Colonisation and structure of faunal communities in epiphytic tank bromeliads in Ecuador: An experimental assessment of the roles of water volume and surface area

By

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1.0 ABSTRACT

Several studies have utilised tank bromeliads to assess the factors which influence community composition. It has often been assumed that bromeliad size is an indicator of age, but little consideration has been given to the effects of bromeliad size and age on species composition when age and bromeliad size are separated. In this study in the cloud forests of Ecuador, 522 artificial bromeliads were utilised in two experimental manipulations over a four week period which allowed the effects of reservoir surface area, reservoir volume, and time, upon species richness, abundance, and diversity to be analysed separately. This was achieved using two surface areas and three water volumes. The results indicated that when age is not controlled for, volume has the main positive influence on community composition, and is best explained by species oviposition preferences. However when age is included, detritus mass and productivity appear to best describe the relationships found with species richness and abundance. Oviposition preferences, environmental factors and the occurrence of stochastic events provide better explanations of the similarity of assemblages between each week, while species accumulation was best explained by island biogeographic theory. These results highlight the importance of considering the effects of age in explaining bromeliad community structure, separate to the effects of size, whilst also illustrating that both abiotic and biotic factors are highly influential. It is possible that the results are applicable to all phytotelm habitats.

2.0 INTRODUCTION

2.1 Bromeliads as phytotelmata

The term phytotelmata (Greek = "plant pond") was introduced in 1928 by Varga (cited in Fish 1983, p.2) after noticing how some plants were similar in that they impounded water capable of supporting aquatic fauna. Phytotelmata develop whenever water becomes retained in hollows that form as part of a plants structure (Kitching 2000). The main five types are bromeliad plants, pitcher plants, bamboo internodes, water-filled tree holes, and water collected in the axils of leaves, petals or bracts. In this study, the focus shall be on bromeliads due to the high abundance which occur in the cloud forests of Ecuador. However the conclusions of the study can broadly be related to all phytotelmata habitats, and likewise research of other phytotelmata can be related to this study.

The Bromeliaceae family is the largest and nearly exclusive Neotropical flowering plant family worldwide. The family contains 2,600 species which are thought to originate from a common ancestor dated 20 million years ago (Balke *et al*. 2008). All but one species of bromeliad are known to occur in the tropical regions of the Americas, from central Argentina up to Florida (Kitching 2000); the exception being *Pitcairnea feliciana* in Guinea, West Africa. Of 26 genera, more than half are epiphytic, meaning they attach to another object for support (usually a tree), but derive food and water resources from the atmosphere. The Bromeliaceae family can be split in to three subfamilies; Pitcairnioideae, Tillansioideae and Bromelioideae, with the latter two subfamilies containing species capable of impounding water (Kitching 2000). Such tank bromeliads can be classed as phytotelmata because they retain water in their leaf axils by tightly overlapping them to form watertight hollows. The young inner leaves combine to form a common pool, while the older outer leaves form smaller discrete cavities (Kitching 2000).

Approximately 1000 bromeliad species are estimated to contain phytotelmata (Greeney 2001) which collect litter-fall as well as rainfall, supporting many aquatic organisms by providing spatial refugia, natural breeding sites, and nutrients (Armbruster *et al*. 2002; Araujo *et al*. 2007). It is unsurprising therefore that they have been associated with a highly diverse aquatic fauna of approximately 400 species, inclusive of both insects and amphibians, and many of which rely upon this habitat for survival during either part or all of their life cycles (Balke *et al*. 2008). The presence of isolated aquatic

communites which are held in their waters has resulted in epiphytic tank bromeliads being compared to and studied as islands (Little and Herbert 1996; Trierweiler *et al.* 2005). These island-like, discrete, manageable environments therefore provide the opportunity to study island processes such as species area relationships and colonisation processes, and the effects of these upon the faunal communities (Araujo *et al.* 2007).

2.2 Bromeliads and the Species-Area Relationship

Prior to 1960, it was believed that community structure (species composition) of islands was fixed in ecological time, and only changed if modified by long-term evolutionary processes (Lomolino *et al.* 2006). This paradigm was revolutionised when MacArthur and Wilson first introduced the theory of island biogeography in 1967, applicable to island archipelagos but also to other semi-isolated habitats. One of the patterns the theory was developed to explain is how overall species richness tends to increase with increasing island area (MacArthur and Wilson 1967). Larger islands contain more habitat types containing specialised species restricted to that habitat, as well as having lower extinction rates, allowing them to support higher species richness (Trierweiler *et al.* 2005). In accordance with island biogeographic theory (IBT), it is commonly found that with an increase in bromeliad size, similar increases occur in species diversity and abundance (Richardson 1999). Additionally, larger and therefore older bromeliads naturally hold more water, and studies have found positive relationships between species abundance and water volume (Yanoviak 1999; Araujo *et al.* 2007; Gonzalez 2009), potentially due to greater areas providing a larger space and site for oviposition (Richardson 1999).

Araujo *et al.* (2007) tested the relationship between bromeliad plant size (including variables of water volume, bromeliad height and reservoir diameter) and faunal richness and abundance. Similar to other studies (e.g. Richardson 1999) they found that bromeliad size was important in influencing faunal richness and abundance but noted that larger plants also contained more detritus matter, which may itself influence richness and abundance by providing resources and nutrients. Although not proven, this potentially allows the larger bromeliads to support a greater number of organisms, increasing the likelihood of more species being present. An increased area has also been linked to higher faunal richness in phytotelm communities (Araujo *et al.* 2007). Here, it was attributed to generating increases in habitat complexity, number of microhabitats, spatial distribution of resources, and available oviposition sites (sites

suitable for laying eggs), hence allowing greater coexistence between more species with differing requirements (Araujo *et al.* 2007). Leaf litter has also been found to be particularly important in structuring communities as it can change oxygen saturation levels, conductivity, and abundance of food when it decomposes in such small contained habitats (Burdett and Watts 2009). The reasoning for abundance of food being so important in particular follows the "More Individuals Hypothesis", a theory suggesting that sites which are more productive can support a higher total abundance, of which species richness is an increasing function (Srivastava and Lawton 1998). Although there is general consensus for species richness and abundance to increase with phytotelm size, many underlying causes have been documented. By accounting for a factor such as age (with which detritus mass, habitat complexity and water volume naturally increase), it may be possible to further our understanding of some of the underlying relationships.

2.3 Bromeliads and Colonisation

Another main process of island biographic theory is turnover, documented when it was realised that immigration and extinction are recurrent processes resulting in species turnover as colonists replace extirpated species. Colonisation is a key process in this and the colonisation of organisms to a bromeliad, as like to any island, involves its' dispersal (either active or passive), arrival and establishment (Maguire 1971). The distance travelled and nature of the barriers crossed are particularly influential in determining dispersal rates and colonisation success (Maguire 1971). In terms of dispersal, it is likely that organisms would be able to crawl between bromeliads in the wet tropics due to the high amounts of water in substances such as moss and standing water collected in leaves (Maguire 1971).

Notably, Cresswell (1998) studied the recolonisation of 164 pitcher plants after removal of their infauna over 14 days. He found that pitcher morphology explained 45% of the variation in the accumulation of necromass (drowned animals), and that necromass accumulation rates were correlated positively with pitcher size. Also, the larval inquilines rapidly re-colonised the pitchers after the original infauna was removed, reaching 40% of original abundance within 14 days (Cresswell 1998). Although such studies have been performed looking at the colonisation of pitcher plants using certain species or species groups (Trzcinski *et al.* 2003), they are less applicable when comparing to bromeliads due to the nature of pitcher plants having to re-colonise each year. In contrast, assemblages of bromeliad tanks are not so temporary, and there is

less chance to observe colonisation. For example, Reid and Janetsky (1996) experimentally removed the infauna communities from 10 bromeliads in Jamaica and found many groups took several months to re-establish stable populations. It is important to note that only small amounts of debris had accumulated by the end of their experiment which may have caused stronger competition between arriving individuals or species (Reid and Janetsky 1996). Additionally it appeared that bromeliad size was not accounted for in their study, and Araujo *et al.* (2007) proposed that an interaction between bromeliad height and diameter of the water reservoir may influence colonisation, but this has not been tested to date.

2.4 Experimental Manipulation of Artificial Bromeliads

Yanoviak (1999) and Gonzalez (2009) have both studied phytotelmata by artificially replicating bromeliads tanks using plastic cups. Yanoviak (1999) replicated tree holes and found that species richness and abundance increased with larger hole size; a similar pattern to what is found for real bromeliads as well as real tree holes (Yanoviak 1999). However this species area relationship has not been tested experimentally using replicate bromeliads. An experimental assessment of the relationship between bromeliad size and colonisation (something not previously researched) both incorporating a factor of time and excluding it will allow the effect of age to be seen, a factor not accounted for in any previous studies. Such manipulation of tank bromeliad faunal communities could therefore provide fundamental insights into the underlying factors which influence and govern community composition, and could help to disentangle the relationships and decipher which factors (for example; detritus mass, productivity, habitat complexity, resource distribution, available oviposition sites, food supply) it is more plausible to attribute relationships to.

