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COMMUNITY STRUCTURE IN WATER-FILLED TREE HOLES OF PANAMA: EFFECTS OF HOLE HEIGHT AND SIZE

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ABSTRACT. Abiotic conditions differ from canopy to understory in rain forests. Many taxa are more diverse or abundant in the canopy and/or have vertically stratified species distributions. Water-filled tree holes are common aquatic habitats in many neotropical forests, yet little is known of factors influencing their biodiversity. I compared community parameters (species richness, abundance, and composition) of tree hole macroorganisms at different heights (canopy, midstory, understory) in the forest of Barro Colorado Island, Panama. Data from multiple censuses of 40 artificial tree holes during three wet seasons (1995–1997) revealed a small but significant decrease in the average number of species present with increasing height above the ground. Species richness and abundance were greater in larger holes. Similar patterns were observed in 206 natural tree holes. Of seven top predator species, one was not found in holes > 7 m above the ground; four other species occurred only in understory holes (ca. 1 m above the ground). Chemical properties of tree hole water did not differ with height, but canopy tree holes dried out more frequently and were thermally less stable than midstory and understory holes. Harsh thermal conditions and higher disturbance frequency may be responsible for the decline in species richness with height.

Key words: canopy, community, disturbance, tree hole, tropics

INTRODUCTION

Data from insecticide fogging and other methods (Erwin 1995, Basset et al. 1997) suggest that rain forest canopies harbor the bulk of global biodiversity and are more species-rich than lower forest levels (e.g., Erwin 1982, Kitching et al. 1993). Forest canopies contain a variety of patchy microhabitats, such as litter packs (e.g., Nadkarni & Longino 1990), tank bromeliads (e.g., Pittendrigh 1948) and tree holes (e.g., Galindo et al. 1951) with partly or wholly concealed faunas that cannot be sampled effectively by fogging (Adis 1990, Stork & Hammond 1997). The biotic diversity of these habitats in the canopy and along vertical gradients within tropical forests is not well known, partly because data collection tends to be especially labor- and time-intensive (Tobin 1995).

Many organisms have vertically stratified distributions in temperate and tropical forests, including epiphytes (e.g., Pittendrigh 1948, Benzing 1995); invertebrates (e.g., Longino & Nadkarni 1990, Brühl et al. 1998); lizards (Reagan 1995); birds (e.g., Pearson 1971); and mammals (Harrison 1962). Among tropical insects, height-specific distributions are best known for sylvan mosquito species (e.g., Bates 1944, Mattingly 1949, Galindo et al. 1950, 1951, 1955, Trapido et al. 1955). The forest canopy is drier and windier and receives more light than lower forest levels (e.g., Chazdon & Fetcher 1984, Parker 1995). Differences in physiological tolerances among species with respect to one or more of these factors generally are thought to cause stratified distributions. Other factors that may influence the vertical ranges of some species include predation pressure (e.g., Papageorgis 1975); resource availability (e.g., Basset 1992); and distributions of preferred hosts (e.g., Dunn et al. 1968).

Tree holes are phytotelmata created by collections of rainwater in tree cavities that serve as breeding sites for several neotropical pest species and disease vectors. As a result, most tree hole research has focused on the biology of economically significant groups, especially mosquitoes. Community-level studies of Central American tree holes are few (e.g., Snow 1949), although tree hole predator assemblages in Panama have been well studied (e.g., Fincke 1992a, 1994, 1998, 1999). In understory tree holes, the coexistence of major predators depends on asymmetrical interspecific competition and seasonal drying; abiotic factors other than hole volume are not predictive of species occupancy. Little is known of the abiotic and biotic factors affecting diversity in tropical tree holes at canopy and midstory heights.

Water-filled tree holes are suitable for community ecology studies, given their relatively small size, clearly defined boundaries, and characteristic animal assemblages (e.g., Kitching 1971, Lounibos 1983). Species inhabiting natural tree holes also colonize artificial container habitats (e.g., Pimm & Kitching 1987, Fincke et al. 1997, Yanoviak 1999), thus providing a means to control multiple factors in ecological experiments.

