddlewood individuals carrying *Aechmea* was undertaken by direct observation along two main trails radiating from the research facility. A total of 18 individuals were found; all of them along a single trail of approximately 7km. Only 15 trees were deemed accessible. Accessibility was determined by ease of reach from the trail and if physical conditions allowed climbing the tree safely.

The position of the accessible Fiddlewood trees was recorded using a Garmin 60CSX GPS device. The Universal Transverse Mercator system (UTM) was chosen to mark tree position because it allows placing the points in a quadrant, making it easier to represent the plot area on a mapped grid. Subsequently, the approximate height of each tree was determined using a Nikon laser range finder pointed from the base to the highest available branch. Tree circumference at breast height was also recorded using a 30m measuring tape.

Collection of bromeliads was carried out in June 2010 between 09:00hrs and 17:00hrs; collection outside that time frame was avoided to be able to obtain more consistent temperature readings. To collect the *Aechmea* individuals from the canopy, tree-climbing techniques were necessary. Single and double rope techniques were used to access different levels of the canopy depending on the height of the trees and the bromeliad position. Collection was carried out by up to two climbers at a time depending of the complexity of the canopy structure (Figure 2B and 2C).

When a bromeliad individual was reached and before it was detached from the tree, a temperature reading was taken from the plant core by inserting an electronic probe HANNA HI 93510N thermistor thermometer. Additionally, the height of the bromeliad from the ground (bromeliad position) was measured with a 30m measuring tape from the base of the bromeliad in a vertical line straight to the ground (Figure 2D).

Subsequently, the bromeliad was tied with a rope, closing the leaves to prevent fauna from leaving the plant (Figure 3). Although most of the inhabitants would seek refuge inside the plant - a behaviour also described by Richardson (1999).

After the plant was secured, it was sawn from the lowest point of its base. Once detached, the plant was slowly lowered down, wrapped in a plastic bag and placed in a plastic box (Figure 3C). Each plant was placed in individual bags and boxes to avoid fauna from moving from plant to plant when there was more than one plant collected at a time. A total of 25 bromeliads were collected from 15 Fiddlewood trees.

Bromeliads were immediately taken to the field laboratory for dissection (Figure 3C) to avoid loss of fauna. In the laboratory, bromeliads were measured from the base of the plant to the end of its longest leaf. This measure is an estimator of plant size (Araújo et al. 2007). The plants were stripped one leaf at a time and plant material was stored while organic content and fauna was kept in a plastic box. Dissected bromeliads and their organic matter were weighed without water. This weight was also used as an estimator of plant size. Macro-invertebrates were stored in vials, preserved in ethanol and classified into morpho-species (Richardson 1999; Araújo et al. 2007; Jabiol et al. 2009) by experts at The University of Manchester, United Kingdom. Macro-invertebrates were classified into morpho-species due to a general lack of knowledge about tropical invertebrate species. Classifying macro-invertebrates into morpho-species has its limitations since some members of the same species appearing in different life stages might be classified as different species. However, these different life stages may play very different ecological roles in these communities, thus making morpho-species a desirable classification for this kind of study (Richardson 1999; Armbruster et al. 2002). Since ants were too numerous to be counted in some plants and because many fled the plant during collection and transportation, I simply assigned a figure of 1 to denote the presence of ant species in a plant (Appendix 1), since the interest of the present study was to asses physical variables affecting species richness and not abundance.

Bromeliad weight and bromeliad length were used as parameters to determine bromeliad size. This method is an approximation and can only roughly estimate the overall size of the plant, because some rather small individuals can present very long leaves, even though their cores and tanks might not have a large capacity. Bromeliad temperature refers to the water temperature in the bromeliad tank where most of the organisms are found. It is therefore desirable to test for a relationship between this important abiotic variable and species richness. Bromeliad position was defined as the distance from the base of the plant to the ground in a straight line; it was tested if plant position throughout the vertical gradient (Figure 4) has an effect on the macro-invertebrate species richness. Tree width and tree height were also considered to test if tree size features have an effect on species richness.

Fig. 2. A) Bromeliad from the genus *Aechmea*. B) Fiddlewood tree (*Vitex gaumeri*) carrying several bromeliads. C) Climbing to reach the sample. D) Taking tree and bromeliad measurements. Photos: Joaquín Urrutia

Fig. 3. A) Salamander found inside a bromeliad. B) Unidentified macro-invertebrate at the base of a bromeliad. C) Preparing the plant for dissection and collection of macro-invertebrates. Photos: Joaquín Urrutia

3.3. Statistical analyses

The adequacy of sampling was assessed by plotting the cumulative frequency of species against sampling effort, a sample-rarefaction curve computed 50 times with EstimateS 8.2 for mac (Colwell et al. 2004). Non-metric multi-dimensional scaling (MDS) ordination was performed to test for similarities between the macro-invertebrate assemblages found in the *Aechmea* bromeliads collected.