This study therefore aims to experimentally assess the roles of water volume, water surface area, and age in structuring tank bromeliad faunal communities. This was fulfilled by conducting two separate experiments with the following objectives:
1) to determine the effects of surface area and volume on species composition
2) to account for the factor of time, and assess how surface area and volume affect the colonisation of species and species composition
3) compare the results of the two experiments to find underlying factors in structuring species composition

3.0 MATERIALS AND METHODS

3.1 Site Description

All field work was performed between 30th May and 17th July 2010 at Reserva Las Gralarias (00°00´33"S, 78°44´15"W), in Pichincha Province, Ecuador (Fig. 3.1). Located in the sub-tropics, west of the Andes mountain range, the 1063 acre private reserve consists of primary and secondary cloud forest with some areas of regenerating pasture (RLG 2010). Annual rainfall ranges from 2000 to 3000mm, with mean temperature approximately 18-22.8°C (RLG 2010). Elevation ranges from 1790m to 2370m above sea level and incorporates the range of most epiphytes in Ecuador (Bussman 2001), with phytotelmata occurring in the form of epiphytic bromeliads abundantly throughout the forested areas of the reserve.

Fig. 3.1. A map of Ecuador highlighting the geographical position of the study location in Pichincha Province

3.2 Field Methods

3.2.1 Faunal Sampling

Methods for sampling real bromeliads often involve the destruction of the plant (Armbruster *et al*. 2002; Frank *et al*. 2004), which is not desirable for conservation purposes. Previous studies have used plastic cups as surrogates for bromeliad tanks, finding between 1 and 15 individual organisms per cup after a one month period (Gonzalez 2010). Following this, 522 plastic cups were used as substitutes for real bromeliads and were assembled at 33 stations (Fig. 3.2) in two experimental designs.

Design 1. To assess the effects of water volume and surface area on faunal composition, a set of 6 cups were left out at all stations for 28 days before collection. For both designs a set of six cups comprised two surface areas (A1 (smallest) and A2 (largest)) and three set water volumes (100ml, 200ml and 400ml) (See Appendix A).

Design 2. At 18 stations, four sets of six cups were assembled (this included 18 of the 33 stations used in design 1). A set was collected after 7, 14, 21, and 28 days to compare weekly accumulation rates and species composition between cup sizes. Upon collecting the cups from the stations after 7, 14, and 21 days the set of six was chosen at random. At each station cup were positioned to ensure the same cup sizes were not adjacent at every station.
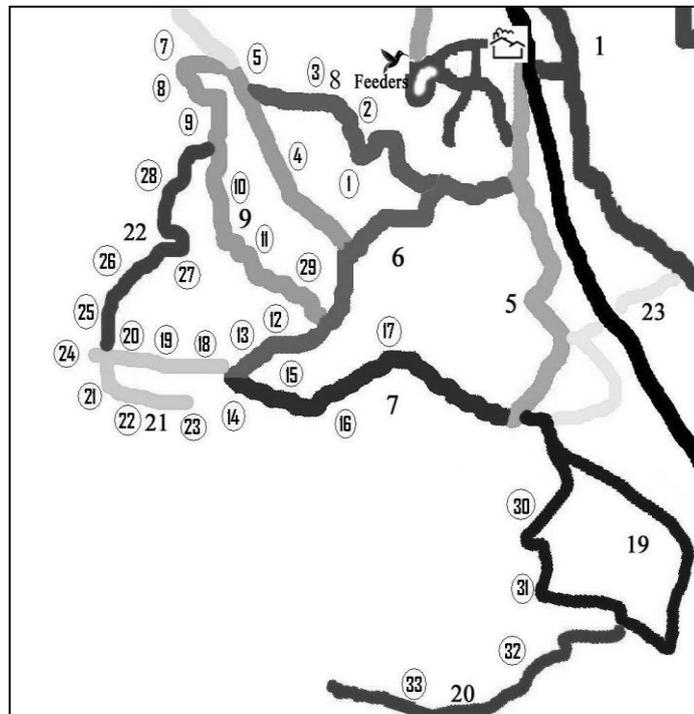
Fig. 3.2. Locations of the 33 stations positioned along existing trails at Reserva Las Gralarias (station numbers are circled)

All cups were positioned within 67m altitudinal range, between 1932m and 1999m, and placed 1m above the ground (Yanoviak 2001). String was used to attach cups to trees going through two opposite drainage holes positioned at the correct heights for experimental volumes (corresponding to 100ml, 200ml and 400ml) (Appendix B). The string rested on the water surface and so created an oviposition site in every cup. The cups were filled with tap water at the start of the experiment and topped up daily thereafter if required, though most were rain fed. They were not placed directly below real bromeliads and ideally would not have been placed within two metres of a bromeliad to ensure that dispersal distance had a more equal effect on colonisation rates per cup (Trierweiler *et al.* 2005). However, this was not possible due to the high abundance of bromeliads in the cloud forest. Finally, cups were painted black on the outside prior to assembling them as this colour has been shown to optimise organism abundance in artificial microcosms (Yanoviak 2001).

Upon collecting cups, they were carefully removed from trees and transported back to a work room in re-sealable ziplock bags to ensure no water was lost. Cups were emptied and thoroughly rinsed with clean water to ensure all invertebrates were obtained. Invertebrates were picked out under 10X magnification in a white tray and preserved in 70% ethanol solution in 64ml airtight plastic containers (Araujo *et al.* 2007). Due to the high abundance of species associated with Neotropical bromeliads (2900 had been described as of 2008 (Frank and Lounibos 2008)), species were classified to morphospecies level following Stork (1987) as adapted by Armbruster *et al.* (2002) using "Encyclopedia of South American aquatic insects" series by Heckman (2001; 2002; 2003; 2006) and "How to know the immature insects" by Chu and Cutkomp (1992) to help identification. Morphospecies were assigned using primary diagnostic features including wing veination, antennal segmentation and structure, overall body form, tarsal structure, mouth part structure and chaeotaxy (the arrangement of setae). The main problem in using morphospecies is misidentification; for example, different life-cycle phases or different sexes of the same species may be classed as different morphospecies. However, Oliver and Beattie (1996) proved morphospecies richness to be a suitable surrogate for species richness when identification by non-specialists was compared to that of specialists. The abundance of each taxonomic unit was also recorded per cup.

3.2.2 Environmental Data

The effect of bromeliad age upon faunal assemblages (larger tanks tend to be found on older, larger bromeliads) is potentially related to debris accumulation and time available for colonisation by organisms (Field, 2010, *pers. comm.*). Wet detritus mass was recorded after organism collection from each cup to measure the influence it had on species assemblages (Trierweiler *et al*. 2005) (dry mass would have been preferred but was not possible due to equipment restraints at the field location). Light intensity was measured using a spherical densiometer at each station to ensure stations were positioned in shaded areas (canopy cover ranged between 82.58% and 92.98% across all stations) to minimise exposure which may reduce species richness and abundance (Montero *et al*. 2010). In measuring canopy cover, as the stations were linear due to restrictions of entering the forest from the trails, four readings were taken along a line through the station and averaged. Finally, altitude was recorded using a handheld GPS (Garmin eTrex H).

3.3 Data Analysis

In order to determine species composition for each cup, species richness (the number of different species (Hill 1973)), number of individuals and two diversity indices (Margalef and Simpson's (1-D)) were calculated using PISCES Species Diversity and Richness v. 3.03 software. Although many different diversity indices exist, these were chosen with care based on their applicability to this study. More than one index was chosen to increase the robustness of the comparisons and to ensure the inclusion of different components of diversity. The Margalef index is easy to calculate and interpret but being a richness measure is sensitive to sample size and the increasing number of rare species as sample size goes up (Richardson 1999). Despite this, species richness measures have been found to discriminate between samples greater than do evenness and dominance measures (Magurran 1988). Shifts in community compositions amongst sites may not be picked up however, and measures of heterogeneity (combining both richness and evenness components of diversity) should also be used (Richardson 1999). Simpson's index (1-D) primarily measures the evenness of the community and is heavily weighted toward the most abundant species in the sample (Magurran 1988). Additionally where accidental species are concerned (e.g. species which are washed into cups from the canopy) and where some species dominate a community, the Simpson's index may provide an improved measure of underlying differences within a community than richness measures (Richardson 1999).