The primary objective of this study was to determine how communities of macroorganisms in tree holes differ in terms of species richness, abundance, and composition with vertical position in the forest. Two secondary objectives were to assess the influence of tree hole size (volume) as a determinant of community structure and to determine how abiotic conditions such as water chemistry and temperature vary with height above the ground.

MATERIALS AND METHODS

The study site was the lowland moist forest of Barro Colorado Island (BCI), Panama (see Leigh et al. 1996 for a site description). Water-filled tree holes are common and widely distributed in the BCI forest during the wet season (May–December), and they typically dry out by late dry season (Fincke 1992a). BCI tree holes range in volume from < 0.05 to > 50 l and occur at all heights within the forest. In this study, midstory and canopy tree holes were accessed using modifications of the single-rope climbing technique (Perry 1978).

Natural Tree Holes

The macrofauna in 206 natural tree holes was censused on BCI over three wet seasons (May–December 1995, May–August 1996, July–December 1997). Of the tree holes examined, 22 were at midstory height (10–20 m) and 30 were in the canopy (>20 m). Height classes were based on the arbitrary vegetation divisions of Hubbell and Foster (1990). Although sample sizes were low at midstory and canopy heights, I censused these holes with greater frequency (up to five times per year) than understory holes (generally once or twice each season). Midstory and canopy holes were found by searching for overflow stains on tree trunks or branches; by visually scanning nearby tree crowns while climbing for this and other projects; and by observing monkeys drinking from holes during their movements through the canopy.

Tree holes were censused by removing their contents to a white plastic pan. A siphon (2 cm inside diam.) was used to empty large holes and a turkey baster to drain small holes. Most of the remaining detritus and sediments were hand-collected to a depth of 3 cm (depending on hole morphology), and each hole was washed up to three times to dislodge animals clinging to interior walls. After collecting subsamples of taxa that could not be identified in the field, I returned water, organisms, and detritus to the hole.

Height above the ground, maximum volume, and host tree species were recorded for the majority of holes censused. Volume estimates of very large holes were made from their linear dimensions and shape. Volume was used as a measure of size because it is relatively easy to quantify in the field and is correlated with hole surface area (Fincke 1994, Yanoviak 1999).

Artificial Tree Holes

In May 1995, two sizes of artificial tree holes (black plastic containers; small, 0.65 l, and medium, 1.5 l) were placed in canopy trees of primary forest at three heights (understory, 1.0–1.3 m; midstory, 10–16 m; canopy, 21–35 m). The factorial array of six artificial tree holes (2 sizes × 3 height classes) was replicated in each of six trees: one *Ceiba pentandra* (L.) Gaertn. and three *Pseudobombax septenatum* (Jacq.) Dug. (Bombacaceae), one *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), and one *Hymenaea courbaril* L. Caesalpiniaceae. In all, 18 small and 18 medium containers were distributed evenly among the three heights. In addition, a large (6.65 l) pan-shaped container was placed at canopy height in each of the six trees.

Artificial tree holes were secured to tree trunks or branches using 6 mm polypropylene rope. Most (90%) of the artificial tree holes remained in place for the entire 3-year span of the study. An alternative method—suspending containers from tree branches with a rope and pulley system (e.g., Loor & DeFoliart 1970)—proved inefficient; contents were lost because of disturbance from canopy mammals or spillage during collection.

Leaf litter from the forest floor was added to each container at the time of setup and monthly thereafter during the 1995 wet season. Natural litterfall was allowed to accumulate in the holes. The initial quantity of litter placed in each container was ca. 33% of the total container volume (uncompressed litter measured in a large graduated cylinder), and within the range of litter densities observed in natural holes. Subsequent litter inputs were $\leq 10\%$ of total container volume. Litter was added to containers in 1996 and 1997 only when their contents had been removed or otherwise disturbed between censuses. Each container was filled with rainwater or filtered lake water, and a piece of tree bark was inserted to serve as an oviposition site for insect colonists.

