

Colonisation of *Heliconia caribaea* by aquatic invertebrates: resource and microsite characteristics

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Abstract. 1. Colonisation of ephemeral aquatic habitats via oviposition by invertebrates may be influenced by a variety of factors, such as the quality of aquatic habitat and the characteristics of the surrounding terrestrial environment. The water-holding bracts of *Heliconia caribaea*, a subtropical herb that produces ephemeral aquatic habitats, are colonised by a variety of aquatic invertebrates. To date, no experiments have been conducted to identify the cues that affect colonisation patterns via oviposition selection in *Heliconia*.

2. Artificial bracts were used to assess the influence of two types of resources found in bracts (plant produced carbohydrates and terrestrial snail faeces) on oviposition site-selection by invertebrate taxa via a replicated factorial design at four locations in the Luquillo Experimental Forest of Puerto Rico, U.S.A. Eleven microsite characteristics thought to affect oviposition were measured for each experimental container.

3. Most taxa responded in a minor way to microsite characteristics, whereas site selection by the most numerically dominant groups (e.g. Syrphidae) were influenced principally by resources within artificial bracts. Overall, the greatest response by particular taxa was to the presence of snail faeces. At the community level, total abundance, richness, and evenness of invertebrates increased with increasing biomass of faeces. Variation in sugar produced a more complex response.

4. In general, the terrestrial matrix surrounding these aquatic habitats was only a secondary determinant of population and community attributes; the principal factor affecting site selection was the quality of the aquatic habitat.

Key words. Aquatic insects, bottom-up, community, diversity, faeces, phytotelmata.

Introduction

Where females lay their eggs is important in shaping population dynamics, species distributions, and community structure of invertebrates. Such behaviour is likely under strong selection, as is illustrated in numerous ecologically specialised life-history phenotypes (Resetarits, 1996). In addition, oviposition behaviour of aquatic invertebrates may have direct fitness consequences for those females capable of assessing the quality of larval habitat (Blaustein & Kotler, 1993; Reich & Downes, 2003). Egg-laying decisions are driven by characteristics of the aquatic environment, including visual, chemical, and tactile cues. Visual cues are likely used over long distances to find ap-

propriate types of habitats (pre-oviposition behaviour), whereas chemical or tactile cues offer more specific information about the quality of a particular site (oviposition behaviour) (Bentley & Day, 1989). Beyond abiotic factors, some taxa also respond to the presence of predators (Blaustein *et al.*, 2004; Eitam & Blaustein, 2004) or conspecifics (Reiskind & Wilson, 2004). Although some species may be highly specialised for a particular habitat type, species that lay eggs in or near aquatic environments probably exploit or share a similar suite of cues for oviposition (e.g. pH, salinity, temperature). Understanding the interplay among factors affecting oviposition choice by most invertebrates is superficial, partly because multiple factors likely influence such choices.

Detrital resources play an important part in aquatic communities (Anderson & Macfadyen, 1976) influencing population and community dynamics of animals. The effects of detritus in small ephemeral aquatic communities, termed phytotelmata (Frank &

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Lounibos, 1983), have been studied extensively. For instance, the effects of leaf litter (e.g. Léonard & Juliano, 1995; Walker *et al.*, 1997; Srivastava & Lawton, 1998), nutrient-bearing stem flow (e.g. Kitching, 1971; Carpenter, 1982; Walker *et al.*, 1991), and dead invertebrates (Yee & Juliano, 2006) on populations and communities of invertebrates is well documented in tree hole microsystems. In pitcher-plant microsystems, external inputs of dead insects shape patterns of invertebrate abundance and diversity (Istock *et al.*, 1976; Cresswell, 1998, 2000; Sota *et al.*, 1998). Several studies have focused on water-filled bracts of the plant genus *Heliconia* (for reviews see Seifert, 1982; Kitching, 2000), as they are highly replicated and isolated containers, containing numerous individuals representing a diversity of invertebrate species (Seifert, 1975; Seifert & Seifert, 1979; Seifert, 1982; Naeem, 1990a). These invertebrate communities have been used to examine a wide variety of ecological questions, including those related to community structure (Seifert, 1975; Naeem, 1990a; Richardson *et al.*, 2000) and species interactions (Seifert & Seifert, 1979; Naeem, 1990b). Recently, Richardson *et al.* (2000) showed that the abundance of different species of invertebrates in *H. caribaea* (Lamarck) in Puerto Rico differed among bracts depending on their age. Although these data support the hypothesis of niche partitioning among habitats, it is unclear if oviposition choices, resource availability (i.e. decaying plant material), abiotic factors, or some combination of factors determine the differences in the distribution of species or individuals among bracts. Naeem (1990a) concluded that resource heterogeneity plays a significant part in determining community structure in bracts of *H. imbricata* (Kuntze) in Costa Rica, although the magnitude of response may depend on resource levels (i.e. flower parts within bracts). No experiments, observational or manipulative, have been conducted to identify the cues that affect colonisation patterns via oviposition selection in *Heliconia*.

