

ABIOTIC FACTORS CONTROLLING SPECIES RICHNESS, DIVERSITY, AND ABUNDANCE IN THE BROMELIAD *HOHENBERGIA POLYCEPHALA* (BROMELIACEAE)

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Abstract. We investigated invertebrate communities of aquatic microcosms created by leaf axils of the bromeliad plant *Hohenbergia polycephala* in order to detect abiotic and biotic determinants of species richness, diversity, and abundance. We found a total of 15 species from 83 invertebrate communities formed in tanks on 36 bromeliad plants on the north coast of Jamaica. Tank volume, depth, temperature, dissolved oxygen concentration, and levels of leaf litter differed according to the relative age of the bromeliad tank. Species richness and diversity did not differ with relative tank age, however abundances of a midge and a mosquito species did. Species richness (S), and both Shannon-Wiener and Simpson's diversity indices were best explained by independent PCA factors involving leaf litter, water volume, dissolved oxygen concentrations, and tank light levels. However, community structure, in general, was poorly explained by the physical attributes of tanks. It appears that a complex combination of several abiotic and biotic factors (including possible priority effects) influences community composition in these microcosms.

Key words: bromeliads, *Hohenbergia polycephala*, phytotelmata, species richness, invertebrates, Jamaica, leaf axils, microcosm.

INTRODUCTION

Aquatic microcosms are often used in the study of community ecology (Srivastava *et al.* 2004). Plants holding water in floral parts, leaf axils, and nutrient-gathering organs commonly support a diverse fauna of invertebrates (Seifert & Seifert 1976, Janetzky & Vareschi 1992). Termed by Varga (1928) and the followers (e.g. Maguire 1963, Frank & Lounibos 1983, and references therein) as phytotelmata, these plant-held bodies of water contain small animal communities based primarily on allochthonous inputs of detritus (Kitcing 1987). Phytotelmata have been well studied for the banana plants *Heliconia imbricata* (Naeem 1988, 1990a,b) and *Heliconia wagneriana* Peters (Seifert & Seifert 1976), and the pitcher plants *Sarracenia purpurea* (Fish & Hall 1978, Bradshaw 1983, Heard 1994a,b, 1998; Miller *et al.* 1994, Nastase *et al.* 1995) and *Darlingtonia californica* (Naeem 1988). Tree holes (e.g. Schmidl *et al.* 2008), bamboo internodes (Kovac & Streit 1996), and the leaf axils of bromeliad plants also have been studied, with tree holes receiving particular attention (see Kitcing 2000 for a comprehensive review).

Communities within phytotelmata are small, numerous, frequently species-rich, exist in various degrees of isolation from each other, and undergo rapid ecological transformations (Maguire 1971, Seifert 1984, Little & Hebert 1996) or dramatic synchronized changes in response to large-scale variation in the temperate climate (Schmidl *et al.* 2008). Hence, phytotelmata may be readily manipulated and observed (Naeem 1990a; Addicott 1974). Microcosms such as phytotelmata are often thought of as suitable model systems permitting general inferences from small-scale ecological systems (Drake *et al.* 1996).

In this paper we investigate the abiotic environment and the relatively unknown aquatic invertebrate communities living in the phytotelmata formed by the leaf axils of the bromeliad plant *Hohenbergia polycephala* (Family Bromeliaceae). Picado (1913) first studied the flora and fauna in bromeliad tanks, and very little research has been conducted since (Frank & Lounibos 2009). The plants we studied are located in the dry limestone scrub forest of northern Jamaica, the habitat not included in the island-wide survey conducted by Little & Hebert (1996). Other recent work on Jamaican bromeliads concentrated on the taxonomy of copepods (Janetzky *et al.* 1996).

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The tanks are filled by rainwater and are ephemeral microhabitats whose duration is determined by changes in plant morphology and life span. We recorded their physical aquatic environment, including tank water volume, temperature, salinity, dissolved oxygen concentration, pH, light exposure, and amounts of organic debris (i.e. leaf litter). We attempted to identify abiotic and biotic factors that may influence the composition of the invertebrate community, its species richness and diversity within the bromeliad microcosms.

Previous studies of phytotelmata have found that habitat age may play a role in structuring the invertebrate community (Fish & Hall 1978, Seifert & Seifert 1979, Nastase *et al.* 1995). While past research on bromeliad phytotelmata has been concerned with the identification of organisms and the measurements of abiotic variables (Laessle 1961), no study has examined whether community structure and/or composition may change according to habitat age, and thus whether succession in microinvertebrate communities reflects dynamics of plant growth.

MATERIALS AND METHODS

Study site and communities. We collected the samples from the bromeliad plant *Hohenbergia polycephala* in the dry limestone scrub forest around Discovery Bay on the north coast of Jamaica. Typical of this forest zone, there is sparse vegetation cover of low forest trees and tall scrub growing from a limestone rock base (Asprey & Robbins 1953). We sampled only ground bromeliads on a strip of land extending from the coastal rocks about 300 m inland between December 28, 1997 and January 7, 1998. We encountered some epiphytic bromeliads but these were not sampled. Sample collecting was done between 08:00 h and noon to reduce variability of physical parameters due to the time of day.