Species composition and abundance of macroorganisms (body size ≥ 1.0 mm) in artificial tree holes were recorded 20 times, every 14th day from late May to early December 1995 ($N = 13$ censuses); once monthly from May to August 1996 ($N = 3$ censuses); and once monthly from July to October 1997 ($N = 4$ censuses).

For each census, the contents of a container were emptied into a white plastic pan, individuals of each species were counted, and all material was returned to the container. The time required to complete a census varied with container size and macroorganism abundance but did not exceed 60 min. per container. All containers on a given tree were censused on the same day.

Two of the large artificial tree holes fell from the canopy within 4 months of placement, the rope securing them having been cut by *Azteca* spp. ants. Rope subsequently was replaced with wire where necessary. The large containers repeatedly were disturbed and occasionally drained by monkeys. These holes were refilled and censused because they provided useful qualitative species composition and distribution information; however, this size class was excluded from statistical analyses.

Abiotic Factors

Measurements of pH were made once in each of 194 natural holes and in all artificial tree holes on eight census dates. I used Hydrion® colorimetric test paper or a Corning® modular electronic meter, depending on availability. Values did not differ by method (paired $t = 0.88$, $df = 14$, $P = 0.39$). Conductivity and dissolved oxygen (DO) were measured in 86 natural holes and 36 of the 40 remaining artificial holes (once each) in 1997 with an electronic meter. Measurements were made at ca. 4 cm depth (10 cm for conductivity) immediately prior to censusing the hole.

Variation in the water temperature of artificial tree holes was measured along the vertical gradient by submerging a Taylor® minimum/maximum thermometer in each of the three medium volume containers on a tree for 24 hours. Simultaneous measurements were made of min./max. air temperatures with a second thermometer secured to the tree next to each medium container. This procedure was repeated twice for each tree during the 1995 wet season.

Another experiment was conducted to determine how volume and exposure affect the drying frequency of artificial tree holes during the wet season–dry season transition. Small artificial tree holes, each containing 0.1, 0.2, 0.3, 0.4, or 0.5 liters of tap water, were placed in the forest understory. Drain holes prevented filling beyond experimental volumes, and container rims were trimmed so that they exceeded the maximum water level by ca. 3 cm. An identical group of five containers was placed in the lab clearing in direct sunlight, where temperature and humidity are similar to canopy conditions (S. Paton pers. comm.). The presence or absence of water in each cup was recorded daily for 175 days beginning mid-August 1997.

Data were tested for normality with normal probability plots prior to analysis. The $\log(x+1)$ transformation was used to correct variance heterogeneity when necessary (Sokal & Rohlf 1981). All means presented in results are ± SE (standard error) and were calculated from untransformed data. Means were compared with Ryan-Einot-Gabriel-Welsch multiple range tests when ANOVA results were significant.

Mosquito species were determined using Darsie's (1993) keys and an unpublished key to the mosquitoes of Panama (Gorgas Mem. Lab., Ancon, Panama). Taxonomic assistance was provided by J. Gelhaus (Diptera: Tipulidae), J. Polhemus (Hemiptera), N. Powers (Diptera: Culicidae), F.C. Thompson (Diptera: Syrphidae), A.S. Rand (Vertebrata), and N. Woodley (Diptera: Stratiomyidae). Vouchers were deposited at the Smithsonian Tropical Research Institute, Panama, and the U.S. National Museum, Washington, D.C.

RESULTS

Mean macroorganism species richness in natural tree holes was lower in the canopy than at midstory and understory heights (ANOVA: $F_{2,74} = 4.07$, $P = 0.02$), but macroorganism abundance did not differ among height classes ($F_{2,72} = 0.12$, $P = 0.88$; TABLE 1). The number of species and individuals in a hole were correlated with hole size (richness $r = 0.45$, $N = 201$, $P < 0.01$; abundance $r = 0.43$, $N = 185$, $P < 0.01$). Larger holes generally contained more predator species, and tadpoles of *Agalychnis callidryas* and *Physalaemus pustulosus* only occurred in holes > 3 l. Effects of hole size on species richness and abundance did not differ among height classes (ANCOVA: richness $F_{2,74} = 1.40$, $P = 0.25$; abundance $F_{2,72} = 1.31$, $P = 0.28$).