In the Luquillo Experimental Forest (LEF) of Puerto Rico, terrestrial gastropods are commonly associated with *Heliconia* leaves, stems, and bracts (Willig *et al.*, 1998). Faeces of the land snail, *Caracolis caracolla* (Linné), are associated with *Heliconia* in the LEF (Cary, 1992; Secrest *et al.*, 1997; Willig *et al.*, 1998) and snails defecate in bracts (Maguire *et al.*, 1968). Indeed >20% of bracts that were surveyed during June 1996 contained *C. caracolla*. The input of faeces by these gastropods may affect patterns of colonisation, and thus represents a potential bottom-up control on diversity. Bract fluid, including carbohydrates, is supplied through active transport by the plant, although precipitation also can augment fluid levels in bracts (Seifert, 1982). In addition to containing rain water, congeners of *H. caribaea* secrete a sugar-rich nectar into bracts (Bronstein, 1986; Wootton & Sun, 1990). Plant-secreted sugars may represent bottom-up controls because they provide nutrition to some invertebrates or to the microorganism prey of invertebrates (Seifert, 1982; Merritt & Cummins, 1996). Because communities in phytotelmata are resource limited (Kitching, 2000), it was hypothesised that the kind and quantity of resources in bracts should affect the pattern of colonisation via oviposition by invertebrates, and thus have significant composition or structure effects on the communities. In fact, invertebrates have been shown to respond positively to increasing organic detritus

(Richardson *et al.*, 2000) and flower parts (Naeem, 1990a) in bracts of *Heliconia*, corroborating the limiting effect of resources in this system.

In this study, two resources (terrestrial snail faeces and carbohydrates) were manipulated to determine how they influenced patterns of invertebrate colonisation in containers that simulated bracts of *H. caribaea*. Use of simulated bracts facilitated control of variation among bracts (e.g. bract volume, opening size, bract age, odour, colour) that may otherwise influence colonisation patterns. In addition, a suite of microsite characteristics that might influence oviposition choice by invertebrates were quantified. This design facilitated an examination of the interaction between internal (i.e. aquatic environment) and external (i.e. terrestrial environment) factors in shaping colonisation dynamics.

Methods

Study site

The LEF occupies 11 330 ha on the eastern side of Puerto Rico (U.S.A.). Average annual rainfall is 3460 mm (McDowell & Estrada-Pinto, 1988) and monthly temperatures range from 21 to 25 °C (Brown *et al.*, 1983). Rainfall is slightly seasonal (Brown *et al.*, 1983), with lower quantities from January to April (dry season) and higher quantities from May to December (wet season).

Although many horticultural varieties of *Heliconia* occur on Puerto Rico, only *H. caribaea* occurs in the Tabonuco forest in the vicinity of El Verde Field Station (18°20'N, 65°49'W). This herb typically grows in clusters in moderately sunlit locations, including road-sides, stream and river banks, rocky slopes, forest openings, clearings, and fields. It reaches a height of 5.5 m, and has large, elongated leaves. Flowers occur within bracts that are produced sequentially to form a raceme. Racemes are large (up to 35 cm in length) and comprise two to 20 bracts.

Experimental design

Artificial bracts of *H. caribaea* were placed within two watersheds defined by the Quebrada Sonadora and Quebrada Prieta, in the LEF. Quebrada Prieta is a second-order stream averaging 20% slope with sand, silt, cobble, and boulder substrates (Masteller & Buzby, 1993). It is characterised by heavy canopy overgrowth resulting in moderate to low influx of sunlight, with slow and sporadic water flow. In contrast, Quebrada Sonadora, a third-order stream, averages 24% slope, and is characterised by moderate to large boulders with a nearly continuous presence of water (McDowell & Asbury, 1994). Although this stream is bordered by mature forest, the wide channel facilitates high light levels throughout most of the day.

A total of 120 containers (250 ml Histoplex[®]), representing a single bract, were placed north and south of the Quebrada Sonadora and Quebrada Prieta ($n = 480$ total). Containers were attached to the stems of *H. caribaea* with fine gauge wire. In this way, containers corresponded to spatial distribution and experienced microsite conditions similar to those of naturally occurring

H. caribaea at each location. Attachment to the stem was near the emergence point of leaves and occurred only on plants that lacked racemes so as to avoid direct colonisation between open racemes and containers on the same stem. Other *Heliconia* that held racemes would provide a source pool of colonists and provide long-distance cues for adults. A stratified random protocol was used to select plants for attachment of containers. A small plastic canopy was positioned above each artificial bract to prevent rainfall from appreciably diluting initial resource concentrations.