Sorenson's similarity coefficient was used as a beta-diversity measure of overlap between species compositions found in different cup sizes (all replicates were pooled for each cup size) (Yanoviak 2001), and to compare overlap between weeks for each cup size using Community Analysis Package v. 2.15. Sorenson's index gives equal weighting to all species and during an in depth study, it was found to be the best measure of similarity (Smith, cited in Magurran 1988). Species accumulation curves were calculated for the colonisation data by averaging the data from all stations per cup per week. Fifty randomisations were conducted to smooth the curves using PISCES Species Diversity and Richness v. 3.03.

In order to analyse the effects of water volume, surface area and environmental variables on the faunal assemblages, two Generalised Estimating Equations (GEE's) were run in SPSS v. 16.0; one on all the data collected after 28 days (design 1) and another on the data obtained from the colonisation experiment collected after 7, 14, 21 and 28 days (design 2). Species richness, number of individuals, and the two diversity indices were included as the dependent variables. Station was included as a random effect, and area and volume as fixed effects. The covariates were canopy cover, altitude and week (for the colonisation experiment GEE only). Detritus mass was input as a dependent variable and also a covariate in the other GEE's. Interaction terms between area, volume and, where applicable, week, were included in the model. WCM (Working Correlation Matrix) structure was set to exchangeable to allow for sampling effects as some cups were collected from the same station and may therefore be correlated. Species richness and number of individuals were entered as having poisson distribution and a Generalised Linear Model (GLM) was used to test whether the data was a good fit using deviance divided by degrees of freedom. All diversity measures were entered as having a linear distribution with Log 10 or square-root transformation applied where necessary to achieve normality in the residuals. Non-significant terms ($P>.05$) were extracted from the model in order to simplify it, and where interaction terms were significant, a model was also run without any interaction terms to ensure the significance of the main effects.

4.0 RESULTS

A total of 4890 individual organisms of 144 morphospecies were collected over the study period. The organisms included both pre-adult and adult life stages and were comprised of terrestrial and aquatic species. Of the 144 morphospecies in the study, 1 was identified to species, 1 to genus, 22 to family, 105 to order, and 12 only to phylum, while 4 were classified as unknown. Although non-aquatic organisms are sometimes excluded from studies on phytotelmata, they have been found to be associated with each other (Greeney 2001). Therefore they have been included in this study, with the morphospecies identified summarised in Appendix C. Two cups which accumulated no organisms were considered anomalous and removed from the analysis. Additionally one cup from station 26 (size A2 200(ml)) was damaged and not included in the analysis. The morphospecies abundance distribution of the total sample (including data from both experimental designs) is presented in Fig. 4.1. Twenty-two of 144 morphospecies (15%) were represented by a single individual, and 14 (9%) were represented by two individuals.
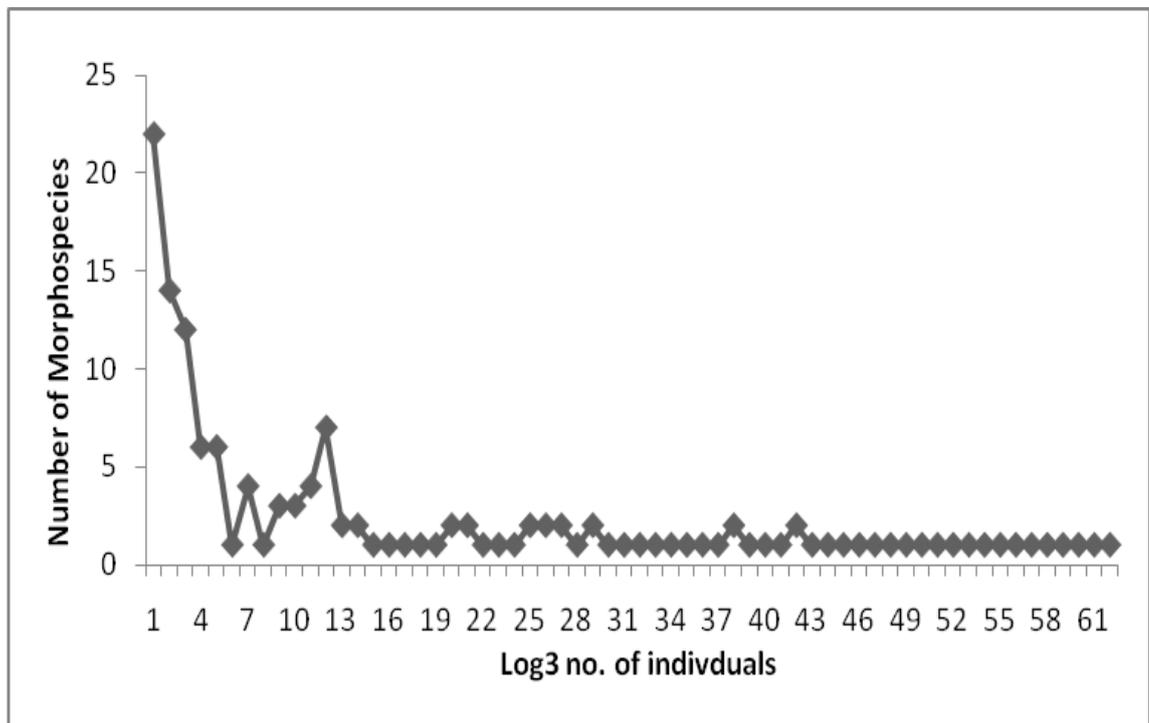
Fig. 4.1. Morphospecies abundance of entire fauna collected from 522 cups in Reserva Las Gralarias, Ecuador.

4.1 Species-Area Relationship (Design 1)

A total of 98 species were found in 198 cups collected after 4 weeks, comprising 1879 individual organisms. Each individual cup on average had 9.5 individuals of 6.5 species. Average species richness was highest in cups of the greatest water volume (400ml), and was lowest in cups of the smallest volume (100ml). Average number of individuals was highest in 200ml volume cups and lowest in those of 100ml volume. Margalef and Simpson's diversity values were highest in 400ml cups and varied for other volumes. No consistent difference was seen between cup areas (Fig. 4.2).
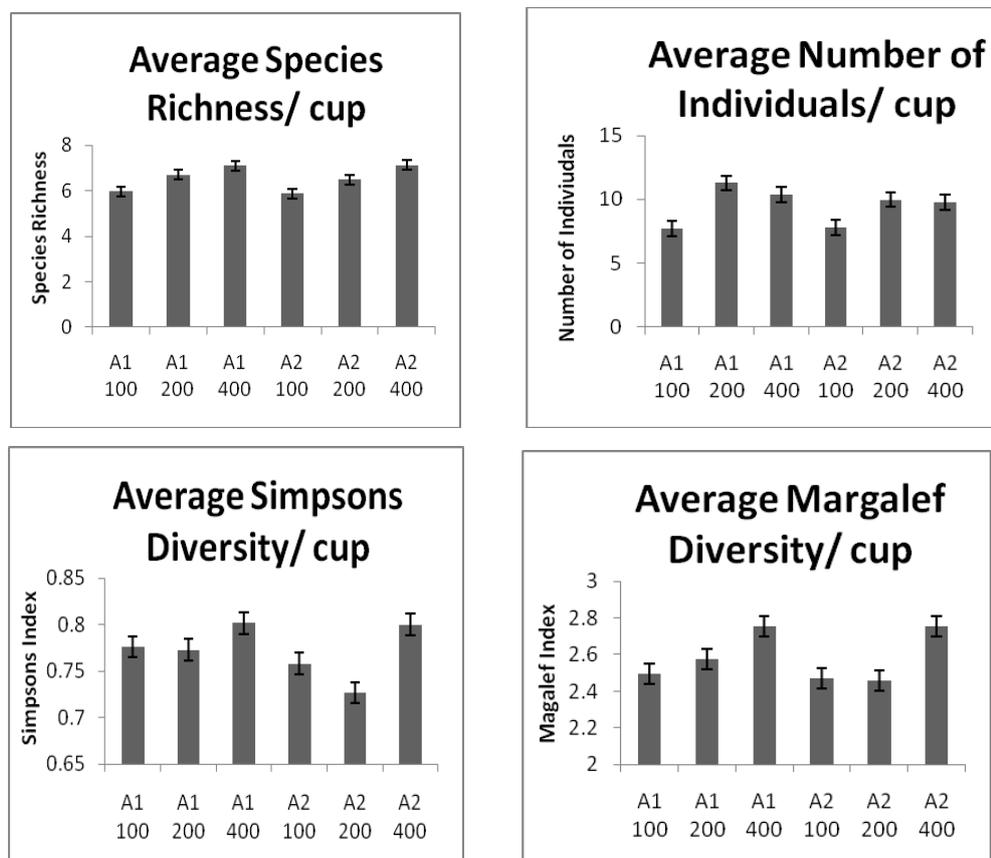
Fig. 4.2. Visual comparisons of the average species composition values per cup size for the data collected after 4 weeks. 95% error bars are shown.