Average species richness in artificial tree holes was lower in midstory and canopy than in the understory (repeated measures ANOVA: $F_{2,30} = 3.78$, $P = 0.03$), but mean abundance did not differ among heights ($F_{2,30} = 0.92$, $P = 0.41$; FIGURE 1). Medium volume artificial holes contained more species ($F_{1,30} = 4.99$, $P = 0.03$) and individuals ($F_{1,30} = 26.6$, $P < 0.01$) than small holes (FIGURE 2). There were no interactions among main effects of height and volume for species richness and abundance in artificial tree holes (2-way repeated measures ANOVAs: $F_{2,30} < 0.43$, $P > 0.65$ for both tests), and time*treatment effects were not significant ($P > 0.25$ for all tests).

TABLE 1. Means (±SE) of community parameters and abiotic factors in natural tree holes at different height classes. Not all variables were measured in all holes; ranges are in brackets and sample sizes in parentheses.

Parameters/factors	Understory	Midstory	Canopy
Richness	5.9 ± 0.17 [1–14] (154)	4.3 ± 0.74 [0–10] (22)	3.1 ± 0.34 [0–6] (30)
Abundance	31.7 ± 2.36 [1–153] (150)	30.3 ± 8.16 [0–147] (18)	41.4 ± 14.2 [0–373] (28)
Volume (l)	1.08 ± 0.23 [0.02–29.8] (154)	5.81 ± 2.3 [0.02–45.8] (22)	1.77 ± 0.78 [0.013–12.8] (25)
Conductivity (μS)	286 ± 23.5 [55–951] (65)	462 ± 194 [117–1982] (9)	324 ± 34.4 [146–540] (12)
pH	5.96 ± 0.06 [3.4–8.0] (150)	6.34 ± 0.17 [5.0–7.5] (20)	6.06 ± 0.12 [5.0–7.0] (24)

About 60 species of macroorganisms are associated with water-filled tree holes on BCI (Yanoviak 1999). Of these, two mosquito species, *Haemagogus lucifer* and *Trichoprosopon digitatum,* were found only in understory tree holes. These distributions generally agree with the findings of Galindo et al. (1950, 1951). Larvae of the giant damselfly *Megaloprepus coerulatus* were not found in artificial or natural holes above 7 m, and the frog *Physalaemus pustulosus* only colonized holes near ground level. Artificial holes lacking *M. coerulatus* typically were occupied by other top predator species, and there was a negative association between the presence of *M. coerulatus* and *Mecistogaster* spp. in nat-

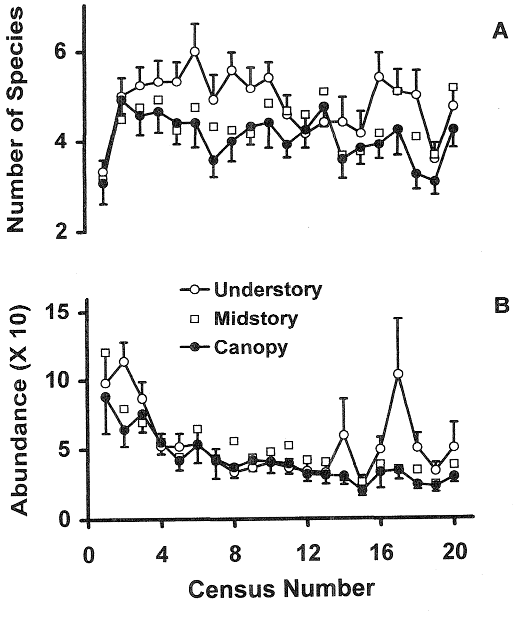

FIGURE 1. Mean (±SE) macroorganism species richness (A) and abundance (B) in artificial tree holes at three heights. The sharp increase in abundance on census 17 was caused by excessive nutrient inputs—fruits of *Gustavia superba* fell into understory holes 2 weeks prior to that census.