Fresh faeces were collected from *Caracolus caracolla* that were found on *H. caribaea*. Faeces were mixed to form a homogeneous mass, placed in a 50°C drying oven for 24 h to desiccate, and ground finely. This approach assured that variation in faeces quality among snails would be eliminated across replicates. One of three concentrations of faeces (0, 2, and 6 g/l) was placed in 50 ml of distilled water within each artificial phytotelmata. These concentrations approximately correspond to none, two, and six defecations by snails. For sugar levels, 50 ml of a sucrose solution was added to each container. Sucrose was added in four concentrations: 0, 1, 4, and 16 g/l of water (observed sucrose range in fluid of *H. caribaea* during March 1996, 0–16 g/l). In instances when both resource types were used in a single container, dry faeces was added to the 50 ml sucrose solution.

Each watershed contained 20 replicates of each of 12 combinations of sugar (four concentrations) and faeces (three masses) in artificial bracts ($n = 120$ containers per location, two locations per watershed). Within each location, each container randomly (without replacement) was assigned to a treatment combination. Because mosquito larvae typically are the first invertebrates to pupate in bracts of *Heliconia* (10–12 days after oviposition; Seifert & Seifert, 1979), all cups were removed 8 days after placement to maximise the capture of larvae. This design, where communities were destructively sampled after 8 days, most likely is indicative of oviposition responses of females to treatments, as little opportunity existed for death as a result of disease, disturbance (i.e. desiccation), or species interactions. At collection, all invertebrates were killed using 70% isopropyl alcohol; individuals subsequently were removed, sorted, and identified to the lowest possible taxonomic level. Because of taxonomic uncertainties regarding the larvae of subtropical invertebrates, some specimens were assigned to morphospecies based on consistent anatomical differences. Unless otherwise noted, the terms species and morphospecies are used synonymously. After identification of invertebrates, richness (S), evenness (E), and total abundance (N) were determined for each artificial bract. Richness was equal to the number of species within a container. Evenness is a measure of equitability with which individuals are apportioned among species. In this case, an evenness index ranging from 0 (all individuals belonging to a single species) to 1 (totally even distribution of individuals among species) was used in which

$$E = \frac{H'}{\ln(S)}$$

where H' , the Shannon Index of diversity (Magurran, 1988), is given by

$$H' = -\sum p_i \ln p_i$$

Eleven microsite characteristics were measured for each artificial bract: the percentage of the slope toward and away from each river, canopy openness above each container, total number of *H. caribaea* bearing racemes within a 3 m radius, total number of *H. caribaea* lacking racemes within a 3 m radius, distance to closest raceme, distance to the closest artificial bract, height of the artificial bract, height of the plant bearing the artificial bract, distance to the river, and distance to the nearest paved road. A clinometer was used to determine the percentage of the slope. Canopy openness was determined using a spherical densiometer positioned 0.5 m away from phytotelmata in each cardinal direction. The average of these four values provided a single estimate of canopy openness.

Statistical analyses

Because of strong correlations among the eleven microsite variables, Principal Components Analysis (PCA) (PROC Factor, SAS Institute Inc., 1990) was used to extract independent principal components (PCs) that represent major environmental gradients that may reflect colonisation dynamics. Principal components with eigenvalues greater than 1.00 were used (Hatcher & Stepanski, 1994) as covariates in subsequent analyses. All covariates (PCs) by main factor (faecal mass, sugar concentration, location) interactions were tested; if not significant, microsite characteristics did not alter the effects of main factors. As such, all non-significant covariate by main effect interactions were eliminated from subsequent analyses. Only those species with densities greater than one individual per container (i.e. >480 total individuals) were analysed. Species with densities less than this would likely be absent from most containers. The response of each taxon was assessed using a separate analysis of covariance (ANCOVA; PROC GLM, SAS Institute Inc., 1990). Sugar ($a = 4$), faeces ($b = 3$), and location ($c = 4$) were categorical factors. As only the strong relationships between main effects and microsite characteristics were of interest, a more stringent significance level for analyses for each taxon was used (i.e. $\alpha = 0.01$). Total abundance, richness, and evenness were analysed using ANCOVA to determine if communities of invertebrates responded to main effects and microsite characters. For community patterns, $\alpha = 0.05$. To enhance normality and homoscedasticity, total abundance was square-root transformed and richness was transformed as $\log(x + 1)$. For analyses of richness and evenness, a Bonferroni correction (Sokal & Rohlf, 1995) was employed to reduce the risk of committing a Type I error.

Results

Fifteen invertebrate species representing eight families were collected from artificial phytotelmata (Table 1). The most species-rich family was Syrphidae, with six species, followed by Ceratopogonidae, with two species. Remaining families were each represented by a single species.

A small proportion of artificial bracts were excluded from analyses because of unplanned additions of rainwater or because

Table 1. Aquatic invertebrates collected from artificial bracts of *Heliconia caribaea* in the Luquillo Experimental Forest.