Sorenson's coefficients obtained for assemblages in each cup size are presented in Table 4.1. The highest similarity in assemblages occurred between cup sizes A2 100 and A2 400, whereas the least similar cup sizes were A1 100 and A2 400 (notably the smallest and the largest cup sizes). Relatively low similarity was also found between cups of different areas; A2 400 and A1 200, and A1 100 and A2 100, whereas relatively high similarity was also found between cups of the same areas; A2 100 and A2 400.

Table 4.1. Sorenson's similarity coefficients for faunal assemblages collected after 4 weeks occurring among the 6 different cup sizes replicating artificial bromeliads

Cup Size	A1 100	A1 200	A1 400	A2 100	A2 200	A2 400
A1 100	-	-	-	**-**	-	-
A1 200	0.7119	-	-	**-**	-	-
A1 400	0.735	0.7227	-	-	-	-
A2 100	**0.661**	0.7333	0.7395	-	-	-
A2 200	0.7288	0.75	**0.8403**	0.7333	-	-
A2 400	**0.6607**	**0.6667**	0.7434	**0.8246**	0.7368	-

The GEE models are summarised in Table 4.2. Detritus mass was explained by area (X^2=16.200, df=1, P<.001), with cups of smaller area having a lower mass than cups of larger area. Following this, detritus mass was entered as a covariate with species richness, number of individuals and the diversity indices as dependent variables. Volume was the only variable to have a significant affect upon species richness (X^2=20.363, df=2, P<.001) and number of individuals (X^2=13.990, df=2, P=.001). In both cases 100ml volume cups had lower species richness and number of individuals than 200ml and 400ml cups, with 400ml cups having the highest number of individuals. Volume was also the only variable to significantly influence Margalef diversity (X^2=10.359, df=2, P=.006), and was the only significant variable remaining in the model for Simpson's diversity (X^2=5.943, df=2, P=.051). Margalef diversity was most negatively associated with cups of 100ml volume and most positively with cups of 400ml volume, while Simpson's diversity showed the most negative relationship with 200ml cups and the most positive with 400ml cups.

Table 4.2. Summary of GEE models performed to assess the effects of cup size and environmental factors on faunal composition components and detritus mass for all data collected after 4 weeks (design 1). Non-significant terms (P<.05) were removed to simplify the model.

Full Model	Dependent Variable	Minimum Adequate Model	Significance
Area Volume Canopy Cover Altitude Area*Volume	Y = Detritus Mass	Area	<.001
Station Area Volume Canopy Cover Altitude Detritus Mass Area*Volume	Y = Species Richness Y = Number of Individuals Y = Simpson's Diversity Y = Margalef Diversity	Volume Volume Volume Volume	<.001 .001 .051 .006

4.2 Colonisation (Design 2)

Table 4.3 summarises the total number of species and individuals collected per week from the 424 cups, with most species and individuals collected after week 3.

Table 4.3. Total number of species and number of individuals each week including all cup sizes

Week	Total Number of Species	Total Number of Individuals
1	88	750
2	92	959
3	98	1302
4	85	1108

Fig. 4.3a shows average number of individuals per cup size each week. Cup size A2 400 was highest after the first week and A2 100 the lowest. Cup size A2 100 saw the biggest increase in number of individuals between weeks 1 and 2, while cup size A2 200 had the biggest increase from weeks 2 to 3. From week 3 to 4 cup size A1 100 lost the most individuals on average, and cups of size A1 200 were the only cups to gain individuals in week 4.
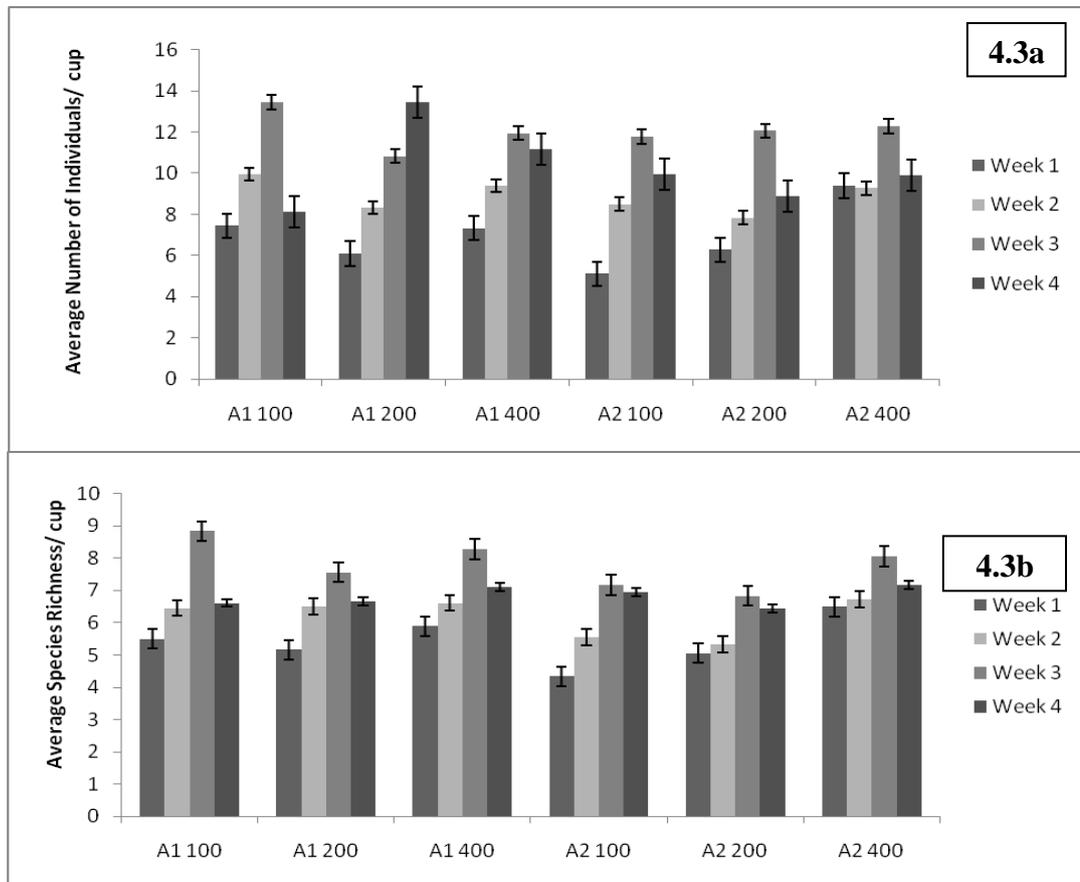
Fig. 4.3a. Average number of individuals for each cup size in each week. **4.3b.** Average species richness for each cup size in each week

Fig. 4.3b shows average species richness was highest in week 3 for all cup sizes. In weeks 1, 2 and 4 it was highest in cups of the greatest volume for each given area. Between weeks 2 and 3 cups of size A1 100 saw the largest increase in species richness, and throughout week 4 all cup sizes saw a decrease in species richness, with A1 100 cups having the steepest decline.

Rates of species accumulation were quickest over the first week for all cup sizes (Fig. 4.4), with A1 100 cups accumulating species at the fastest rate. Between weeks 1 and 2 cups of size A2 200 accumulate species at a faster rate than other cup sizes, while over the final 2 weeks accumulation rates of all cup sizes slow down, but they continue to increase at similar rates. In total, A1 100 accumulated the most species and A2 400 the least.
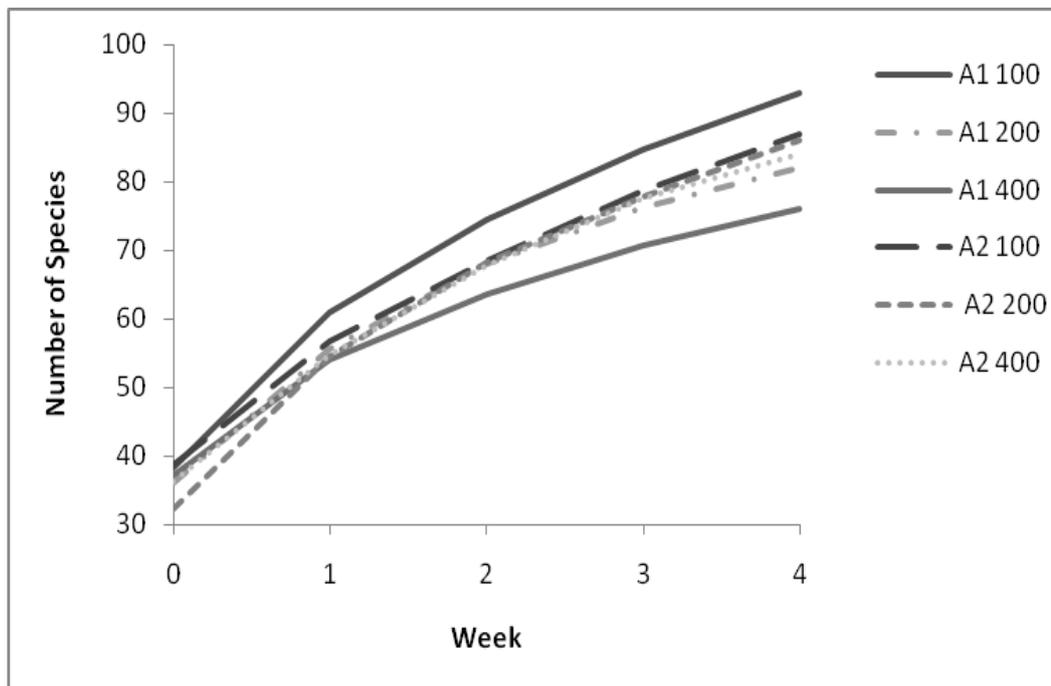
Fig. 4.4. Species accumulation curves for each cup size plotted as a function of time