We obtained samples from 36 bromeliad plants, including multiple tanks of different ages on the same plant when available. Thus a total of 83 samples was collected from the water-holding receptacles (tanks) formed at the leaf axils (Fig.1). The inner tank (Tank A) is a cone-shaped whorl formed from 3 to 4 overlapping almost vertical leaves. Over time, individual tank size and shape change since the new leaves grow from a whorl in the center of the plant. The leaves become progressively older towards the base of the plant and away from the inner whorl. The older tanks (Tank B - second youngest, and Tank C - the oldest) are contained between two more horizontal leaves

(Fig.1). We sampled plants of similar height (approximately 0.75 to 1 m), leaf width and length. Of the 36 plants sampled, we obtained 36 samples from Tank A, 34 from Tank B, and 13 from Tank C.

Temperature (°C), salinity (‰), dissolved oxygen concentration (mg l⁻¹), and pH were measured in each water-filled tank at mid-depth prior to water extraction. The depth (cm) of the tank was measured from the water surface to the bottom of the receptacle for all tanks, while the diameter (cm) of Tank A was measured at the water surface. Leaf litter was in different stages of decomposition and therefore we could not count the leaves or measure absolute volume of the litter but rather we had to refer to the relative filling up. The amount of leaf litter within the tanks was quantified visually on a scale of 0 to 5 prior to water collection (no leaves = 0, a few leaves = 1, half-full = 3, and full = 5). Turbidity was quantified by visual examination in the lab by first allowing the debris in the sample to settle and then ranking the degree of water clarity. Turbidity ranged from 1 to 5 (very clear = 1 and brown water with a lot of suspended sediment = 5). Light readings were taken with a Minolta X-300s single lens reflex camera and the suggested shutter speed represented light intensity.

After measuring the abiotic pool characteristics, we collected faunal samples. Unlike Naeem (1988), we used a non-destructive form of sampling to collect biotic samples. The tank contents were thoroughly mixed by sucking up the contents with a large pipette (~2 cm in diameter). We collected 50 ml (when available) of the homogenate from the tank for biotic analyses. The remaining water was extracted, total volume measured, and the water returned to the plant. Within each bromeliad plant, sampled tanks were not interconnected, and hence invertebrate communities were independent entities. They formed at different times, with younger communities positioned above the older ones. As in any sampling design in a natural habitat, samples closer to each other may, for various reasons, influence each other and thus be more similar. This possibility not only applies to tanks of a single plant but also to whole plants that grow close to each other. We found that tank A (youngest) was on average more similar (Bray-Curtis similarity index on log-transformed abundances) by about 3% to tank B (older) and that tank B was about 23% more similar to tank C (oldest) of the same plant than to all other tanks of the same category on other plants (the latter difference was statistically significant at $p < 0.000005$; ANOVA).