Subphylum	Class	Order	Suborder	Family	Morphospecies	Individuals
Crustacea	Copepoda			Unknown	1	3
Atelocerata	Insecta	Diptera	Nematocera	Psychodidae	1	123
				Ceratopogonidae	1	1
					2	2
				Chironomidae	1	43
				Culicidae: <i>Culex antillumagnorum</i>	1	1933
			Brachycera	Unknown	1	8
				Syrphidae	1	21,083
					2	16,126
					3	26
					4	29
					5	4360
					6	1
				Dolichopodidae	1	120
		Lepidoptera	Ditrysia	Pyralidae	1	29

of spillage during the 8-day field period. None the less, each of the four locations contained 14–20 replicates per treatment combination.

PC analysis distilled the eleven microsite characteristics into four principal components, which together accounted for 74% of variation among microsites. PC1 was associated positively with the number of plants in a 3 m radius with or without racemes and the total number of racemes in a 3 m radius, and negatively to the distance to the nearest artificial bract (eigenvalue = 1.86). PC2 was related positively to plant height, artificial bract height, and the total number of plants without racemes in a 3 m radius (eigenvalue = 1.61). PC3 was related positively to the percentage of the slope (eigenvalue = 1.33). PC4 was related positively to canopy openness (eigenvalue = 1.01).

Four taxa had sufficient densities for analysis, including Syrphidae sp. 1 (occurring in 92.5% of containers), sp. 2 (92.2%),

and sp. 5 (60.8%), and *Culex antillumagnorum* (Dyar) (36.3%). No covariate by main factor interactions characterised any taxon, except *C. antillumagnorum*. Thus, these interactions were deleted and ANCOVA were rerun except in the case of *C. antillumagnorum*. Densities of Syrphidae sp. 1, sp. 2, and sp. 5 each displayed significant interactions involving sugar and faeces, a result that was consistent regardless of location (Table 2). Syrphidae sp. 1 increased in density with increasing mass of faeces, but higher concentrations of sugar dampened this response (Fig. 1). In contrast, Syrphidae sp. 2 responded positively to increasing mass of faeces and concentrations of sugar (Fig. 2). Colonisation by Syrphidae sp. 5 was idiosyncratic, with a variable response to additions of faeces and sugar (Fig. 3A). In addition, the densities of Syrphidae sp. 5 differed among faeces treatments in a site-specific manner (Table 1), with the South Prieta maintaining the greatest response by this

Table 2. Results (*F*-statistic) of three-way (location, faeces, sugar) ANCOVA (PC1 through PC4 are covariates) on particular taxa colonising artificial bracts of *Heliconia caribaea*.

Source of variation	d.f.	<i>F</i> -statistic			
		Syrphidae sp. 1	Syrphidae sp. 2	Syrphidae sp. 5	<i>Culex antillumagnorum</i>
Location (L)	3, 389	2.37*	3.21	7.39*	0.72
Faeces (F)	2, 389	157.36*	59.61*	40.49*	4.78*
Sugar (S)	3, 389	20.27	44.72*	0.23	4.21*
PC1	1, 389	0.21	1.26	0.03	0.01
PC2	1, 389	7.36*	11.31*	2.08	18.79*
PC3	1, 389	3.64	0.34	2.38	0.21
PC4	1, 389	0.05	1.37	30.40	0.01
L × S	6, 389	1.01	1.20	1.16	1.15
L × F	6, 389	1.14	2.75	3.50*	2.09
F × S	9, 389	5.16*	10.76*	3.30*	0.80
L × F × S	18, 389	1.39	1.40	1.86	0.92

*Significance at $P \leq 0.01$.

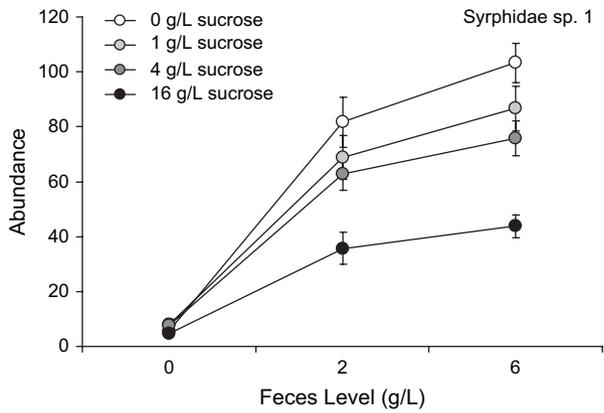


Fig. 1. Results illustrating the significant interaction of faeces and sugar on the mean abundance (± 1 SE) of Syrphidae sp. 1 in artificial bracts of *Heliconia caribaea*.

species (Fig. 3). The response of *C. antillumagnorum* to sugar concentrations differed among locations, but covariate 2 (PC2) also influenced this response (PC2 \times Sugar \times Location $F_{18,389} = 1.39$, $P = 0.006$, Table 3). Based on simple linear regression, three instances occurred when the colonisation response of *C. antillumagnorum* at low sugar concentrations was related positively to PC2 (Table 3).