Stepwise multiple regression analyses were performed in Minitab 15 Statistical Software (2007) to test for the response of species richness to six physical variables: i) tree height, ii) tree width, iii) bromeliad weight, iv) bromeliad length (length of longest leaf), v) bromeliad temperature and vi) bromeliad position.

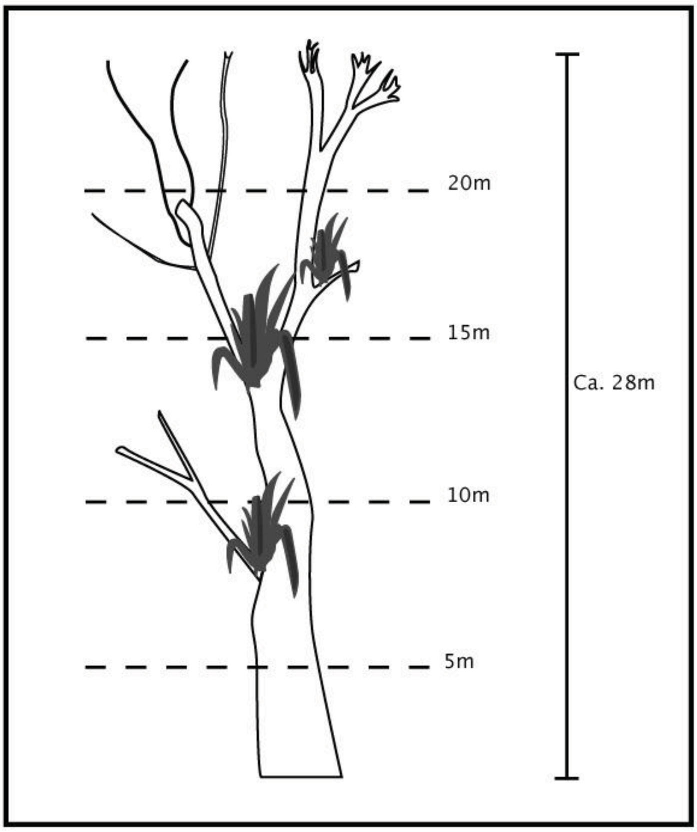

Fig. 4. Illustration of an example of bromeliad position on the tree at the different vertical gradients where bromeliads were found.

4. Results

Twenty-five *Aechmea* bromeliads from 15 Fiddlewood trees were collected. Trees ranged from 16.70m to 29m in height (mean 22.90 ±0.822 SE) and 1.37m to 5.20m in circumference (mean 3.19 ±0.211 SE). Bromeliad position ranged from 3.90m to 16.86m (mean 9.89 ±0.850 SE). Bromeliad longest leaf length spanned from 0.98m to 2.65m (mean 1.88 ±0.0745 SE). The minimum bromeliad weight was 1lbs, while the maximum was 12lbs (mean 4.60 ±0.597 SE). The complete summary of physical variables is found on Table 1.

4.1. *Bromeliad faunal assemblages*

All bromeliads harboured fauna. A total of 136 morphologically different species of organisms were found in the sampled bromeliads (Appendix 1). Grubs were the group with the highest species richness with 34 different morpho-species, followed by spiders with 22 morpho-species.

The bromeliad with the highest species richness contained 23 different morpho-species, while the one with the lowest contained only 4 (mean 12.64 ±1.19 SE). Excluding ants, the highest abundance of individuals in a single plant was 73 and the lowest number of individuals in a plant was five (mean 23.88 ±3.05 SE). Ants presented the highest abundance of all the different morpho-species, followed by isopods and grubs.

Two species of salamanders were the only bromeliad inhabitants that were not macro-invertebrates. They were found residing inside independent bromeliads that stood on different trees. These bromeliads were located in the middle of the recorded height gradient at 8.45m and 9.15m, respectively.

Table 1. Summary of physical data for the 25 sampled bromeliads.