The diversity indices are summarised in Fig. 4.5 for each week by cup size. Both diversity indices suggest that for week 1, diversity was highest in the largest cup size (A2 400). For week 2 the Simpson's index show A1 200 cups as having the greatest diversity, while the Margalef index show A2 400 cups as having the highest diversity. For week 3 both indices show cups of size A1 100 to have the highest diversity whereas for week 4, Simpson's index put cups of size A2 400 as having the highest values with Margalef index being almost equal for sizes A2 400 (0.800) and A1 100 (0.802).
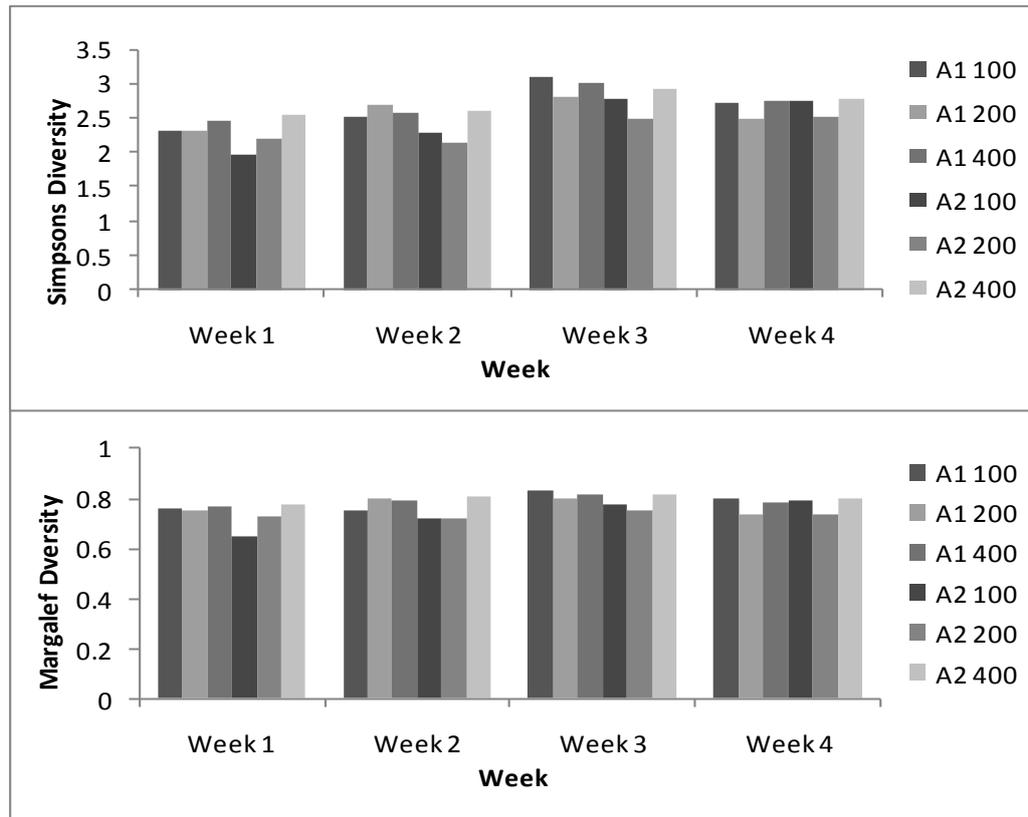
Fig. 4.5. Summary of the diversity indices obtained for each cup size per week

The Sorenson's coefficients show that cup sizes A1 400 contained the most similar assemblages throughout the 4 weeks, as well as between the first and last week (Table 4.4). In contrast, A1 200 cups reveal the most change in assemblages from the first to the last week, accentuated by being the least similar from week 1 to 2 and 2 to 3.

Table 4.4. Sorenson's coefficients showing similarity of faunal composition for each cup size between each week and between the first and last week

	Weeks 1 and 2	Weeks 2 and 3	Weeks 3 and 4	Weeks 1 and 4
A1 100	0.5591	0.6667	0.6346	0.5435
A1 200	0.4938	0.64	0.6392	0.4615
A1 400	**0.6517**	**0.7551**	**0.7071**	**0.647217**
A2 100	0.5641	0.6531	0.6471	0.5366
A2 200	0.5926	0.6667	0.6337	0.4719
A2 400	0.6	0.6444	0.6374	0.5055

The Generalised Estimating Equations model was primarily used to determine if differences in species composition between weeks was significant (P<.05), including week as a covariate in addition to those mentioned in design 1 (Table 4.5). Detritus mass was shown to have a positive relationship with week (X^2=216.232, df=1, P<.001). Interactions between area and week (X^2=6.884, df=1, P=.006) and between area, week and volume (X^2=9.928, df=4, P=.042) also explained detritus mass; the positive relationship between the week*area interaction was weaker for smaller sized cups. Species richness was explained by volume (X^2=8.662, df=2, P=.013) and a positive association with week (X^2=51.592, df=1, P<.001), with cups of 200ml having the most negative association with species richness, and 400ml cups the most positive. Week also showed a positive influence upon number of individuals (X^2=41.163, df=1, P<.001/ X^2=37.084, df=1, P<.001) (when interactions were included/ excluded from the model respectively) while interactions between area and volume (X^2=28.106, df=5, P<.001), and area, volume and week (X^2=14.091, df=5, P=.015) also significantly influenced number of individuals. Cups of size A1 200 had the most negative association and A2 400 the most positive. All cup sizes had positive relationships with number of individuals, but cup sizes A2 100 and A2 200 showed significant and larger relationships. Positive associations between week (X^2=26.888, df=1, P<.001), and altitude (X^2=4.017, df=1, P=.045) with Margalef diversity occurred. Volume (X^2=7.995, df=2, P=.019) also explained Margalef diversity, with cups of 200ml volume having the most negative association. Finally Simpson's diversity was positively associated with week (X^2=7.475, df=1, P=.006/ X^2=7.430, df=1, P=.006) and altitude (X^2=4.398, df=1, P=.036/ X^2=4.400, df=1, P=.036), and was also affected by an interaction between volume and week (X^2=7.145, df=2, P=.028) (when including/ excluding interactions from the model respectively). Volume also explained Simpson's diversity (X^2=6.508, df=2, P=.039/ X^2=6.127, df=2, P=.047), with cups of 400ml volume showing the most positive relationship.

Table 4.5. Summary of GEE models performed to assess the effects of cup size, week and environmental factors on faunal composition components and detritus mass for all data collected after each week (design 2). Non-significant terms (P<.05) were extracted to simplify the model. [+] indicates that values were taken from a GEE model run without interactions

Full Model	Dependent Variable	Minimum Adequate Model	Significance
Area Volume Canopy Cover Altitude Week Area*Volume Area*Week Week*Volume Area*Week*Volume	Y = Detritus Mass	Week[+] Area*Week Area*Week*Volume	<.001 <.001 .019
Station Area Volume Canopy Cover Altitude Week Detritus Mass Area*Volume Area*Week Volume* Week Area* Week*Volume	Y = Species Richness	Volume Week	.013 <.001
	Y = Number of Individuals	Area*Volume Week Area *Week *Volume	<.001 <.001 .015
	Y = Simpson's Diversity	Volume[+] Week[+] Altitude[+] Volume*Week	.045 .006 .036 .028
	Y = Margalef Diversity	Volume Week Altitude	.019 <.001 <.001

5.0 DISCUSSION

Tank bromeliads form the ideal habitats to test aspects of island biogeography theory as they support discrete faunal communities and have been found to behave like islands (Richardson 1999). The aim of this study was to assess the roles of surface area and volume in structuring the faunal communities found in tank bromeliads, as independent variables, and also over time.