For community characteristics, no significant interaction occurred between covariates and main effects. As a result, these interactions were eliminated from subsequent analyses. In addition, no two-way or three-way interactions involving main effects (faeces mass, sugar concentration, or location) were significant. All main effects as well as PC1 significantly affected total abundance. Specifically, total abundance was greater in artificial phytotelmata from the North Sonadora as compared with the South Sonadora ($F_{3,338} = 3.7$, $P = 0.012$), but other locational contrasts were not significant (Fig. 4A). Total abundance was significantly greater in moderate sugar concentrations ($F_{3,338} = 4.6$, $P = 0.003$) as compared with other

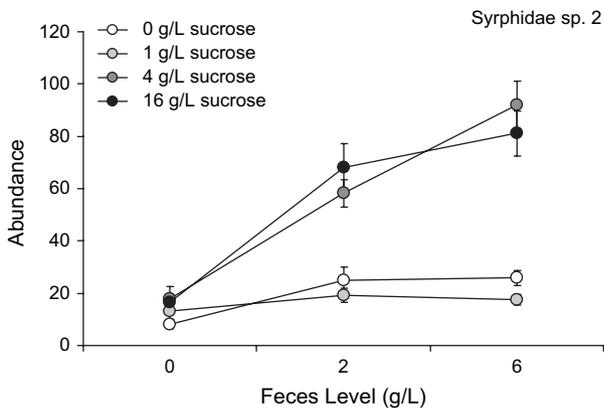


Fig. 2. Results illustrating the significant interaction of faeces and sugar on the mean abundance (± 1 SE) of Syrphidae sp. 2 in artificial bracts of *Heliconia caribaea*.

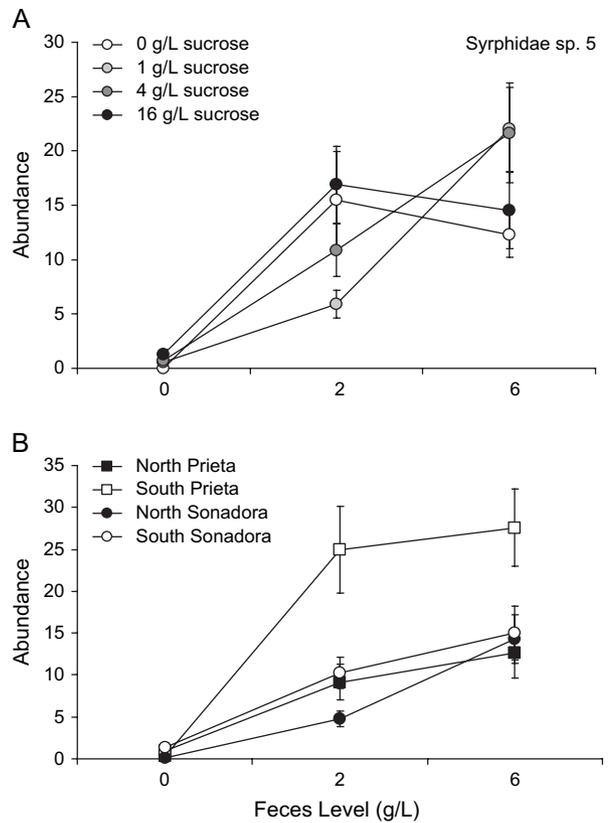


Fig. 3. Results illustrating the significant interaction of (A) faeces and sugar and (B) sugar and location on the mean abundance (± 1 SE) of Syrphidae sp. 5 in artificial bracts of *Heliconia caribaea*.

concentrations (Fig. 4B). Finally, total abundance increased nearly sevenfold ($F_{2,338} = 226.9$, $P < 0.001$) with increasing faecal mass (Fig. 4C). Both richness and evenness differed as a consequence of faecal additions ($F_{3,338} = 8.9$, $P = 0.002$), with significantly higher evenness in the presence versus the absence of faeces (Fig. 5). Richness ($F_{3,338} = 41.29$, $P < 0.001$) was greater when faeces was present than absent (Fig. 6).

Discussion

Resources within artificial bracts were more important than microsite characteristics in determining patterns of colonisation by invertebrates as a consequence of female ovipositing. Females locate suitable ovipositing sites via a number of general and specific cues (Bentley & Day, 1989; Merritt & Cummins, 1996). In the case of *Heliconia*, females most likely use flower aroma and colour to locate patches of potential oviposition sites (Seifert, 1982), and then use specific cues (e.g. resource amount) associated with particular bracts of different ages to choose where to deposit eggs (Richardson *et al.*, 2000). The results presented here reinforce this supposition, as most of the common species responded to variation in specific cues, such as faeces mass or sugar concentration, and not to more general cues, such as microsite characteristics.