Tree Num	Location Quadrant 16Q	Bromeliad Number	Species Richness	Bromeliad Temp.	Bromeliad Height	Bromeliad Weight	Longest Leaf Length	Tree Width	Tree Height
		18	15	22.9 °C	13.0m	2lbs	1.91m	3.20m	21.0m
1	0288311, 1851136	19	3	23.1 °C	13.0m	2lbs	1.32m		
		10	20	21.7 °C	9.06m	2lbs	1.69m		
2	0288620, 1850925	11	11	21.7 °C	9.15m	5lbs	1.87m	1.37m	24.0m
3	0289142, 1850765	7	23	23.4 °C	16.50m	7lbs	2.21m	3.60m	23.6m
		1	18	25.0 °C	6.0m	4lbs	1.77m	2.60m	17.7m
		2	13	25.0 °C	6.0m	5lbs	2.01m		
4	0289176, 1850788	3	23	24.0 °C	6.10m	12lbs	2.13m		
5	0289214, 1850830	4	17	25.4 °C	7.62m	11lbs	2.07m	3.14m	20.0m
		23	6	25.6 °C	12.70m	6lbs	2.17m	3.65m	26.0m
6	0289214, 1850830	24	13	25.7 °C	12.70m	2lbs	2.11m		
7	0289335, 1850945	14	9	24.3 °C	10.90m	2lbs	0.98m	2.90m	20.0m
		15	5	23.3 °C	3.90m	1lbs	1.63m	2.40m	28.4m
8	0289804, 1851093	16	5	24.2 °C	3.90m	3lbs	1.66m		
		5	14	25.0 °C	5.25m	8lbs	2.03m	2.90m	18.5m
9	0289849, 1851099	6	12	25.5 °C	5.25m	5lbs	1.95m		
10	0289895, 1851124	25	9	24.7 °C	8.45m	7lbs	2.56m	3.94m	26.0m
11	0290130, 1851215	8	13	24.0 °C	7.60m	6lbs	2.20m	1.41m	16.7m
		9	12	25.1°C	14.0m	3lbs	1.26m		
		12	20	24.2 °C	14.6m	4lbs	1.93m		
12	0290237, 1851200	13	15	24.2 °C	14.6m	5lbs	1.84m	3.57m	25.4m
13	0290763, 1851614	17	6	24.3°C	7.45m	2lbs	1.77m	5.30m	25.7m
	0290989, 1851741	21	20	25.9°C	16.86m	8lbs	2.65m		
14		22	4	24.8°C	16.86m	2lbs	1.88m	5.20m	29.0m
15	0290466, 1851385	20	10	26.5°C	5.90m	1lbs	1.57m	3.60m	17.4m

The slope of the rarefaction curve declined as sample sizes increased, but did not approach an asymptote (Figure 5). New species are therefore expected to be added with increased sampling effort. This is supported by the MDS ordination, which shows that each bromeliad sampled contained very dissimilar faunal assemblages in terms of composition and abundance, represented by the relatively wide scattering of samples in ordination space (Figure 6).

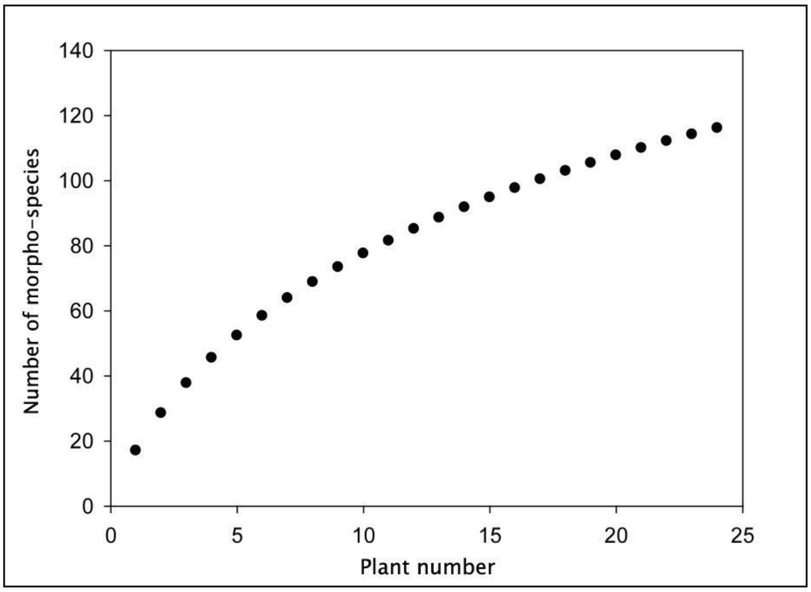

Fig. 5. Cumulative total of morpho-species collected as a function of bromeliad individuals in the sample.

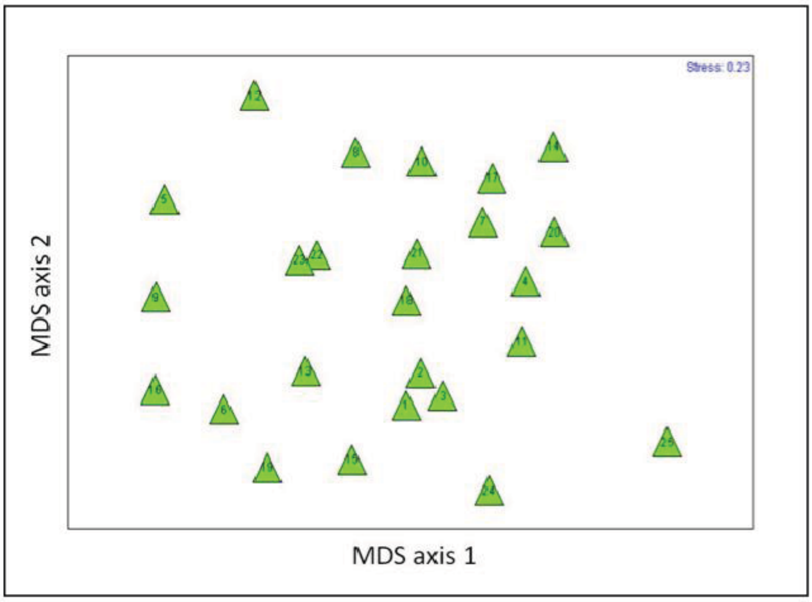

Fig. 6. Non-metric multi-dimensional scaling (MDS) ordination of the macro-invertebrate fauna in *Aechmea* bromeliads in the Chiquibul forest reserve. Samples are plotted based on species composition and abundance. Numbers represent bromeliad number in Table 1 and Appendix 1.