5.1 Species Area Relationship

The results showed that volume, but not area, was an important predictor of species richness, abundance and diversity values (Simpson's and Margalef), with highest richness and diversity values occurring in cups of the highest water volume. However, the results still conform to island biogeographic theory as species can inhabit the phytotelmata at any depth, and so the relationship where inhabitable areas increase (volume in this case) with species richness is still creditable. Meanwhile, surface area was found to be the most important determinant of detritus mass. Similarly to this study, Richardson (1999) also found an increase in debris correlated with an increase in plant size, suggesting the positive relationship between plant size and detritus mass occurs due to area rather than volume, as would occur naturally with the rate of leaf litter input being determined by the area of the opening of the phytotelmata (Sota 1996). Armbruster *et al.* (2002) found that the detritus volume was the most important explanatory variable in influencing the morphospecies richness of tank bromeliads. In their study detritus mass provided the measure of resources available to support the food chain (Armbruster *et al.* 2002), supporting studies which promote the importance of nutrients in influencing species richness by increasing the potential length and/ or complexity of the food web. It is also thought that species richness increases with phytotelm size when different habitats are promoted, as would occur naturally as a bromeliad becomes older (Araujo *et al.* 2007). Increased habitat complexity allows a greater faunal diversity to occupy an aquatic area (Burdett and Watts 2009) by creating more niches for species, reducing the amount and frequency of competitive encounters, and by allowing more species to coexist (Srivastava 2006).

However, the results of this study found that volume is fundamental in structuring communities and not detritus mass, directly nor indirectly through area. Additionally, Burdett and Watts (2009) found experimentally that food availability was more important in controlling community structure than was physical structure in closed small

aquatic communities. This suggests that either other factors may have been more important in providing nutrients than detritus mass, or as Srivastava and Lawton (1998) found in their experiment, oviposition preferences of species are based on other factors. Although it may be that as larger bromeliads naturally hold larger water reservoirs and greater water volumes, they potentially provide a larger space and site for oviposition (Richardson 1999). Thus, it is the adults that get affected by oviposition decisions, whereas larvae have to endure survivorship, growth, and abundance. Therefore oviposition preference could be controlled by larvae survivorship, with adults choosing positions that provide resources and enhance reproductive and emergence success. This may not only be based on productivity or area however, but also on drought resistance (Srivastava and Lawton 1998). Sota (1996) found that species would colonise the applicable sized holes based on their development characteristics; for example, species without drought-resistant immature stages would colonise tree-holes that were larger and thus more resistant to drought. Such larger reservoirs are usually deeper rather than wider as wider holes will endure more evaporation, and so this relationship is based more on volume than surface area. However, this relationship may be difficult to understand as it may be a natural occurrence whereby drought resistant tree-holes also tend to be larger, and therefore contain more debris which in turn increases productivity (Srivastava and Lawton 1998). Despite this theory, it has been shown that some species such as *Wyeomia* mosquitoes have no preference to ovipositing in debris filled leaf axils of bromeliads compared to clear tap water alone (Fish 1983), showing that oviposition preferences are species dependent and cannot be generalised.

Oviposition preferences may also help to explain why the number of individuals was highest at an intermediate water volume. Srivastava and Lawton (1998) tested the "More Individuals Hypothesis", a theory which assumes that species richness increases as a function of total abundance, and that community abundance is limited by productivity. However, upon testing this theory on tree-hole communities, it was found that more productive tree-holes supported higher species richness but not more individuals as the theory suggests. They concluded that productivity could not explain the results as the theory did not account for local colonisation or extinction processes, including oviposition preferences (Srivastava and Lawton 1998). Further, although many species colonise phytotelm habitats, some do not spend their whole life cycles there. They may become extinct, or individuals may leave, resulting in a weakening of the relationship between number of individuals and species richness as predicted by the "More Individuals Hypothesis".

In contrast to volume being the most explanatory variable of species composition, cups of the same areas appeared to contain more similar assemblages than those of different areas according to Sorenson's similarity measure. It was noted by Preston (1962) that the species-area curve comes about due to the sampling of larger areas in which more individuals and more species are obtained, because some of the new individuals will be rare species not previously sampled. This would help to explain the similarities between the areas if the larger areas attracted similar species to each other which were not sampled by the smaller area cups, but the argument could also hold true with greater volumes sampling more individuals and rare species making it hard to disentangle the underlying causes. Blakely and Didham (2010) also found that disturbance and habitat heterogeneity have strong influences upon species identity and composition, however all cups received the same treatments (none were noticeably disturbed). Again it is possible that oviposition preferences play a role as similar species may select cups with similar surface areas resulting in a similarity amongst the same surface areas. It is also possible the similarities may have occurred by chance or due to factors not being accounted for in the study. Such factors would therefore not only be applicable to this trend, but also to all the results of both experimental designs. For example, no attempt was made to distinguish the effects of trophic structure, which may covary with habitat structure (Srivastava 2006). Habitat structure is more applicable to real bromeliads due to the structure of their leaves, and was therefore not measured in the artificial cups. However habitat structure could change depending on the amount and in particular type of detritus mass. A change in habitat structure may affect predatory distributions which in turn could affect the composition of the rest of the population; Yanoviak (1999) found that species richness and abundance was greater in larger tree-holes with larger holes containing more predator species.

5.2 Colonisation

In this experiment, volume was found to significantly affect species richness, as did week, making it plausible for detritus mass to have an indirect influence upon species richness as detritus mass also increased each week. This differs slightly to the conclusions made from design 1 where detritus mass was not found to be related to species richness based just on looking at the different cup sizes. It is therefore possible that the underlying cause for detritus mass showing an indirect relationship in this experiment is age. Older bromeliads naturally contain more detritus (as shown by the association between week and detritus mass). The cups in design 1 were all the same

age (left out for the same amount of time) and detritus differences were solely based on area. Although smaller areas were shown to contain less detritus mass than larger areas, it is possible that resources (the energy input with detritus mass) have to accumulate and so significant differences can only be seen if a factor of time is included. In support of this, Blakely and Didham (2010) manipulated the mechanisms affecting species richness and revealed that species richness does not increase with increasing size of an ecosystem as an individual mechanism, but rather that resource concentration drives the species-area relationship as larger areas retain greater resources. An alternative possibility is that species richness is not driven by processes itself.

For example, number of individuals also increased each week for all cup sizes, but volume did not independently affect number of individuals. Rather it was an interaction between area and volume, where cup sizes of the largest area and volume had significantly more individuals than other cup sizes. As detritus mass is related to area, it is very plausible to suggest that detritus mass may have more of an influence on the number of individuals which then affects species richness. Detritus mass is a good indicator of the productivity of a site and sites which are more productive can naturally support a higher number of total individuals (Srivastava and Lawton 1998). However where number of individuals is closely related to productivity, species richness is closely related to number of individuals. Firstly, more productive sites can support a higher number of total individuals which in turn increases the number of species, as low abundance populations are more likely to become extinct. Hence at more productive sites, higher species richness is also likely to be found (Srivastava and Lawton 1998). Secondly a higher productivity has more chance of containing more resource types, meaning that more specialist species can be supported which endure less competition leading to higher species richness (Srivastava and Lawton 1998). Thirdly, increased productivity could lead to the addition of a trophic level which reduces the size of populations. This in turn leads to less competitive exclusion, resulting in an increase in diversity (Srivastava and Lawton 1998). Even if this was the case however, the relationship between volume, area, and number of individuals was not revealed in the experiment where age was not included. This suggests therefore that age has a greater influence on species composition than do area, volume, or oviposition preferences as discussed previously.

On average, species richness and number of individuals were highest in the cups of the greatest volume over each of the 4 weeks. The diversity indices suggest that the

largest cups (in area and volume) exhibit the highest diversity and evenness in the first and last weeks, but after the third week the smallest cup size (in area and volume) had the highest values. It follows the species-area arguments described above that the larger cups (with more detritus) have higher richness, abundance, diversity, and evenness values. However it is interesting that in week three diversity and evenness were highest in the smallest cup size, and that the Margalef index was equally as high for the smallest cup size as the largest in the final week. Species richness and number of individuals also follow the same trend of being highest in the third week overall, showing a rise to a peak in this week followed by what appears to be the start of a fall, as well as in the smallest cup size. Similar observations were observed by Beaver (1983) in pitcher plant populations. Beaver concluded that the input of food followed a similar curve. However, bromeliads are dissimilar to pitcher plants as pitcher plants do not often live beyond a year resulting in a constant turnover of the plants themselves, and faunal communities are not able to reach an equilibrium state (Fish 1983).