Table 3. Results of simple linear regressions for the abundance of *Culex antillumagnorum* versus PC2 within combinations of location and sugar concentration.

Location	Sugar (g/l)	Slope	Intercept	Adj. R^2	P -value
North Sonadora	0	3.95	3.17	0.30	0.002
	1	6.08	5.50	0.11	0.055
	4	1.96	-1.42	0.01	0.290
	16	0.85	0.32	0.00	0.738
South Sonadora	0	5.01	2.53	0.03	0.213
	1	8.09	7.54	0.25	0.019
	4	2.65	2.17	0.03	0.212
	16	1.86	1.04	0.03	0.203
North Prieta	0	9.03	5.14	0.12	0.049
	1	5.78	5.09	0.11	0.069
	4	6.45	1.18	0.00	0.787
	16	1.01	-0.31	0.00	0.509
South Prieta	0	15.03	9.56	0.05	0.159
	1	3.93	0.51	0.00	0.702
	4	2.47	2.99	0.09	0.098
	16	2.28	1.87	0.00	0.447

The majority of species that oviposited in artificial bracts were consistent with those encountered by Yee (1999), who surveyed 148 natural racemes (1095 bracts) within the LEF during the same time. Species that were numerically dominant in this study (e.g. Syrphids 1, 2, *Culex antillumagnorum*) also were common in natural bracts (Yee, 1999), although relative abundance distributions may be misleading, if the variation in combinations of sugar and faeces in natural bracts were not similar to the levels used in this study. Yee (1999) did not find dolichopodids or pyralids in natural bracts, and it is possible that these two groups are generalist species that oviposit in a variety of small aquatic containers. Many species that are *Heliconia* specialists are adapted to oviposit in bracts of one or a few species of *Heliconia* (Seifert, 1982, and references therein), although several species appear to be phytotelm generalists (Richardson *et al.*, 2000). Even though some species require tactile cues (e.g. wall surface) to elicit oviposition, other species land directly on the water surface, and use cues associated only with the aquatic environment (e.g. mosquitoes, Bentley & Day, 1989). Richardson and Hull (2000) suggest that colour and odour alone would not be sufficient to explain patterns of colonisation in natural bracts, but differences in chemistry (e.g. sugar concentrations) or detritus among bracts are used to make oviposition decisions. Artificial bracts used here did not have general cues associated with *H. caribaea* (e.g. colour or odour), although bracts were attached to existing *H. caribaea* plants that occurred within large clumps of flowering plants. Many general cues (e.g. odour) were apparent to attract adults to artificial bracts, although this work suggests that oviposition decisions were made based on the quality of the larval habitat. The interplay between general and specific cues likely determine oviposition decisions by many insects.

Input of snail faeces influenced population (Figs 1–4) and community (Figs 5 and 6) attributes of these invertebrates more than carbohydrates did. Snail faeces is a complex resource derived from digested plant tissue, whereas sugar represents a single carbohydrate. Faeces provides food for saprophagous and

coprophagous invertebrates (Seifert, 1982; Merritt & Cummins, 1996), including Ceratopogonidae, Chironomidae, Psychodidae, and Syrphidae. These taxa inhabit stagnant aquatic systems such as septic lagoons and sewers (Stehr, 1987; Thorp & Covich, 1991) as well as bracts of *Heliconia* (Seifert, 1982; Yee, 1999; Richardson & Hull, 2000). Indeed, most common syrphid taxa were significantly more abundant in treatments with high concentrations of faeces, whereas the effects of sugar were more variable. Although some aquatic invertebrates consume carbohydrates (Seifert, 1982; Wigglesworth, 1984; Ziegler, 1985), it is more likely that sugar concentrations indirectly influence invertebrates through the consumption of microorganisms that subsist on sugar. Faeces also may provide a medium for the growth of bacteria, protozoans, and fungi. In addition to depositing faeces, *Caracolis caracolla* in the LEF have been shown to readily transport a number of microorganisms, including *Paramecium* and rotifers among bracts of *H. caribaea* (Maguire & Belk, 1967). In this way, faeces may seed communities with cysts and individuals that form the biotic base of the aquatic food web. The complex response of the most abundant syrphids to both resource types may be a consequence of the synergistic effect of faeces and sugar on dynamics of the microorganism food web. Because faeces were dried before use, the abundances of living microorganisms associated with it were likely reduced, although the nutrient quality of faeces was likely unaffected in a significant way.