4.2. *Relationship between species richness and physical variables*

Results of backward stepwise regression examining aspects of physical variables affecting morpho-species richness showed that bromeliad weight was the only variable that yielded significant results (P= 0.005, R^2= 29.77; Figure 7B). The other variables contributed little or no explanatory power of morpho-species richness in sampled bromeliads, since bromeliad weight was the only variable retained in the model (Figure 7A and 7C-F).

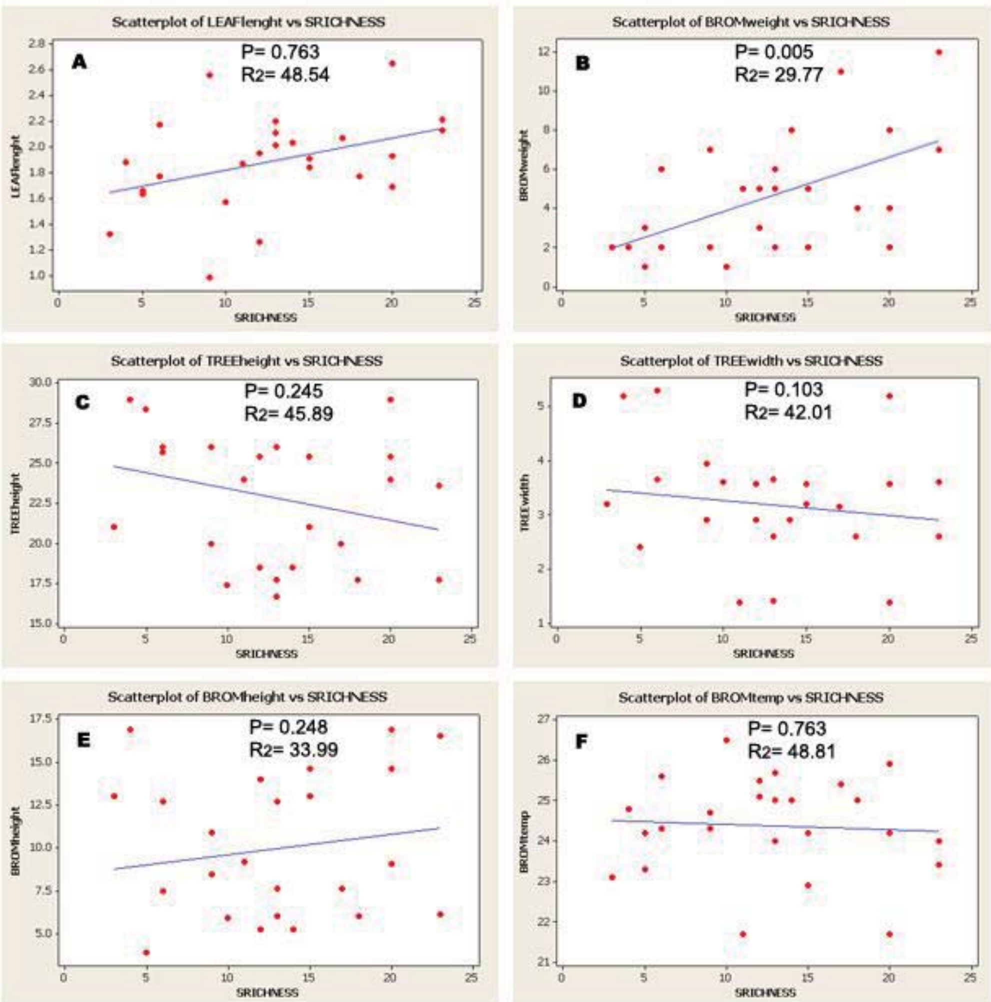

Fig. 7. Relationship between species richness and: A) Leaf length, B) Bromeliad weight C) Tree height, D) Tree width, E) Bromeliad height, F) Bromeliad temperature.

5. Discussion

Overcoming the obstacles of sampling organisms that reside in the complexity of canopy systems is still a challenge. Despite the advancement in canopy access tools, experimental design for sampling epiphytes still does not follow a general protocol. Some studies only sample plants that are found at "hands reach" (Richardson 1999; Armbruster et al. 2002; Araújo et al. 2007). In other studies, climbing techniques were utilized to obtain samples, but some plants that were found lying on the ground were also included (Blüthgen et al. 2000). The latter sampling method may increase the sample, but undermines the accuracy of the organismal community found inside the plants. In the present study, rope climbing techniques were utilized to sample bromeliads and I tried to standardise sampling by sampling bromeliads across the height gradient (Figure 4), recording their exact position and other physical data and restricting sampling to a single tree species.