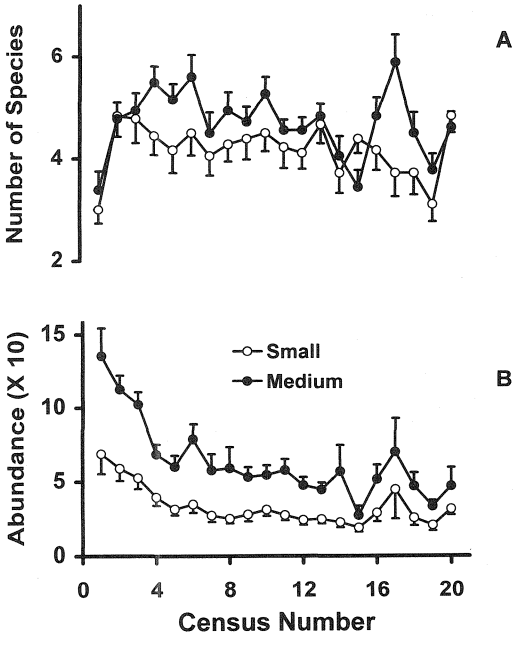

FIGURE 2. Mean (±SE) macroorganism species richness (A) and abundance (B) in different sizes of artificial tree holes.

TABLE 2. Percent occurrence of selected taxa in natural (Nat) and artificial (Art) tree holes among the three forest height classes. Values are cumulative frequencies for natural holes and means across 3 years for artificial holes. Data from multiple censuses of a single hole were pooled. Sample sizes are in parentheses.

	Understory		Midstory		Canopy	
Taxon	Nat (154)	Art (12)	Nat (22)	Art (12)	Nat (30)	Art (16)
Annelida: Oligochaeta						
Dero spp.	28	42	14	8	10	0
Odonata: Aeshnidae	10	36	36	22	7	21
Odonata: Pseudostigmatidae						
Mecistogaster spp.	40	71	50	86	13	69
Megaloprepus coerulatus	32	24	0	0	0	0
Diptera: Ceratopogonidae						
Bezzia snowi	36	44	18	78	7	56
Forcipomyia spp.	10	25	5	36	10	40
Diptera: Chaoboridae						
Corethrella appendiculata	14	8	0	0	0	0
Diptera: Chironomidae						
Chironomus sp.	29	61	9	39	3	33
Diptera: Culicidae						
Aedes terrens spp. complex	53	94	45	81	20	87
Anopheles eiseni	33	53	36	53	3	42
Culex conservator	22	8	14	25	7	13
Culex corrigani	22	33	23	25	3	19
Culex mollis	12	22	9	19	3	4
Culex urichii	12	97	14	94	30	96
Haemagogus (*H.*) spp.	27	42	33	58	34	56
Toxorhynchites theobaldi	5	6	5	3	3	8
Diptera: Psychodidae						
Telmatoscopus spp.	7	8	14	6	3	6
Diptera: Stratiomyidae						
Zuercheria bequaerti	3	3	27	3	3	4
Diptera: Syrphidae						
Copestylum rafaelanum	5	19	5	16	13	38
Diptera: Tipulidae						
Sigmatomera spp.	40	72	59	78	20	62
Hemiptera: Veliidae						
Microvelia sp.	35	14	50	14	3	6
Paravelia myersi	3	0	14	8	3	8
Coleoptera: Dryopidae	12	0	36	11	7	2
Coleoptera: Scirtidae						
Prionocyphon & Scirtes spp.	43	72	50	83	33	62
Anura: Dendrobatidae						
Dendrobates auratus	5	14	5	8	13	10

ural holes ($G = 5.14$, $df = 1$, $P < 0.025$). Immature stages of the phantom midge *Corethrella appendiculata* were found only in understory holes (TABLE 2). Mean species richness did not differ between similar size holes with and without *C. appendiculata* ($t = 1.70$, $df = 35$, $P = 0.10$).