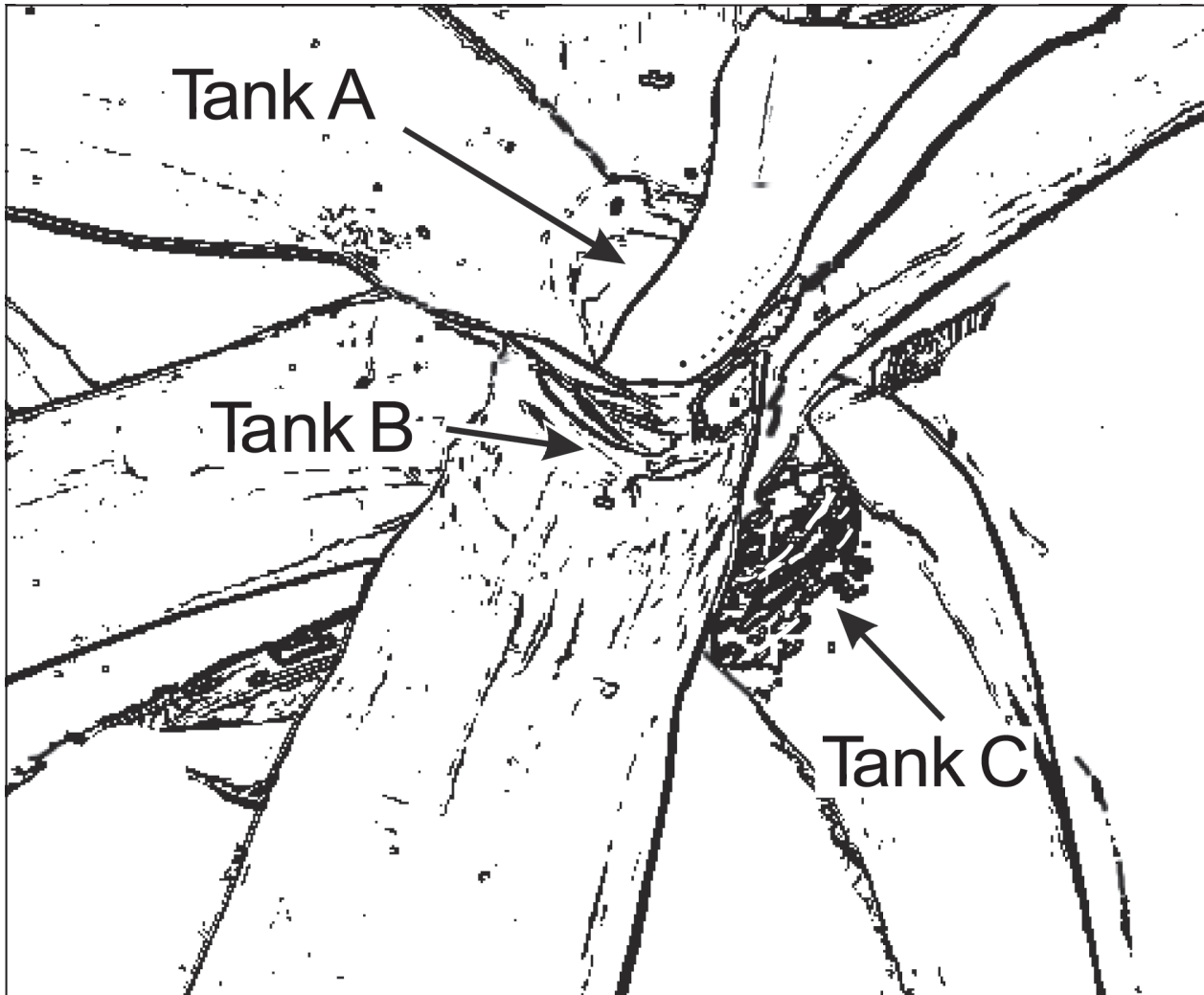


FIG. 1. Schematic representation of the central part of *Hohenbergia polycephala*. Axils marked as Tanks A – C contain water and are progressively older. Older axils usually hold no water due to their leaf orientation.

Consequently, we have put more weight on interpretations that did not depend on intra-plant similarities. Individual tank contents were mixed prior to water extraction to dislodge clinging organisms from detritus and the tank wall, and to evenly distribute organisms within each tank.

Organism counting, identification, and analyses. The invertebrates were sorted while alive from each sample within 24 hours of collection and preserved in 60% ethanol for later identification and counting.

Species richness, Shannon-Wiener diversity index (H') and Simpson's diversity index (D) were calculated for all 83 communities sampled.

Principal component analysis (PCA) was used to reduce the number of variables in the analyses and to generate independent variables based on abiotic tank characteristics (i.e. temperature, pH, dissolved oxygen, leaf litter, turbidity, depth, volume, and

amount of light at each tank). Regression analyses were used to show the relationships between community structure and abiotic variables. Analysis of variance was used to determine the differences between tanks of different relative ages. Statistical analyses were performed with Statistica 5.0 '97 Edition at a significance level of $\alpha = 0.05$. Canonical correspondence analysis (CCA) was used to relate overall community patterns to environmental attributes of tanks using the CANOCO software package (ter Braak & Šmilauer 1998) and extracted axes were tested using Monte Carlo permutations.

RESULTS AND DISCUSSION

Abiotic measurements. Tank water volume ranged from 20 to over 400 ml, while the depth of water within the tanks ranged from 3 to 26 cm (Table 1).

TABLE 1. Minimum, maximum, and mean values for abiotic variables measured in the bromeliad tanks.

Variable	Minimum	Maximum	Mean Value
water volume (ml)	20	410	124.3
water depth (cm)	3	25.5	12.1
water temperature (°C)	26	22.5	24.2
dissolved oxygen (mg l ⁻¹)	0.2	5.8	2.2
pH	3.6	7.3	6
salinity (‰)	0	0	0
leaf litter (scale 0-5)	0	5	1.7
turbidity (scale 0-5)	0	5	2.1
diameter (cm) Tank A only	4.5	11	6.1
tank light level	1	30	4.47

Water temperature varied by less than 4°C, and dissolved oxygen concentration ranged from 0.2 to 5.8 mg l⁻¹ (Table 1). Dissolved oxygen concentration is likely influenced by water temperature, a variable that is negatively correlated with oxygen (df = 1,81; F = 9.514; p = 0.0028; R² = 0.1051). However, no correlation was found between detritus and dissolved oxygen concentrations (df = 1,81; F = 0.3927; p = 0.5316; R² = 0.0048). This finding was unexpected since more decomposing material should consume more oxygen.

Salinity in all water samples was consistently 0‰, indicating that all tanks sampled contained only fresh, likely rain water. An earlier bromeliad study by Laessle (1961) reported pH values ranging from 4.0 to 6.0, although occasionally reaching higher levels to a maximum of 7.0. The pH measured during our study ranged from 3.6 to 7.3, with an average of 6.0 (Table 1). The slightly higher mean pH values compared to Laessle's (1961) findings may be attributed to the calcium content of leaves falling into the tanks used in this study. Laessle (1961) proposed that fallen leaves in calcareous regions, such as dry limestone scrub forests, may have higher calcium content than found in non-limestone regions, thereby accounting for the high average pH values recorded in our study. While pH is generally lower in environments containing high levels of detritus like dead leaves (rich in dissolved organic matter), we found positive relationships between pH and turbidity and between pH and leaf litter. Bromeliad tanks were less than one-quarter filled with leaves on average (generally about 5 leaves). Turbidity was posi-

tively correlated with leaf litter (df = 1,81; F = 10.40; R² = 0.1148; p = 0.0018; Table 1).