Despite this it is still possible that nutrient inputs may have resulted in the pattern across cup sizes, but the high values in week three for the smallest cup size appear to be anomalous considering the rest of the data, and no theoretic explanation can be found to give reasons why the pattern occurred. Although all stations were positioned in shaded areas of the forest, individual cups may have been subject to slightly different microhabitats which were more or less exposed than other cups; this was not accounted for in the environmental data. For example, Laessle (1961) found that plants exposed to strong light sources contained higher amounts of algae and therefore higher oxygen and lower carbon dioxide levels than shaded plants, and subsequently had less stable gas levels. Additionally, temperatures were shown to fluctuate greater in more sun-exposed plants. However, differences in bromeliads in sun and shade documented by Montero *et al.* (2010) found that sun plants had higher water volumes, less detritus mass, and were shorter than shade plants, but despite this they found no differences between the phytotelm macrofauna species richness and abundance. Also, to obtain the same result on average across the cup size suggests that either that cup size was preferred to other cup sizes, although if this was the case a steep decline in values in week 4 would be unlikely to have happened, or more likely, the result occurred by chance or due to different weather conditions in week 3.

Species accumulation was quickest throughout the first week of data collection with the smallest cup size (in both area and volume) accumulating the most species over the four weeks. It is well known that regarding the species-area relationship, the number of

species inhabiting an ecosystem will increase rapidly at first but at a slower rate for larger ecosystems (Lomolino 2000). This would explain the higher accumulation rate over the first week and also in the smallest cup size, however it is probably due to the abnormally high values accumulated in week three that this cup size accumulated more species overall. Meanwhile, cup sizes varied in their similarity between the weeks, but cup size A1 400 contained the most similar assemblages from week to week, suggesting that colonisation preferences may differ dependent on cup size, with this cup size providing preferential conditions for specialist species, while the other cup sizes provide ideal conditions for more generalist species. In a colonisation experiment on pitcher plants Cresswell (1998) concluded three possible explanations for the species richness of a fauna inside the pitcher at any one time. These can be adapted to bromeliad fauna as well and help explain the results found here. Firstly, faunal composition may be determined by a sequence of unique stochastic events. Second, it is possible that colonisation is a successional process which, in conjunction with the first point, would help explain the lack of similarity for each cup size between each week as different cups were used to collect the data from each week. Finally, seasonality may affect faunal composition if studies occur for short periods of the year. However, as all cups were left out for the same period, seasonality would not affect the differences found between cup sizes. Instead this may have affected differences between weeks as the study occurred during the transition from the wet to the dry season, and rainfall was recorded to fluctuate throughout the study period (Lyons, 2010, *pers. comm.*). This could explain why there was a general lack of similarity between weeks.

5.3 Implications of the findings and concluding points

Considering the results from both experiments, when time was not included and the effects of surface area and volume upon species composition were assessed, it was found that volume was the most important predictor of species composition, and the best explanation for this was oviposition preferences of species based on drought-resistance. However, when time was incorporated in the colonisation study, the results corroborated with previous studies (Reid and Janetsky 1996; Araujo *et al.* 2007; Burdett and Watts 2009) in that detritus mass and therefore productivity were found to be important in explaining the patterns seen. Although environmental factors, oviposition preferences based on drought resistance, and habitat complexity also had possible roles to play, their effects were masked, something which should be considered in future work. In relation to real bromeliads, the size of any bromeliad is a

good indicator of its age and the time taken to accumulate the communities held. However, as age has been revealed as an important factor in accumulating detritus mass and nutrients separately to the effects of size, it should be incorporated as an independent factor where possible in future studies. Similarity between cup size or between weeks for the same cup size was the hardest to explain and highlighted the limitations to the experiment as well as the possible effects of other factors which could not be included in this study. Further research is needed to determine the driving factors behind the similarity of the assemblages. In terms of the colonisation experiment conducted here, the species accumulation curves did not appear to be reaching an asymptote suggesting that colonisation rates were still higher than extinction rates, and although IBT provided the best explanation up to this point, caution should be taken in making conclusions. In order to correct this, the best approach would be to extend the study over a longer time period. Beaver (1983), has already shown that the number of species present in a pitcher plant varies over time in a 7 month long study, with the highest dominance in plants of 2-3 months old, and a similar time frame could be adopted for a study on bromeliads.

In terms of applicability of the results to real bromeliads care should be taken. By replicating bromeliads with cups it is uncertain as to whether the organisms which colonised them actually resembled what would be found in a real bromeliad in terms of composition. Bromeliads usually have three types of associations with invertebrates, the first of which is least likely to be represented; invertebrates that feed on the plants, organisms which are aquatic at least in some part of their development, and terrestrial organisms which use bromeliads for shelter, prey, or humidity (Frank *et al.* 2004). Additionally some species are bromeliad specialists and it is unlikely these will have been represented. Rather bromeliad generalists will have been represented. In regards to generalising the results to phytotelmata, Lopez *et al.* (2009) found that species communities within bromeliads differed from those in nearby continental freshwater ponds and swamps. The endemism of the bromeliad fauna was attributed to the bromeliads altering the water chemistry by being highly efficient in retaining nutrients from detritus (such as N and P) (Ngai and Srivastava 2006), resulting in many pond species being unable to successfully colonise the bromeliads. Similarly, some pitcher plants release a water-soluble substance from their leaves into the tank area which attracts species to it, and likewise some species are attracted to fruits such as the mosquito *Eretmapodites subsimplices*, which oviposits in young Saba fruits (Fish 1983), again promoting applicability to generalist fauna but also generalist phytotelmata (e.g. phytotelm species which do not release chemicals). Additionally, Seifert and

Seifert (1976) reported that in *Heliconia spp.* inhabiting faunal populations and larval densities increased during flowering, a period when the results of this study would not be applicable.

To conclude, tank bromeliads provide a container habitat that has allowed many studies to research factors which affect taxonomically unrestricted discrete communities and provide insight into the processes that control community assemblages. Research on real bromeliads will potentially always involve full or part destruction of a plant, and using artificial bromeliads should be preferentially chosen as they provide useful tractable surrogates for real bromeliads, and can be utilised to find out underlying processes in the community ecology of the ecosystems as has been shown by this study. As discussed here and by Srivastava *et al.* (2004) using artificial microcosms (small, contained ecological systems such as phytotelmata) provides the advantage of being able to control habitats and detect the subtle effects of processes which are occurring. However, the general applicability of any results to natural ecosystems would have to be tested in natural phytotelmata to see if the same results can be obtained. Therefore, to prove the results of this study and go beyond theorising the effects of age, a study on real bromeliads as well as other phytotelmata needs to be employed. Finally, it should be remembered phytotelmata often represent the sole permanently abundant lentic (still water) habitat in Neotropical forests (Balke *et al.* 2008). It is important not only for the conservation of the bromeliads themselves, but also the abundant and diverse fauna which rely upon them for survival, and for future research, that much effort is put into conserving tropical forests around the world in order to protect these abundant microcosms.

REFERENCES

Araújo, V.A., Melo, S.K., Araújo, A.P.A., Gomes, M.L.M. & Carneiro, M.A.A. (2007) Relationship between invertebrate fauna and bromeliad size. *Brazilian Journal of Biology,* **67:** 611-617.

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

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

Beaver, R. A. (1983) *The Communities living in Nepenthes Pitcher Plants: Fauna and Food Webs.* In: Frank, J. H. & Lounibos, L. P. (eds) Phytotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing Inc, NJ: USA.

Blakely, T. J.& Didham, R. K. (2010) Disentangling the mechanistic drivers of ecosystem-size effects on species diversity. *Journal of Animal Ecology*, no. doi: 10.1111/j.1365-2656.2010.01729.x.

Bubb, P., May, I., Miles, L., Sayer, J. (2004) *Cloud Forest Agenda.* UNEP-WCMC: Cambridge, UK.

Burdett, A. S. & Watts, R. J. (2009) Modifying living space: an experimental study of the influences of vegetation on aquatic invertebrate community structure. *Hydrobiologia*, **618:** 161-173.

Bussman, R. W. (2001) Epiphyte diversity in a tropical Andean forest – Reserva Biologica San Francisco, Zamora-Chinchipe, Ecuador. *Ecotropica*, **7:** 43-59.

Chu, H. F. & Cutkomp, L. K. (1992) *How to know the immature insects: an illustrated key for identifying the orders and families of many of the immature insects with suggestions for collecting, rearing and studying them.* 2nd edition. McGrawHill: USA.

Cresswell, J. E. (1998) Morphological correlates of necromass accumulation in the traps of an Eastern tropical pitcher plant, *Nepenthes ampullaria* Jack, and observations on the pitcher infauna and its reconstitution following experimental removal. *Oecologia*, **113:**383-390.

Field, R. (2010) *Bromeliads.* [email] (Personal communication, 23/03/2010).

Fish, D. (1983) *Phytotelmata: Flora and Fauna.* In: Frank, J. H. & Lounibos, L. P. (eds) Phtotelmata: Terrestrial Plants as Hosts for Aquatic Insect Communities. Plexus Publishing Inc, NJ: USA.

Frank, J. H. & Lounibos, L. P. (2008) Insects and allies associated with bromeliads: Insects and allies associated with bromeliads: a review. *Terrestrial Arthropod Reviews*, **1:** 125-153.