5.1. *Bromeliad faunal assemblages*

The obtained number of macro-invertebrate morpho-species is comparable with that obtained in other studies. Jabiol et al. (2009), found 44 invertebrate morpho-species in a much larger sample of 158 bromeliads. Additionally, Richardson (1999) found a lowest sample of ca. 85 morpho-species and a highest of ca. 200 in groups of 20 bromeliads for different forest types in different sampling years. Nevertheless, the accumulation curve presented in this study (Figure 5) did not reach an asymptote, and therefore suggests that further sampling is necessary. However, it did not climb as steeply as the accumulation curves in the study by Armbruster et al. (2002) despite their sample reaching ca. 200 bromeliad individuals. However, the Yasuní reserve in Ecuador, where the latter study was carried out, is a region with one of the highest plant and invertebrate diversity in the world (Valencia 1994; DeVries 1999), which may explain why the accumulation curve is so steep even at such a large number of samples. The results in the present study show a slight settling tendency, which suggests that sampling effort does not need to increase significantly for the curve to reach a plateau. The above trend is also consistent with the general decrease in species richness seen along the latitudinal gradient from equatorial to polar regions (e.g. Rohde 1992; Chown and Gaston 2000).

5.2. *Relationship between species richness and physical variables*

This study aimed strictly to assess the effect that physical variables have over macro-invertebrate assemblages in epiphytic bromeliads - especially those that have been considered the least in other studies (e.g. bromeliad position). Bromeliad weight (an estimator of plant size) was the best predictor for species richness. This is consistent with other studies, which have found a significant correlation between bromeliad size and macro-invertebrate species richness, where water volume and detritus mass were of particular significance (Armbruster et al. 2002). My results are therefore probably attributed to the fact that in a bigger plant there is more room for water and litter, which creates a suitable environment for a larger amount of macro-invertebrates.

Other physical variables were non-significant. Physical variables from the host tree (height and width) therefore appear to have no effect on species richness. This suggests that bromeliad characteristics are those that could have an effect on species richness and that macro-invertebrates are not affected by tree features. Bromeliad position shows a slight positive trend with some of the highest plants presenting elevated species richness and many of the plants in a medium height gradient with a moderate amount of species. *In situ* observations in earlier studies demonstrate that epiphytes exhibit a clear vertical zonation within the host tree with few species shared between the tree crown and the trunk base (e.g. Jarman & Kantvilas 1995). However, the MDS in the current study suggests that species composition and abundance can be very distinct across all the bromeliads sampled independent of vertical differences, which may explain the non-significant results found here. In any case, the above trends are important given that some species of macro-invertebrates are exclusive to certain bromeliad species (Diesel 1992). Furthermore, the rare presence of other animal groups like salamanders – which have also been recorded in other studies (Jiménez-Centeno 1994; Richardson 1999) – may suggest a predator specialization to these habitats.

Macro-invertebrate richness appears to be concentrated at a temperature range of 23ºC-26ºC. A reason for macro-invertebrates to avoid the warmest plants could be due to lower rates of evaporation in cooler plants. Bromeliad temperature was expected to rise at increased heights due to elevated sun exposure; still there is not a clear positive tendency in this data to link height and temperature (Figure 8). This pattern is perhaps explained by canopy structure and emergent trees affecting the amount of sunlight that is received, generating microclimates that make temperature uneven across the height gradient.

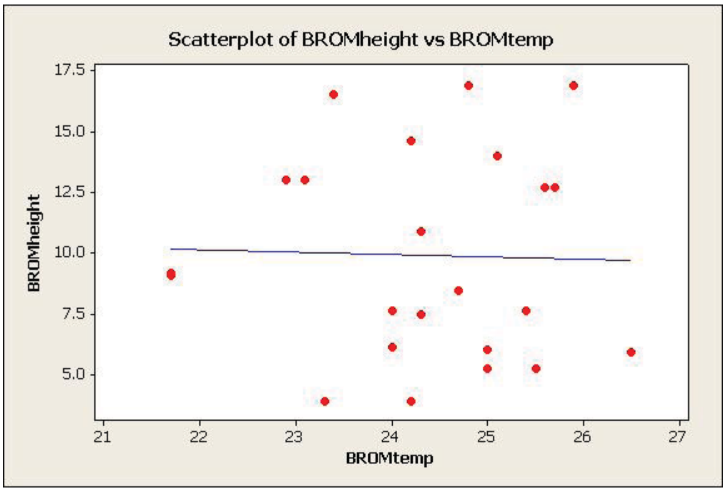

Fig. 8. Relationship between bromeliad position and bromeliad temperature (P=0.905).

5.3. *Implications for conservation and climate change*

Studying and understanding patterns of community structure still remains an important goal for ecological studies due to their implications for the conservation of biodiversity (Armbruster et al. 2002). Policy makers need reliable and substantial scientific evidence to take action on reducing the rate of biodiversity destruction.