Species identified. A total of 15 invertebrate species (Turbellaria, Oligochaeta, Crustacea, and Insecta. Microfauna of Rotifera, Nematoda, and Gastrotricha were not collected) was found in the bromeliad tanks, although Kitching (2001) mentions that some tanks can host up to 20 species. However, it is not clear whether his observation was referring specifically to Caribbean bromeliads or some other tropical regions. No single species inhabited all the bromeliad tanks sampled. Dipteran species included two ceratopogonid larvae (*Bezzia* and *Forcipomyia*), two unidentified herbivorous midge species (Chironomidae), one *Pericoma* (Psychodidae), and one tanypodid midge species. We found two species of mosquito larvae and pupae belonging to the genera *Aedes* and *Wyeomyia* (Diptera, Culicidae). One ostracod and one harpacticoid copepod species were also found. The ostracod appears to be one of the two poorly distinguished species of *Candonopsis* (Little and Hebert, 1996). The harpacticoid appears to be closely related to *Attheyella mervini* Janetzky *et al.* 1996 but does not entirely conform to the original description. One species of turbellarian, *Geocentrophora sphyrocephala* Man. 1876, and one species of aquatic beetle, *Desmopachria* (Coleoptera, Dytiscidae) were also identified. Oligochaetes included *Dero* sp. (Naididae) and two unidentified species.

We obtained many of the same types of organisms that Laessle (1961) identified in his earlier examination of bromeliad phytotelmata. These included ostracods, flatworms, oligochaetes, mosquito larvae (*Aedes*, *Wyeomia*), and *Bezzia*. Laessle (1961) found two species of copepods, a cyclopoid form and harpacticoid form, and indicated that these two species preferred not to coexist, with a majority of his tanks containing one or the other. We found only the harpacticoid species. It is possible that the cyclopoid species avoids bromeliads of the limestone scrub forest, or that the harpacticoid species outcompetes the cyclopoid species in the study area. However, studying a system of erosional rock pools, Azeria & Kolas (2008) found both cyclopoids and harpacticoids coexisting. Additionally, Laessle (1961) identified several species of *Aedes* and *Wyeomia*, including *Ae. inaequalis* Grabham, *Ae. walkeri* Theobald, and *Ae. stenei* Thomson. We have not been able to identify our mosquitoes to species level but all specimens appear to represent single morphospecies belonging to the genera of *Aedes* and *Wyeomyia*.

The average number of species per tank was 4.39, with a range of from 1 to 8 species. This is slightly lower than the 5.94 species identified by Maguire (1971) in bromeliads sampled in Puerto Rico, and may be a result of biogeographical differences or habitat differences. A study by Reid and Janetzky (1996) of Jamaican bromeliads reported comparable but slightly higher numbers, although their species counts were based on whole plants and not individual tanks. *Aedes* spp. inhabited the greatest number of bromeliad tanks (Fig. 2). This observation emphasizes the role of phytotelmata as breeding sites

for mosquitoes, which were found to act as vectors of malaria in Trinidad (Pittendrigh 1948). The high frequencies of occurrence of *Aedes*, midge 1, and *Dero* may indicate they are habitat generalists and are capable of tolerating a wide range of tank conditions or that they are particularly good dispersers. Similarly, Laessle (1961) found that oligochaetes were very tolerant of fluctuations in temperature, dissolved oxygen, and CO₂ which may explain the high occurrence of *Dero* in this study (60% of the sampled tanks). In contrast, Reid and Janetzky (1996) found oligochaetes (*Lumbriculus*) much less frequently.