Trichoprosopon digitatum only occurred in artificial holes during the first census date and was rare in natural tree holes (two of 206 holes). Species of *Haemagogus* could not be differentiated based on larval and pupal characters in the field. Adults reared from subsamples, however, indicated that *H. lucifer* was replaced by *H.*

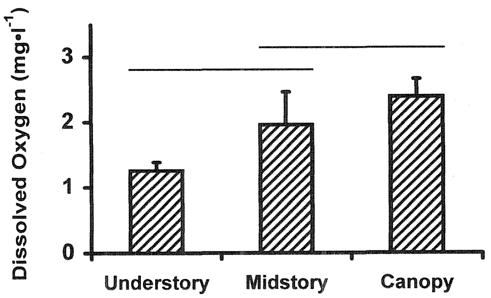

FIGURE 3. Mean (+SE) dissolved oxygen content of natural tree holes in different height classes. ANOVA: $F_{2,83} = 6.22$, $P < 0.01$. Horizontal bars connect means that are not significantly different. Understory $N = 65$, midstory $N = 9$, canopy $N = 12$.

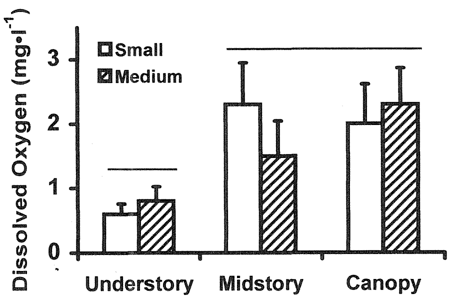

FIGURE 4. Mean (+SE) dissolved oxygen content of small (open bars) and medium (hatched bars) artificial tree holes in different height classes. Two-way ANOVA: height $F_{2,28} = 5.51$, $P = 0.01$; size $F_{1,28} = 0.01$, $P = 0.94$; height*size $F_{2,28} = 0.75$, $P = 0.48$. Horizontal bars connect means that are not significantly different.

equinus at higher forest levels. Subsample rearings also indicated that these two species do not co-occur in understory holes, but more consistent and thorough sampling is required before drawing this conclusion. The frog *Physalaemus pustulosus* did not colonize the artificial tree holes used in this study and only occurred in three natural holes.

Average DO content of water in natural tree holes increased with height (FIGURE 3), but height had no effect on conductivity (ANOVA: $F_{2,83} = 1.98$, $P = 0.14$) or pH ($F_{2,191} = 2.14$, $P = 0.12$; TABLE 1). Chemical variables were not correlated with hole volume ($r < 0.15$, $P > 0.17$ for all tests). The DO content of artificial tree hole water was lower in the understory than in midstory or canopy (FIGURE 4). Conductivity did not differ among heights or sizes of artificial tree holes (2-way ANOVA: height $F_{2,28} = 0.39$, $P = 0.68$; size $F_{1,28} = 0.01$, $P = 0.96$; height*size $F_{2,28} = 0.51$, $P = 0.60$), nor did average pH (2-way repeated measures ANOVA: height $F_{2,30} = 0.87$, $P = 0.43$; size $F_{1,30} = 0.15$, $P = 0.71$; height*size $F_{2,30} = 0.43$, $P = 0.66$; time*treatment $P > 0.25$ for all tests).

Minimum artificial tree hole water temperatures were similar to air temperatures and did not differ among height classes (2-way ANOVA: air/water $F_{1,30} = 0.20$, $P = 0.66$; height $F_{2,30} = 0.10$, $P = 0.90$; air/water*height $F_{2,30} = 0.31$, $P = 0.73$), but maximum temperatures were lower in the understory than in midstory and canopy (FIGURE 5). Natural tree hole temperatures were not measured in the canopy with sufficient consistency for statistical analysis, but water temperatures of both natural and artificial holes in the canopy often exceeded 40°C on cloudless days. The water temperature of natural tree holes in the understory was consistently lower (24.7°C ± 0.14) than the surrounding air temperature (26.7°C ± 0.22) during daylight hours (paired $t = 11.1$, $df = 37$, $P < 0.001$).