Richness and total abundance significantly increased with the addition of faeces. This is consistent with the work of Richardson *et al.* (2000), who documented that abundance of invertebrates was related positively to total organic detritus (although not significantly so). Communities were more even in treatments containing faeces. Many species that were dominant in treatments without faeces were in low abundance in treatments containing faeces (e.g. *Culex antillumagnorum*, Pyralidae, Dolichopodidae). The increase in evenness was reflected in an increase in species richness, through the addition of several taxa that appeared only at 6 g/l of faeces (Syrphidae sp. 4, sp. 5, and

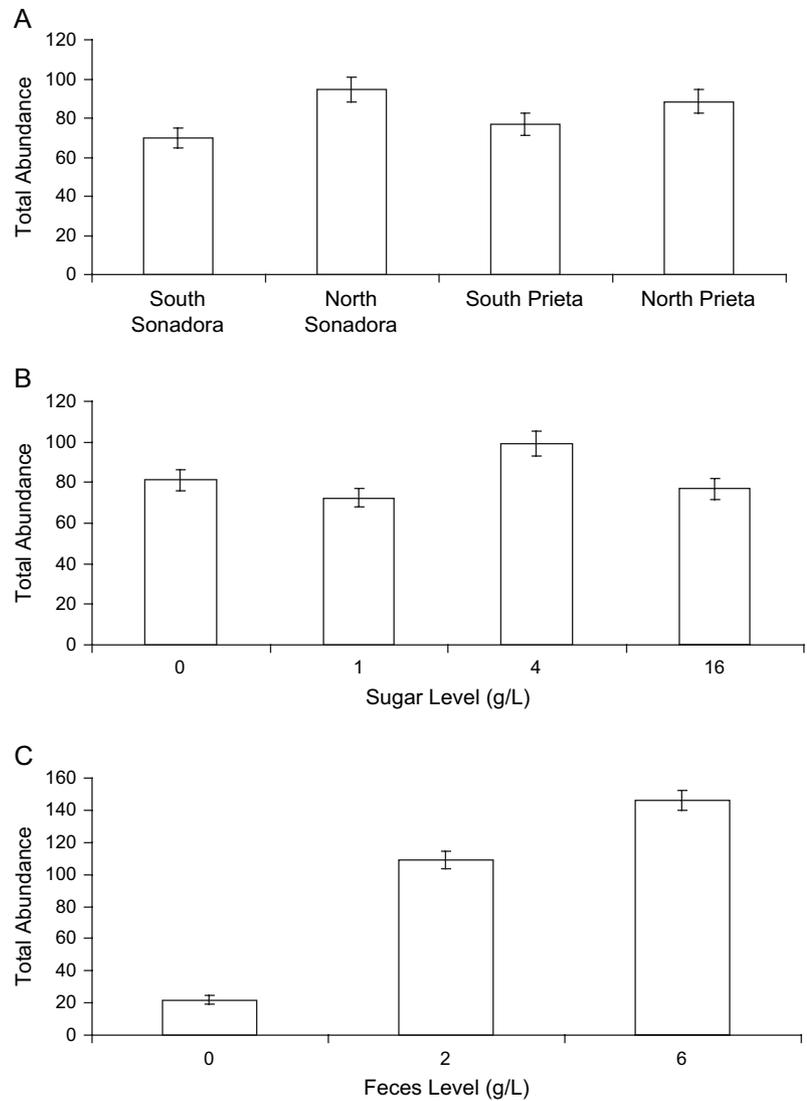


Fig. 4. Comparisons of total abundance (± 1 SE) of invertebrates in artificial bracts of *Heliconia caribaea* with respect to (A) location, (B) sugar, and (C) faeces. Treatment levels that share a letter above bars are statistically indistinguishable ($P > 0.05$).

sp. 6, and Psychodidae). Two of these species, Syrphid sp. 4 and Psychodid sp., attained abundances similar to more common taxa, including chironomids and dolichopodids. This is in contrast with results from *Heliconia* in Costa Rica, where evenness increased only via increases in the abundance of common taxa, rather than through the addition of new or rare species (Seifert, 1975). The strong influence of faeces on invertebrate colonisation in this study suggests that *Caracolus caracolla* plays an integral role in determining the abundance and richness of invertebrates in bracts of *Heliconia caribaea*.

The interaction of microsite characters and resources affected the abundance of one taxon (*Culex antillummagnorum*, Table 3). Densities of this mosquito decreased with increasing levels of sugar (mean abundance ± 1 SE, 0 g/l sugar = 7.76 ± 1.85 , 1 g/l = 5.79 ± 1.62 , 4 g/l = 3.87 ± 1.18 , 16 g/l = 1.80 ± 0.59). Hudson (1956) determined that two species of culicids displayed

differential responses to ovipositing in glucose. As concentrations of glucose increased from 0 to 80 g/l, *Culex molestus* (Forskål) increased whereas *Aedes aegypti* (L.) decreased egg deposition in laboratory containers. Female *C. molestus* also showed a preference for drinking the same water in which it showed an oviposition preference (Hudson, 1956), indicating that adult requirements (e.g. sugar) may interact with larval habitat quality to shape oviposition decisions. In this study, the response of *C. antillummagnorum* to different sugar concentrations also increased with changes in plant and artificial bract height for three of the 16 interactions (i.e. PC2, Table 3). *H. aurea* (Rodríguez) in Venezuela supports three species of mosquitoes that differed in abundance among bracts at different heights on the same raceme (Seifert, 1980). Spatial partitioning of mosquito species has been hypothesised to result from oviposition choice by females (Seifert, 1980; Seifert & Barrera, 1981).