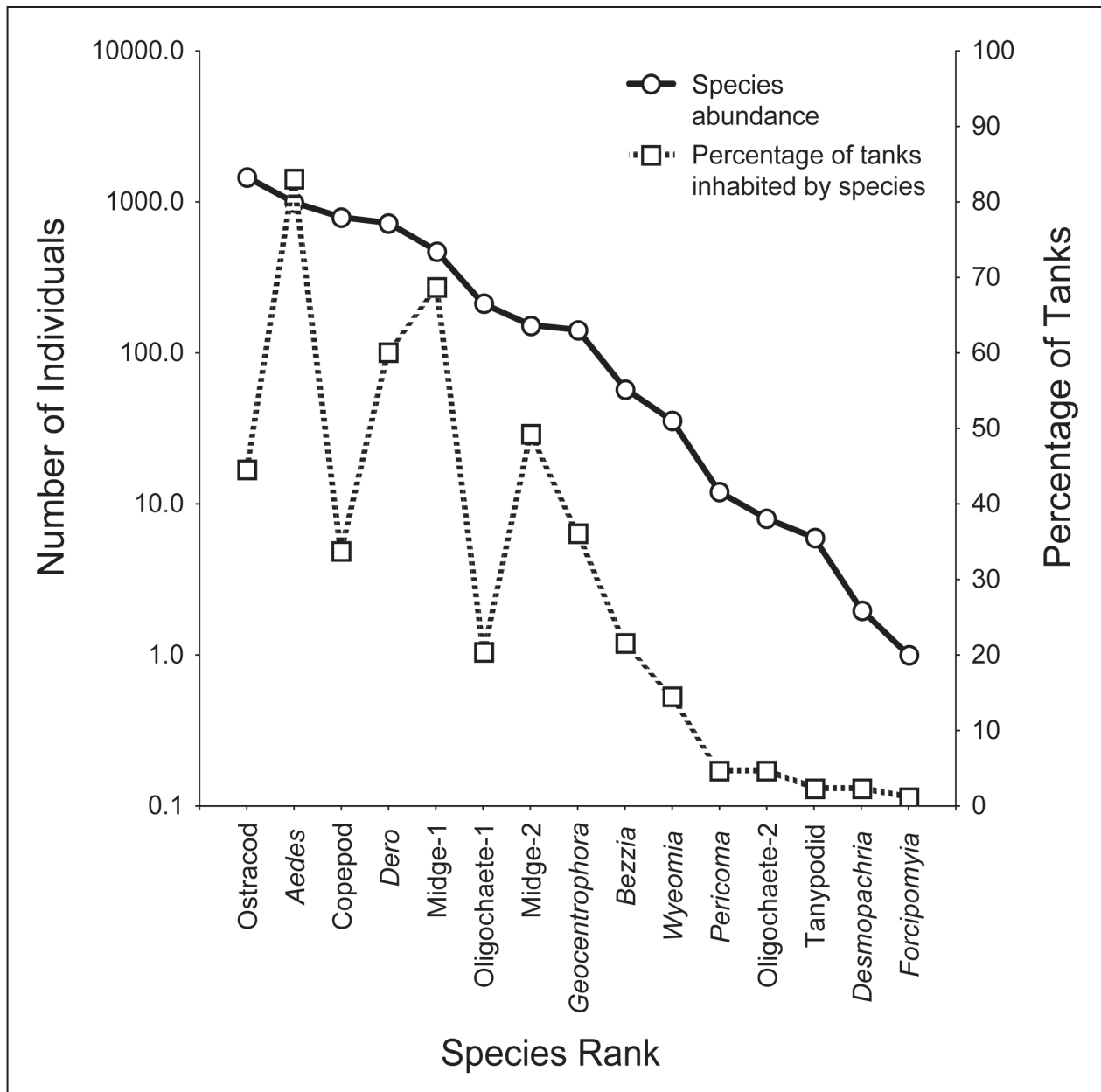


FIG. 2. Mean abundance of species ranked from highest to lowest and their corresponding frequency of occurrence pooled over all the *Hohenbergia polycephala* communities sampled.

Relationships between abiotic and biotic factors. Species richness was best explained by a multiple regression model based on PCA factors (Table 2) which included large tanks, high dissolved oxygen, lower levels of light, and lower levels of leaf litter (df = 4,73; F = 3.89; p = 0.0066; R² = 0.0371). Additionally, a significant positive correlation between leaf litter and species richness was revealed using a simple regression model. This result may be due to the direct effect of habitat properties associated with leaf litter, to time effect (both litter and species accumulate with time), or both combined. Experiments conducted by Reid and Janetzky (1996) showed that a complete colonization of Jamaican bromeliad tanks takes about one year. Thus higher species richness in older tanks is to be expected, unless environmental conditions in those tanks are inferior. Seifert (1984) found that larger *Heliconia* bracts had greater insect species richness than smaller bracts, and associated this with the greater habitat heterogeneity provided by larger bracts. Greater heterogeneity may foster coexistence of a greater number of species within the tank by permitting a broader range of resources as well as providing shelter from predators. Also, the greater number of individuals that can exist in a larger tank may reduce the probability of stochastic extinction (e.g. Schmidl *et al.* 2008).

We attempted to determine whether any of the environmental gradients could explain diversity patterns. However, a multiple regression model for the Shannon-Wiener diversity index (H'), with a summary of environmental conditions in individual tanks represented by the Principle Component (PCA) scores as independent predictors, was not significant