Tank bromeliads are important for forest ecosystem functions. They are a water sinks in the forest canopy and may therefore be of great importance for diverse ecosystem proceses and invertebrate populations (Holz et al. 2002). Epiphytic bromeliads create within them unique and complex environments that harbour diverse assemblages of common and rare species of macro-invertebrates.

They are, therefore, true microcosms and not simple phytotelmata as they often have been regarded (Richardson 1999). They may in fact be keystone species that allow many others to thrive – particularly in parts of the tropics where rainfall is highly seasonal.

Furthermore there is a need to consider the effects that removal of host trees can have over epiphytic bromeliads and their macro-invertebrate communities. The fiddlewood tree is an endangered species with a study showing virtually no individuals in 10-year-old logged stands in the Yucatan peninsula (Gutiérrez-Granados et al. 2011). If bigger and more mature plants carry a higher amount of macro-invertebrate species, removing the oldest trees can have a negative effect over bromeliad communities since they rely on the trees for support and bigger trees have the capacity to harbor more and larger plants.

Nadkarni and colleagues (2001) have performed the first field experiments, where epiphytes were moved from one local climatic condition to another. To simulate global climate change, they shifted epiphytes in Costa Rica from moist montane tree crowns to lower valley situations where it is sunnier and drier. As predicted, the result was increased mortality of epiphytes and slower growth. This suggests that these plants may be valuable indicators of climate change. Such new approaches to studies of canopy plants are important, as scientists increasingly play a role in global conservation policies (Lowman 2001).

Conclusion

The current study suggests that bromeliad weight (a variable related to size) has a positive effect on the number of species found in tank bromeliads (Figure 7B). This result is incredibly important for directing future studies, because a review of all available publications on the ecophysiology of vascular epiphytes over the past 80 years revealed that more than 75% of the 153 articles did not specify the size of the study organisms at all (Schmidt et al. 2001). Only around eight percent, provided a clear description of the actual size of the study organisms, e.g., plant height, length of the longest leaf or plant dry mass. In other words, most authors unwittingly treated individuals of unspecified size as representative for a given species (Schmidt et al. 2001).

Additionally the importance of descriptive studies documenting bromeliad communities and their interactions should not be underestimated, Jabiol et al. (2009) states that this is a crucial step towards optimizing the design of new surveys (e.g. biomonitoring) and/or experiments (e.g. hypothesis testing on some targeted insect communities), while improving our understanding of the levels and dynamics of biodiversity in tropical habitats.

Future studies should also clearly take advantage of the newest canopy sampling techniques and consider sampling bromeliads with a detailed size and height gradient. Linking bromeliad size to its life stage may also draw data on which detailed size or maturity of the plant is preferred by macro-invertebrates. Additionally, tree host preference may also be linked to plant size. Such studies could boost forest management schemes and enhance protection for tree species harboring superior canopy diversity.

Appendix 1. Complete list of the 136 morpho-species and their abundance.

Bromeliad Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Morphospecies																									
Grub 1	1	2	2			2		1	2				2		2	1		2	2			1	1		
Grub 2		1	2			1	2											2	3	1				2	
Grub 3			12																	1					
Grub 4																				1					
Grub 5																									1
Grub 6																									
Grub 7										1															
Grub 8																1					1				
Grub 9			1																						
Grub 10																									
Grub 11			2																						
Grub 12	3		8				1						1					3			1	1	1		
Grub 13	1											2													
Grub 14	5	15	13	6	1										3	1					1				
Grub 15																								2	
Grub 16	1		1			2					1							1							
Grub 17	1																	1			1				
Grub 18	1																								
Grub 19	1	1																			1				
Grub 20		1									4														
Grub 21		1	1		1			12										1							
Grub 22				2			2				1														
Grub 23					1								1												
Grub 24					2	1				1	1													1	
Grub 25					2		2	4																	
Grub 26							1											1							
Grub 27							1														1				
Grub 28							1				1														
Grub 29								2																	1
Grub 30								1																	
Grub 31										1															
Grub 32														1											1
Grub 33																						2			
Grub 34																								1	
Myriapod 1			1							1										1				1	
Myriapod 2	1			1																					
Myriapod 3				4										2							1				
Myriapod 4					1							3	1												

Appendix 1. (Continued)