Small exposed holes were dry more often than large understory holes in the drying experiment (FIGURE 6), and the average maximum number of consecutive dry days was greater for containers in the clearing (14.0 ± 1.2) than in the understory (6.0 ± 2.7; $t = 2.7$, $df = 6$, $P = 0.018$). Although not quantified, natural tree holes in the canopy dried out faster and with greater frequency than understory holes of similar volume. Of the artificial tree holes used in the vertical stratification portion of this study, three midstory containers and five canopy containers were completely dry on one or more census dates. None of the understory containers dried out during the wet season. The number of species in a container on a dry census date (1.6 ± 0.73) was less than the number observed on the previous

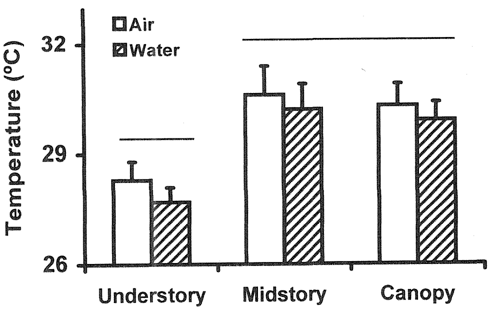

FIGURE 5. Mean (+SE) maximum air (open bars) and water (hatched bars) temperatures in different height classes of artificial tree holes. Two-way ANOVA: height $F_{2,30} = 27.8$, $P < 0.001$; air/water $F_{1,30} = 2.49$, $P = 0.13$; height*air/water $F_{2,30} = 0.07$, $P = 0.93$. Horizontal bars connect means that are not significantly different.

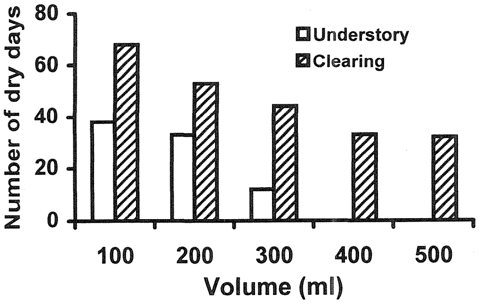

FIGURE 6. Number of days that containers of different volume and exposure level (understory = open bars, clearing = hatched bars) were completely dry out of 175 observations; $\chi^2 = 35.14$, $df = 5$, $P < 0.0001$.

wet census date (4.9 ± 0.83; paired $t = 6.2$, $df = 7$, $P < 0.001$).

DISCUSSION

Results of this study show that species richness and abundance tend to decline with the height of a hole above the forest floor. Similar vertical stratification studies have been conducted in Panama (Galindo et al. 1950, 1951, 1955, Trapido et al. 1955). Although they did not sample natural tree holes in the canopy or record distributions of non-mosquito taxa, their results for open-top containers in lowland forest show larger cumulative numbers of mosquito species in the understory than in midstory or canopy. Kitching (1971) and Copeland (1989) surveyed insects of tree holes > 2 m above the ground as part of their temperate zone investigations. Kitching found larger densities of selected taxa in tree holes above 2 m than in holes closer to the ground and suggested differences in nutrient quality and relative organic matter content as mechanisms for this pattern. Copeland did not address the distribution of tree hole insects with respect to vertical location.

Drying and Temperature Disturbance

Lower species richness in canopy tree holes is partly attributed to frequent hole drying and higher temperatures in tree crowns. Exposed artificial tree holes dried out more often than containers in the understory, and the pattern was similar for natural holes. Although some tree hole invertebrates can survive periodic dehydration (e.g., Fincke 1994, Juliano & Stoffregen 1994, Sota et al. 1994), habitat drying kills many aquatic organisms and affects tree hole community structure (e.g., Lounibos 1985, Bradshaw & Holzapfel 1988). Desiccation destroys eggs of some tree hole mosquitoes (Bates 1949, Galindo et al. 1955), and potential colonists may avoid or deposit fewer eggs in sites lacking water (cf. Frank et al. 1976), especially if wet holes are available nearby (i.e., at lower levels in the forest). These mechanisms are likely responsible for low species richness in artificial holes that had recently dried out.