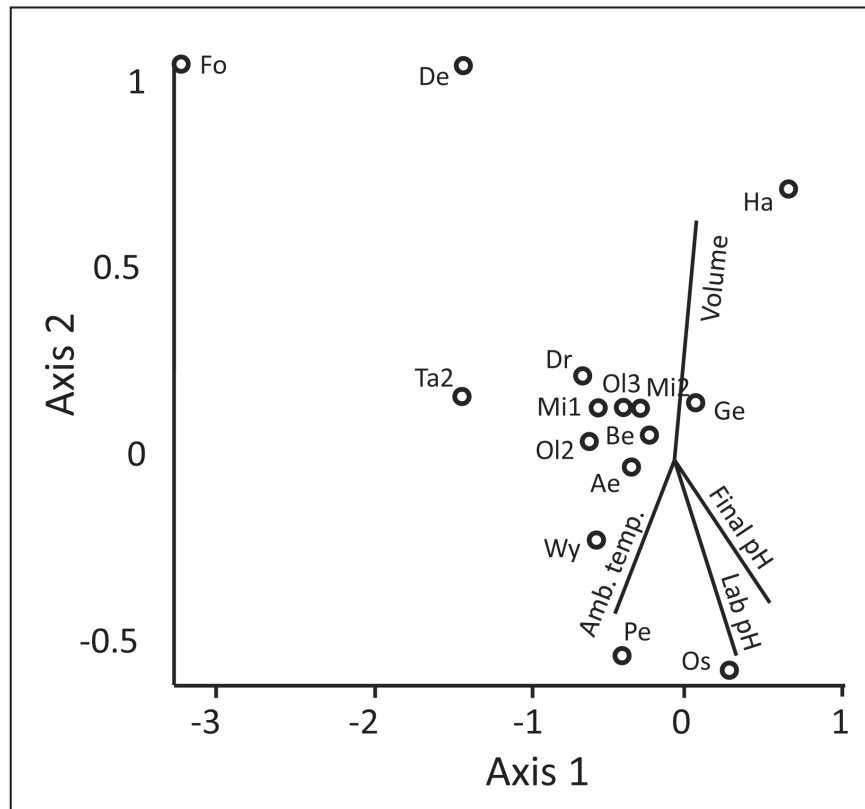
(df = 4,70; F = 1.91; p = 0.1177; R² = 0.1176). In fact only PCA Axis 3 was significantly correlated with H' but did not appear to be ecologically relevant (df = 1,73; F = 5.62; p = 0.0204; R² = 0.0715). Similarly, only PCA Axis 3 was significantly related to the Simpson's diversity index (D) (df = 1,71; F = 6.05; p = 0.0163; R² = 0.0786). This axis was highly weighted by dissolved oxygen concentration (Table 2). Simpson's diversity index and the Shannon-Wiener diversity index yielded similar results when regressed against the PCA factor scores and individual abiotic variables. This finding is significant since both indices emphasize different aspects of relative species abundance or dominance. While Simpson's index emphasizes the most abundant species in the sample, the Shannon-Wiener index weights both rare and common species equally (Magurran 1988). From the similarity of results produced by these two indices we infer that there is no real pattern in the distribution of rare or common species among tanks. This may be due to the complex relationships such as predation, facilitation, and predation known to affect success of individual species in response to presence or absence of their interactors in the bromeliad systems (Heard 1994b, Schmidl *et al.* 2008, Starzomski *et al.* 2010).

Turbidity was related to the abundance of *Aedes* (df = 1,80; F = 5.65; p = 0.0198; R² = 0.0660), ostracods (df = 1,80; F = 5.47; p = 0.0219; R² = 0.0639), and midge 1 (df = 1,80; F = 4.19; p = 0.0439; R² = 0.0498). Turbidity represented the suspended sediment in the tank water, which is presumably caused by the organic inputs by microorganisms, including bacteria, external inputs from

TABLE 2: Principle Component Analysis factor loadings for bromeliad tank characteristics for all 83 tanks. Loadings with absolute values > 0.7000 are marked with an asterisk (*).

Variable	PCA #1	PCA#2	PCA #3	PCA #4
water temperature	0.43	-0.45	0.61	0.21
water volume	-0.79*	0.28	0.22	-0.12
depth of water	-0.78*	0.22	0.08	-0.26
pH	0.48	0.64	-0.05	-0.15
dissolved oxygen	-0.11	0.14	-0.77*	0.52
leaf litter	-0.01	0.80*	0.30	0.10
turbidity	0.67	0.54	0.02	-0.06
tank light level	-0.27	0.21	0.35	0.80*
eigenvalue	2.19	1.74	1.22	1.08
percent variance	27.40	21.77	15.31	13.44

FIG. 3. Ordination of species (CCA) with vectors of the most important environmental variables and ordination scores for species. The vector lengths indicate the relative importance of the factor. Species indentifications: Ae – *Aedes* (dipteran); Be – *Bezzia* (dipteran); Dr – *Dero* (oligochaete); De – *Desmopachria* (coleopteran); Fo – *Forcipomya* (dipteran); Gs – *Geocentrophora sphyrocephala* (turbellarian); Ha – *Nitocra spinipes* (harpacticoid); Mi1 – Midge 1 indet.; Mi2 – Midge 2 indet.; Ol2 – Oligochaete 2 indet.; Ol3 – Oligochaete 3 indet.; Os – Ostracod indet.; Pe – *Pericoma* (dipteran); Ta2 – Tanypodid 2 indet. (dipteran); Wy – *Wyeomyia* (dipteran).



leaf litter and debris, decaying carcasses of invertebrates, and internal production of algae (Laessle 1961, Maguire 1971). Our results were in agreement with Trimble (1979) who found that there was a strong preference of *Aedes togoi* for water containing organic matter. This was due to the increased likelihood that predaceous larvae of *A. togoi* would have access to some organic food if living prey were not immediately accessible. The positive relationships found between turbidity and *Aedes*, ostracods, copepods, and midge 1 abundances may be a reflection of their detritus-related feeding strategies.