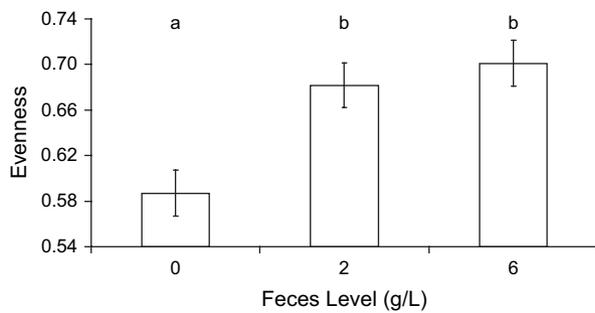


Fig. 5. Comparisons of evenness (± 1 SE) among faeces levels for invertebrates in artificial bracts of *Heliconia caribaea* as a function of faecal mass. Treatment levels that share a letter above bars are statistically indistinguishable ($P > 0.05$).

Vertical selectivity of oviposition sites has been shown for other mosquitoes (Yap & Foo, 1984). Such differences in oviposition selectivity may reflect different larval requirements that correspond to conditions in particular ages of bracts, or may be a way to reduce interspecific competitive interactions among similar taxa (Bentley & Day, 1989). Knowledge is lacking regarding how adult and larval habitat requirements differ in insects with complex life cycles, and how such differences shape spatial distributions in nature.

Phytotelm systems are resource limited, and thus are controlled by bottom-up (i.e. resource) rather than top-down (i.e. predator) forces (Kitching, 2000), especially in *Heliconia* bracts (Seifert, 1982; Richardson *et al.*, 2000). The large quantitative effect of resources on communities and populations appears to be ubiquitous in aquatic microsystems (Naeem, 1990b; Jenkins *et al.*, 1992; Srivastava & Lawton, 1998). This may be a consequence of their ephemeral nature. Invertebrates in bracts of *Heliconia* lack substantial first-order interactions (Seifert & Seifert, 1976, 1979; Richardson *et al.*, 2000). Instead, the transitory nature of these systems leads to communities that result from the oviposition choices of females (Seifert, 1982). Moreover, species within natural bracts exhibit distant evolutionary relationships (Seifert, 1984), and thus they exhibit dis-

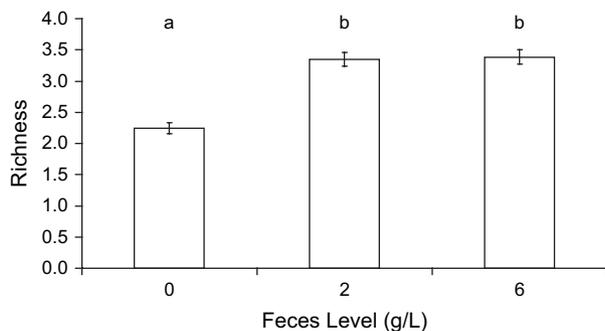


Fig. 6. Comparisons of richness (± 1 SE) among faeces levels for invertebrates in artificial bracts of *Heliconia caribaea* as a function of faecal mass. Treatment levels that share a letter above bars are statistically indistinguishable ($P > 0.05$).

tinctive life cycle specialisations. Little likelihood for resource competition exists, because even when overlap in resource utilisation occurs, low densities of species effectively reduce the negative demographic consequences of competition (Seifert, 1984). First-order interactions may also be absent because of the short life span of bracts. Most *Heliconia* bracts only are viable to invertebrate habitation for a few months (Seifert, 1982). As such, invertebrate species that dwell within them mirror the short life span of bracts and may not interact in a competitive manner (Seifert, 1982). Based on the results of this research, and because similar evanescent systems lack strong first-order interactions, resources appears to be one of the few forces structuring the communities within phytotelmata. Moreover, these results indicate that resources provide a strong cue for oviposition by females, who select resource-rich habitats rather than resource-poor habitats.

Natural selection should favour the ability of invertebrates to locate bracts in a timely manner, due to the limited period that these habitats are available for colonisation (Seifert, 1975). Variation in resources among bracts may be a primary cue used by females to select oviposition sites, an interpretation consistent with the results for other *Heliconia* communities (Seifert, 1982; Naeem, 1990a; Richardson & Hull, 2000). This work underscores the importance of aquatic resources in this system, and provides further evidence of the complex life-history adaptations exhibited by species that are microsystem specialists.

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