High temperatures in canopy tree holes probably contributed to lower species richness by causing local extinctions of some taxa. Water temperatures in canopy tree holes often exceeded the thermal tolerances reported for many mosquito species (Bates 1949). Lower diversity in canopy tree holes may also reflect lower colonization effort. Although oviposition data were not gathered in this study, some diurnally active tree hole mosquitoes deposit fewer eggs at higher temperatures (Bates 1947).

Dehydration and high temperatures may have indirectly reduced species richness in canopy tree holes by influencing nutrient availability. Leaf litter is the energy base for food webs in most water-filled tree holes (Kitching 1971). It is degraded by the activities of bacteria and fungi, which are consumed by macroinvertebrates (e.g., Fish & Carpenter 1982). Litter drying reduces the productivity of decomposer microbes (Clein & Schimel 1994) and the organisms that consume them (e.g., Aspbury & Juliano 1998), when the litter is subsequently immersed in rainwater. Some microbial processes associated with litter decomposition are temperature-sensitive (Webster & Benfield 1986). If dehydration and high temperatures reduced microbial productivity in canopy tree holes, secondary consumers (e.g., mosquitoes) may have become food-limited and locally extinct.

Species Distributions

Five species had vertically restricted distributions, making the regional pool of tree hole-associated taxa larger in the understory than at other levels in the forest. This difference had minimal if any effect on mean species richness in tree holes at different heights. Two of the understory species, *Trichoprosopon digitatum* and *Physalaemus pustulosus,* were rare, and removing them from the analysis did not change the outcome. *Haemagogus lucifer* appeared to be replaced by *H. equinus* in canopy and midstory tree holes.

Intraguild predation tends to stabilize the number of top predator species within a hole (Fincke 1994, 1999). Where it occurred, *Megaloprepus coerulatus* tended to exclude *Mecistogaster* spp.; other top predators generally occupied holes lacking *M. coerulatus.* These results suggest that the superior competitive ability of *M. coerulatus* compensated for effects of its limited distribution on species richness. The secondary predator *Corethrella appendiculata* can reduce the abundance of some species (e.g., Lounibos 1983), but its effects on macroorganism diversity in BCI tree holes are unknown.

Physicochemical Factors

The positive correlations of species richness and abundance with hole volume shown in this study are typical of phytotelmata (e.g., Frank et al. 1977, Sota 1996). Larger containers are larger targets for colonization, and some colonists adjust the number of eggs they deposit based on water volume (Frank et al. 1976, Fincke 1992b). Larger phytotelmata tend to collect more nutrients in the form of leaf litter (e.g., Sota 1996), which leads to greater species richness and abundance (e.g., Srivastava & Lawton 1998, Yanoviak 1999). In addition, top-down effects of individual predators on diversity and abundance should increase in strength with decreasing volume both among holes and within a drying hole (e.g., Fincke 1994). Hole volume is inversely related to the probability that it will dry out (e.g., Sota et al. 1994), and drying frequency affects the abundance and diversity of species present.

Conductivity and pH had no significant influence on community properties of BCI tree holes and did not vary predictably with hole size or height above the ground. This result was expected; larvae of most tree hole species tolerate a broad range of chemical conditions (e.g., Bates 1949, Snow 1949, Petersen & Chapman 1969, Fincke 1999). The increase in DO concentration with increasing height is attributed to algal growth in the artificial tree holes and windier conditions in the midstory and canopy. Filamentous algae also occurred in some natural tree holes of the canopy. DO is typically very low in tree holes, and most macroinvertebrate larvae in tree holes breathe atmospheric oxygen through siphons and other morphological adaptations.

CONCLUSIONS

Water-filled tree holes on BCI do not follow the pattern of relatively high arthropod diversity in tropical forest canopies shown by fogging and related studies. The species pool of potential tree hole colonists was slightly larger in the understory, and the diversity of macroorganisms in individual tree holes decreased with the height of a hole above the forest floor. Higher disturbance frequency in the form of dehydration and extreme water temperatures in the forest canopy together form the most parsimonious explanation for the latter pattern.

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