Simple regression analyses indicated that a greater number of species inhabit tanks with high levels of leaf litter and turbidity. These habitats may be more spatially heterogeneous and thus provide a wider variety of shelter, food resources, and micro-niches within the bromeliad tank than less turbid or leaf-filled tanks. In turn, such heterogeneity may be more attractive to a greater number of species (*cf.* Kingsolver 1979). While there were positive correlations between species richness and both leaf litter and turbidity, no relationships were found between these abiotic variables and either diversity index.

In view of the generally weak direct relationships between tank attributes and species richness, diversity, and the distribution and abundance of most

species, a question arises as to whether the bromeliad tank community is significantly shaped by micro-habitat properties or by other forces. Those other forces could involve within-tank biotic interactions or inter-tank metapopulation dynamics and dispersal (*cf.* Kitching 2001, Starzomski *et al.* 2010). To address this question we applied a canonical correspondence analysis (CCA) to both species data and tank attributes. CCA performs an ordination of species and constrains it using environmental data. First, CCA organizes species data along a compositional gradient, simultaneously identifies a gradient in the sample (tank) attributes, and finally examines the relationship between the two gradients (Jongman *et al.* 1995). The first three CCA axes explained over 24% of the variance, indicating that there is a fairly strong link between the overall community composition in individual tanks and tank properties, even if much variance cannot be explained by factors included in the study. Furthermore, CCA identifies tank volume, ambient temperature, and pH as major correlates with the community composition gradient (Fig. 3). However, these environmental variables are primarily correlated with Axis 2. Therefore Axis 1 appears to indicate the existence of another source of variation that is not associated with any of the measured physical variables. Possibly factors such as

predation, facilitation, competition, or dynamics of dispersal may exert an even greater influence on the taxonomic make-up of individual tanks than the measured physical factors (see Kitching 2001 for an in-depth review of biological interactions in phytotelmata). Ambient temperature may be an indicator of light and wind conditions and thus be related to the dispersal of propagules. By contrast, volume may have more to do with the conditions in the tank and with the tank age. We address some aspects of the latter in the following section. In sum, both sets of analyses appear to converge in that they indicate a possible large role for biotic interactions, but a smaller role for direct environmental variables.

Relative age of tanks: influence on abiotic and biotic factors. A major focus of this study was to determine whether community composition or any environmental variable differed among phytotelmata with respect to age. There were significant physical differences between Tanks A, B, and C. Leaf litter differed between tanks ($p < 0.00001$), decreasing from a mean of 2.7 in Tank A to 0.8 in Tank C (Table 3). Mean water volume decreased from Tank A to Tank B ($p < 0.00001$) but did not change between Tank B and Tank C (Table 3). Depth also decreased from Tank A to Tank B ($p < 0.00001$; Table 3). Mean tank temperature increased with age, while the mean dissolved oxygen concentration increased from Tank A to Tank B but decreased slightly in Tank C (Table 3).

Significant differences among abiotic factors (temperature, dissolved oxygen concentration, water volume, depth and leaf litter) due to tank age may

be important for determining the habitat suitability. Leaf litter decreased with increasing tank age and may be a result of the outer, older pools being shielded by overlying, wide bromeliad leaves that deflected litter fall accumulation. The most recently formed reservoir (Tank A) had greater depth and volume than the older tanks (B and C). This was attributed to the urn-shaped Tank A and their greater water-holding capacity than the more horizontal, older reservoirs, reflecting changes in plant architecture (Fig. 1). Small differences in mean temperature and mean dissolved oxygen concentration between the tanks of different ages were also detected. Temperature increased from the younger, inner tank to the older, outer tanks. Dissolved oxygen concentration differed among tanks of different ages by only 0.69 mg l^{-1} . Dissolved oxygen concentration increased with increasing age from Tank A to Tank B, but Tank C had dissolved oxygen concentrations only slightly greater than Tank A. Similarly, Laessle (1961) determined that dissolved oxygen concentration was greater in outer tanks than in the inner reservoir, particularly in wooded areas where the inner central tanks were covered with leaves. However, we found no correlation between dissolved oxygen concentrations and leaf litter ($df = 1,81$; $F = 0.39$; $p = 0.5316$; $R^2 = 0.48$).

Previous studies on phytotelmata have found that habitat age may play a role in structuring the invertebrate community (Fish & Hall 1978, Seifert & Seifert 1979, Nastase *et al.* 1995). Fish & Hall (1978) detected successional patterns of organisms inhabiting pitcher plant communities. In the bromeliad

TABLE 3: Summary of ANOVA results between Tanks A, B, and C (relative age). Mean values for each abiotic and biotic variable are given for all samples of the same tank type.