Bromeliad Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Myriapod 5	1		2	2													1								
Myriapod 6												1													
Myriapod 7														1			1								
Myriapod 8															1			1							
Myriapod 9																					2			1	
Pseudoscorpion 1	5	11	11				1	1		1	3		5		4						2			1	2
Pseudoscorpion 2	1											1													
Pseudoscorpion 3							1		1			1													
Cockroach 1	7		1	2						1			1												
Cockroach 2							15		1	3							4		1		4		2	1	
Cockroach 3			4						1			1													
Cockroach 4						1																			
Cockroach 5					1					5															
Cockroach 6										1		1		1											
Cockroach 7																		1							
Cockroach 8																									2
Ant 1																		1*							
Ant 2	1*	1*	1*																		1*				
Ant 3					1*	1*														1*					
Ant 4							1*					1*	1*												
Ant 5							1*																		
Ant 6								1*		1*	1*														
Isopod 1	1	3	4	4			9	2		2	3	1		24			12	7		5	6	2	1		
Isopod 2	1		1									1													
Isopod 3	1						1																	2	
Isopod 4				1								1									2				
Isopod 5									1				9								1				
Isopod 6									1																
Isopod 7												1													
Isopod 8												1													
Snail 1																									
Snail 2	1	3		1																					
Snail 3			1										1												
Snail 4									1																
Worm 1		1			1	1		1									1	1			2				
Worm 2			2										1												
Beetle 1							3			1							1	1		1				3	
Beetle 2		1		1																					
Beetle 3																									
Beetle 4						1																			

Appendix 1. (Continued)

Bromeliad Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Beetle 5							1				2														
Beetle 6																									
Beetle 7									1																
Beetle 8									1			1													
Beetle 9																					1			1	
Beetle 10																									2
Spider 1									1																
Spider 2																				1					
Spider 3																							1		
Spider 4			1																						
Spider 5																									
Spider 6		1		3																					
Spider 7			1																						
Spider 8				1						1													1		
Spider 9				1						1			1	1						3					
Spider 10				1				1				1	1												
Spider 11					2	1			2			1									1				
Spider 12						1																			
Spider 13							2			1		1									1				
Spider 14								1																	
Spider 15										1		1	1	1		1									
Spider 16												1													
Spider 17												1													
Spider 18																									
Spider 19																									
Spider 20																		1							
Spider 21																					1				
Spider 22																								1	
Scorpion 1				1																					
Scorpion 2					1																				
Scorpion 3																									1
Wasp 1																									
Wasp 2					6	6																			
Wasp 3																									
Cricket 1					1																				
Cricket 2			1																						
Cricket 3						1							1												
Cricket 4					2					1															
Cricket 5							1																		
Cricket 6									1																

Appendix 1. (Continued)

Bromeliad Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Cricket 7										1															
Cricket 8										1															
Bug 1			1				1																		
Bug 2				1			1							1											1
Bug 3								1																	
Bug 4											1									1					
Bug 5																1									
Bug 6																		1							
Salamander 1											1			1							1				
Salamander 2																									1
Pupae 1								1																	
Caterpillar 1				1																					
Caterpillar 2																									
Caterpillar 3							1																	1	
Caterpillar 4							1																		
Caterpillar 5							1			5			2												
Caterpillar 6															1										
Caterpillar 7																									
Total Individuals	33	41	73	33	22	18	49	28	14	30	18	22	28	33	11	5	20	24	6	15	31	6	7	18	12
Species Richness	18	13	23	17	14	12	23	13	12	20	11	20	15	9	5	5	6	15	3	10	20	4	6	14	9

*** Denotes presence of ant species**

Acknowledgements

I would like to thank my supervisor Torbjørn Haugaasen whose feedback and insights have been invaluable in the process of completing this study. I would also like to thank Richard Preziosi and the members of the field course in terrestrial and marine biodiversity (Manchester University) for accommodating me in their trip to Belize, without their help this study couldn't have been possible. Moreover, I want to thank: Lisa, Lindsay, Ben and Jacob, the four undergraduate students who made possible the dissection of bromeliads and preliminary identification of morpho-species, as well as for their help while climbing was carried out. Additionally I thank my fellow tree climber Larissa Chambers for all her help.

Furthermore I want to thank my family and friends for supporting me in my decision to come to Norway where I was able to engage on this project, without the help of many of them I wouldn't have been able to reach this point.

References

Araújo V., Melo S., Araújo A., Gomes M., Carneiro M.(2007). Relationship between invertebrate fauna and bromeliad size. *Braz. J. Biol.*, 67(4): 611-617.

Armbruster P., Hutchinson R., Cotgreave P. (2002). Factors influencing community structure in a South american tank bromeliad fauna. *Oikos*, 96: 225-234.

Balke M., Gómez-Zurita J., Ribera I., Viloria A., Zillikens A,Steiner J.,García M., Hendrich L., Vogler A. (2008). Ancient associations of aquatic beetles and tank bromeliads in the Neotropical forest canopy. *PNAS*, 105 (17): 6356-6361.

Barker, M. & Pinard, M. (2001). Forest canopy research: sampling problems, and some solutions. *Plant Ecology,* 153: 23–38.

Benzing, D. (2000). Bromeliaceae: Profile of an Adaptive Radiation. Cambridge Univ Press, Cambridge, UK.

Blüthgen N., Verhaagh M., Blüthgen N. (2000). Ant nests in tank bromeliads – an example of non-specific interaction. *Insectes soc*., 47: 313-316.

Chown, S. & Gaston, K. (2000). Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution* 15: 311-315.

Colwell R., Mao C., Chang J. (2004). Interpolating, extrapolating, and compared incidence-based species accumulation curves. *Ecology,* 85: 2717–2727.