Frank, J. H., Sreenivasan, S., Benshoff, P. J., Deyrup, M. A., Edwards, G. B., Halbert, S. E., Hamon, A. B., Lowman, M. D., Mockford, E. L., Scheffrahn, R. H., Steck, G. J., Thomas, M. C., Walker, T. J. & Welbourn, W. C. (2004) Invertebrate animals extracted

from native Tillandsia (Bromeliales: Bromeliaceae) in Sarasota County, Florida. *Florida Entomologist*, **87:** 176-185.

Gonzalez, A. B. C. (2009) *The effect of bromeliad placement and structure on richness of invertebrate communities in a montane rain forest in Honduras.* PhD, Cambridge: Anglia Ruskin University.

Greeney, H. F. (2001) The insects of plant-held waters: a review and bibliography. *Journal of Tropical Ecology,* **17:** 241-260.

Heckman, C. W. (2001) *Encyclopedia of South American Aquatic Insects: Collembola.* [Kindle Edition] Springer: USA

Heckman, C. W. (2002) *Encyclopedia of South American Aquatic Insects: Ephemeroptera.* [Kindle Edition] Springer: USA.

Heckman, C. W. (2003) *Encyclopedia of South American Aquatic Insects: Plecoptera.* Klewer Academic Publishers: The Netherlands.

Heckman, C. W. (2006) *Encyclopedia of South American Aquatic Insects: Odonata - Anisoptera* [Kindle Edition] Springer: USA.

Hill, M. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54:** 427-31.

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

Kitching, R. L. (2000) *Food Webs & Container Habitats : The Natural History & Ecology of Phytotelmata*, Cambridge University Press, Port Chester, NY, USA

Laessle, A. M. (1961) A micro-limnological study of Jamaican bromeliads, *Ecology,* **42:** 499-517.

Little, T. J. & Herbert, P. D. N. (1996) Endemism and ecological islands: the ostracods from Jamaican bromeliads. *Freshwater Biology,* **36:** 327–338.

Lomolino, M. V. (2000) Ecology's Most General, Yet Protean Pattern: The Species-Area Relationship. *Journal of Biogeography*, **27:** 17-26.

Lomolino, M. V., Riddle, B. R. & Brown, J. H. (2006) *Biogeography.* (eds) Sinauer Associates, Inc: USA.

Lopez, L. C. S., Alves, R. R. & Rios, R. I. (2009) Micro-environmental factors and the endemism of bromeliad aquatic fauna. *Hydrobiologia*, **625:** 151–156.

Lyons, J. (2010) *Weather data from RLG.* [email] (Personal communication, 19/08/2010)

MacArthur, R. H. & Wilson. E. O. (1967) *The Theory 0f Island Biogeography.* Princeton NJ: Princeton University Press.

Maguire, B. (1971) Phytotelmata: Biota and community structure determination in plant held waters. Annual *Review of Ecology, Evolution, and Systematics*, **2:** 439-464.

Magurran, A. E. (1988) *Ecological Diversity and its Measurements*. University Press, Cambridge: Great Britain.

Montero, G., Feruglio, C. & Marberis, I. M. (2010) The phytotelmata and foliage macrofauna assemblages of a bromeliad species in different habitats and seasons. *Insect Conservation and Diversity,* **3:** 92–102.

Ngai, J. T. & Srivastava, D. S. (2010) Predators Accelerate Nutrient Cycling in a Bromeliad Ecosystem. *Science*, **314:** p.963.

Oliver, I. & Beattie, A. J. (1996) Invertebrate Morphospecies as Surrogates for Species: A Case Study. *Conservation Biology*, **10:** 99-109.

Preston, F. W. (1962a). The canonical distribution of commonness and rarity: part I. *Ecology*, 43: 185-215.

Preston, F. W. (1962b). The canonical distribution of commonness and rarity: part II. *Ecology*, 43: 410-432.

Reid, J. W. & Janetzky, W. (1996) Colonization of Jamaican Bromeliads by *Tropocyclops jamaicensis* n. sp. (Crustacea: Copepoda: Cyclopoida). *Invertebrate Biology*, **115:** 305-320.

RLG (2010) *Reserva Las Gralarias.* (online) Available at: http://reservalasgralarias.com/ [Accessed 29.04.2010].

Richardson, B. A. (1999) The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. *Biotropica,* **31:** 321-336.

Seifert, R. P. & Seifert, F. H. (1976) A Community Matrix Analysis of Heliconia Insect Communities. *The American Naturalist*, **110:** 461-483.

Sota, T. (1996) Effects of capacity on resource input and aquatic metazoan community structure in phytotelmata. *Res. Popul. Ecol.* **38:** 65-73.

Srivastava, D. S. (2006) Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad–insect community. *Oecologia,* **149:** 493–504.

Srivastava, D. S. & Lawton, J. H. (1998) Why More Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities. *The American Naturalist*, **152:** 510-529.

Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., Munuia, P., Romanuk, T., Schneider, D. C. & Trzcinski, K. (2004) Are natural microcosms useful model systems for ecology? *TRENDS in Ecology and Evolution*, **19**: 379-384.

Stork, N. E. (1987) Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology,* **12:** 69–80.

Trierweiler, R. W., Hunter, S. A., Jun, J. E. & Nowogrodzki, A. R. (2005) Island biogeography theory as applied to tank bromeliad communities. *Dartmouth Studies in Tropical Ecology,* 51-61.
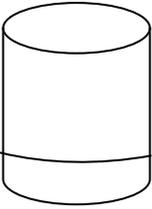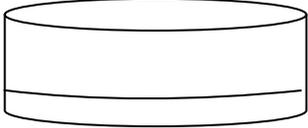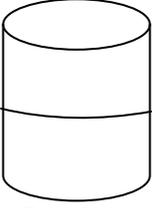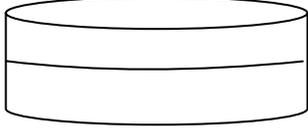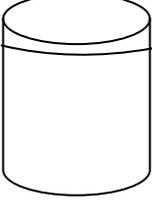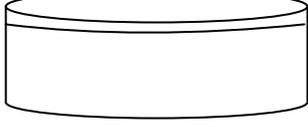
Trzcinski, M. K., Walde, S. J. & Taylor, P. D. (2003) Colonisation of pitcher plant leaves at several spatial scales. *Ecological Entomology*, **28:** 482–489.

Yanoviak, S. P. (1999) Community structure in water-filled tree holes of Panama: Effects of hole height and size. *Selbyana,* **20:** 106-115.
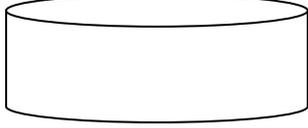
Yanoviak, S. P. (2001) Container colour and location affect macroinvertebrate community structure in artificial treeholes in Panama. *Florida Entomologist,* **84:** 265-271.

APPENDICES

Appendix A: Design for each set of six cups

Volume 100ml, Depth 4cm , Surface Area 28cm^2	Volume: 100ml, Depth 2cm , Surface Area 64cm^2
Volume 200ml, Depth 7.5cm, Surface Area 28cm^2	Volume: 200ml, Depth 4cm, Surface Area 64cm^2
Volume 400ml, Depth 15cm, Surface Area 28cm^2	Volume: 400ml, Depth 7cm , Surface Area 64cm^2

Cup dimensions
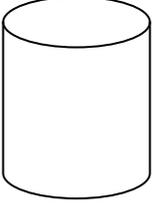
A1	A2
Depth 14cm, surface area 8.8cm	Depth 8cm, surface area 11.1cm

Appendix B: Example photograph of a typical cup (size A2 200) attached to a tree in Reserva Las Gralarias, Ecuador

Appendix C: Taxonomic classification of fauna collected from 522 artificial bromeliads in Reserva Las Gralarias, Ecuador

Taxonomic Grouping	No. of Morphospecies	No. of individuals
Annelida	2	3
Arthropoda		
Arachnida		
Acari	7	611
Opiliones	1	46
Scorpiones	1	1
Other	11	172
Crustacea		
Isopoda	1	249
Insecta		
Blattodea	2	13
Chilopoda	7	262
Coleoptera (larvae)	8	141
Coleoptera (pupae)	2	6
Coleoptera (adult)	23	324
Collembola	1	4
Dermaptera	1	22
Diptera (larvae)	18	1033
Diptera (adult)	12	893
Hemiptera	2	15
Homoptera	3	45
Hymenoptera (ants)	3	348
Hymenoptera (wasps)	4	49
Lepidotpera	9	149
Orthoptera	6	74
Phasmida	2	4
Thysanoptera	1	76
Trichoptera	2	5
Other	1	21
Mollusca	5	31
Nematoda	2	33
Plathyhelminthes	1	4
Unknown	4	146