Variable	df	F	p-value	A	B	C
water volume (ml)	2,80	36.07	7.0×10^{-12}	212.19	80.82	80.08
water depth (cm)	2,80	25.9	2.0×10^{-9}	16.3	10.42	9.6
leaf litter (0 to 5)	2,80	11.46	4.0×10^{-5}	2.69	2.4	0.77
water temperature (°C)	2,80	3.38	0.039	23.88	24.01	24.65
dissolved oxygen (ppm)	2,80	3.56	0.033	2.01	2.7	2.18
<i>Aedes</i> (# individuals)*	1,67	4.29	0.042	8.3	16.6	11.04
Midge 1 (# individuals)	2,79	3.47	0.036	3.47	6.81	9.81
species richness (S)	2,79	0.05	0.951	4.61	4.61	4.46
Shannon Diversity (H)	2,79	0.77	0.466	1.03	1.05	1.16
Simpson's Diversity (D)	2,77	0.48	0.623	2.89	2.72	3.07

* in Tanks A and B only

microcosms we found that species richness and species diversity (H') did not differ between tanks of different ages (Table 3). However, there were some species abundance patterns that changed with tank age. Midge 1 abundance increased with increasing tank age ($p = 0.0355$) and *Aedes* was significantly more abundant in Tank A than Tank B ($p = 0.042$; Table 3). This pattern could be due to a variety of factors, including differential food availability according to tank age (Seifert & Seifert 1979). There may be a resource in a younger tank that gradually degrades with increasing age, and which is accompanied by a temporal succession of species that are able to use that resource. Alternatively, there may be abiotic restraints on particular species leading to distinct differences in species composition among different tank ages. Nastase *et al.* (1995) found positive relationships between abundance of the pitcher plant midge *Metriocnemius knabi* (Coq.) and water volume. They also found positive relationships between the mosquito *Wyeomyia smithii* (Coq.) and younger, larger pitchers with little organic matter. Pitcher plant mosquitoes and midges both lay eggs in larger pitchers (Bradshaw 1983, Heard 1994a, 1998; Nastase *et al.* 1995). In our bromeliad microcosms, female mosquitoes and midges may have specific preferences for oviposition sites, such as more sheltered pools with less leaf litter and less volume. Values of these physical characteristics increased with tank age (Table 3). Significant inverse relationships of volume with *Aedes* abundances ($df = 1,80$; $F = 4.53$; $p = 0.0346$; $R^2 = 0.0536$), and midge 1 abundances ($df = 1,80$; $F = 3.97$; $p = 0.0498$; $R^2 = 0.0472$) may also support this suggestion of oviposition site preferences. Additionally, female dipterans may be drawn by chemical attractants for oviposition (Bentley & Day 1989). They may have site quality preferences such as resource levels, chemical and physical factors, and presence and density of competitors and predators for optimal offspring development (Heard 1994a).

Interspecies relationships. We detected a significant positive correlation between the abundances of *Aedes* and midge 1 ($df = 1,80$; $F = 5.47$; $p = 0.0219$; $R^2 = 0.0639$). Nastase *et al.* (1995) obtained a comparable relationship between pitcher plant midges and mosquitoes. As in their study, we were unable to determine whether this correlation was due to an interaction between the two species or was a function of each species responding to environmental factors in a similar manner.

Community structure is often greatly influenced by predator-prey interactions. According to Naeem (1988), mosquito species and harpacticoid copepods in *Heliconia* bracts may be prey for chironomids (*Pentaneura*). In the bromeliad communities we investigated there were no significant relationships between the *Bezzia* (predaceous midge) and copepods ($df = 1,80$; $F = 1.25$; $p = 0.2676$; $R^2 = 0.0153$), *Aedes* ($df = 1,80$; $F = 1.95$; $p = 0.1161$; $R^2 = 0.0238$), or *Wyeomyia* ($df = 1,80$; $F = 0.06$; $p = 0.8065$; $R^2 = 0.08$). The predaceous tanypodid species was too rare for regression analyses but a similar species was found to have limited effects on bromeliad midge survival in Costa Rica (Starzomski *et al.* 2010). This is in spite of findings that several tanypodids contained heads of midge 1 and midge 2 in their guts.

Conclusion. Fifteen species were found to inhabit the freshwater bromeliad tanks in *Hohenbergia polyccephala*. Species richness was most influenced by PCA factors weighted highly by leaf litter, habitat size, dissolved oxygen concentration and light levels. Species diversity was best explained by a PCA factor heavily weighted by dissolved oxygen concentration. However, as indicated by CCA, overall community composition appeared to be more influenced by tank volume, pH, and ambient temperature. This structure of influential variables differs from a similar study conducted by Schmidl *et al.* (2008) on temperate tree-hole communities. Age of the bromeliad tanks may influence the relative abundance of species within each microcosm, but it did not clearly affect species richness or diversity. There were large unexplained variances in all statistical analyses that appear to point to the importance of complex biotic interactions. Nevertheless this study further illustrates how community composition, particularly in reference to the bromeliad plant *Hohenbergia polyccephala*, is likely influenced by a combination of several abiotic and biotic factors of which leaf litter (an indicator of age?), size of aquatic environment, light, oxygen, and the proximity to another tank community (cross dispersal or similar history?) appear to be the most important.

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