DeVries P., Walla T., Greeney H. (1999). Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biol. J. Linn. Soc.,* 68: 333 – 353.

Diesel, R. (1992). Parental care in an unusual environment: Metopaulias depressus (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads. *Anim Behav.,* 38:561–575.

Forsyth, A. & Miyata, K. (1985). Tropical Nature. *Charles Scribner's Sons*, New York.

Gutiérrez-Granados G., Pérez-Salicrup D., Dirzo R. (2011). Differential diameter-size effects of forest management on tree species richness and community structure: implications for conservation. *Biodiversity and Conservation,* 1-15.

Hölscher D., Köhler L., van Dijk A., Bruijnzeel L. (2004). The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology,* 292: 308-322.

IUCN. (2010). *IUCN Red List of Threatened Species. Version 2010.4*. <http://www.iucnredlist.org>. Downloaded on 01 April 2011.

Jabiol J., Corbara B., Dejean A., Cereghino R. (2009) Structure of aquatic insect communities in tank-bromeliads in an East-Amazonian rainforest in French Guiana. *Forest Ecology and Management*, 257: 351-360.

Jarman, S. & Kantvilas, G. (1995) Epiphytes on an Old Huon Pine Tree (Lagarostrobos-Franklinii) in Tasmanian Rain Forest. *New Zealand Journal of Botany*, 33: 65–78.

Jiménez-Centeno, C. (1994). Utilization of Puya dasylirioides (Bromeliaceae: Pitcairnoidea) as foraging site by Bolitoglossa subpalmata (Plethodontidae: Bolitoglossinii). *Revista de Biología Tropical*, 42 (3): 703-710.

Kelly, D. (1985). Epiphytes and climbers of the Jamaican rain forest: vertical distribution, life forms and life histories. *Journal of Biogeography*, 12: 223-24.

Kelly, M. (2003). Jaguar monitoring in the Chiquibul forest, Belize. *Caribbean Geo*, 13: 19–32.

Lowman, M. & Moffett, M. (1993). The ecology of tropical rain forest canopies. *Trends Ecol. Evol*., 8: 104–107.

Lowman, M. (2001). Plants in the forest canopy: some reflections on current research and future direction. *Plant Ecology,* 153: 39–50.

Luther, H. (2008). An alphabetical list of bromeliad binomials, 11th ed. Bromeliad Society International, Gainesville, Florida, USA.

Maguire, B. (1971). Phytotelemata: biota and community structure determination in plant-held waters. *Annu. Rev. Ecol. Syst*., 2:439-464.

Minitab 15 Statistical Software. (2007). [Computer software]. State College, PA: Minitab, Inc. (www.minitab.com).

Nadkarni, N. (2001). Enhancement of forest canopy research, education, and conservation in the new millennium. *Plant Ecol*., 153: 361–367.

Nieder J., Prosperí J., Michaloud G. (2001). Epiphytes and their contribution to canopy diversity. *Plant Ecology,* 153: 51–63.

Pypker T., Bond B., Link T., Marks D., Unsworth M. (2005). The importance of canopy structure in controlling the interception loss of rainfall: examples from a young and old-growth Douglas-fir forests. *Agric. For. Meteorol*.

Richardson, B. (1999). The Bromeliad microcosm and the assessment of faunal diversity in a neotropical forest. *Biotropica,* 31: 321–336.

Rico-Gray V., Chemas A., Mandujano S. (1991). Uses of tropical deciduous forest species by the Yucatecan Maya. *Agroforestry Systems,* 14:149-161.

Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65: 514–527.

Schmidt G., Stuntz S., Zotz G. (2001). Plant size: an ignored parameter in epiphyte ecophysiology?. *Plant Ecology,* 153: 65-72.

Serramo L., Da Nobrega R., Iglesias R. (2009). Micro-environmental factors and the endemism of bromeliad aquatic fauna. *Hydrobiologia*, 625:151-156.

Smith N., Mori S., Henderson A., Stevenson D., Heald S. (2004). Flowering Plants of The Neotropics. Princeton University Press, Princeton New Jersey.

ter Steege, H. & Cornelissen, J. (1989) Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica*, 21: 331–339.

Valencia R., Balslev H., Miño G. (1994). High tree alpha-diversity in Amazonian Ecuador. *Biodiv. Conser*., 3: 21 – 28.

Winkler, H. & Preleuthner, M. (2001). Behaviour and ecology of birds in tropical rain forest canopies. *Plant Ecology*, 153: 193–202.

Wright A., Romney D., Arbuckle R., Vial E. (1959). *Land in British Honduras, report of the British Honduras Land Use Survey Team. Her Majesty's Stationary Office; Colonial Research Publication* No. 24, London.

Zotz, G. (1997). Substrate use of three epiphytic bromeliads. *Ecography*, 20: 264-270.

Zotz, G. & Hietz, P.(2001). The physiological ecology of vascular epiphytes: current knowledge, open questions. *J. Exp. Bot*., 52(364): 2067.