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Predation, resource availability, and community structure in Neotropical water-filled tree holes

Abstract Predation and resource availability influence community structure in many aquatic ecosystems. Predators (odonates) and resources (leaf litter) were manipulated to determine their independent effects on macroorganism species richness, abundance, and composition in water-filled tree holes of Barro Colorado Island, Panama. Interactive effects of these factors were also investigated in artificial tree holes. Large odonates reduced species richness in natural tree holes, but did not significantly reduce macroorganism abundance. The presence of larvae of the mosquito *Culex urichii* and the ceratopogonid midge *Bezzia snowi* were negatively associated with the presence of large odonate larvae. In natural tree holes, leaf litter addition and removal respectively increased and decreased richness by *c*. 1 species relative to controls, and macroorganism abundance was greater in litter addition holes than in litter removal holes. Independent effects of predation showed similar patterns in artificial holes, but there was no predator×resource interaction, partly due to the short duration of the experiment. Predators grew faster when litter was abundant, and indirectly reduced litter degradation rates when resources were scarce in artificial holes. Both resource availability and predation influence species richness in water-filled tree holes, but act at different time scales; richness follows productivity (litter quantity) over a period of weeks, whereas effects of predation may span several months.

Keywords Abundance · Macroinvertebrates · Phytotelmata · Species richness · Tropics

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Introduction

Top predators can affect prey diversity or abundance in large aquatic settings such as lakes and streams (e.g., Brooks and Dodson 1965; Zaret 1980; Kerfoot and Sih 1987; Blois-Heulin et al. 1990; Diehl 1992; McPeek and Peckarsky 1998), and can indirectly influence populations at basal trophic levels via trophic cascades or "top-down" control (e.g., Power 1990; Carpenter and Kitchell 1993; Pace et al. 1999). Although predator effects and nutrient effects are not mutually exclusive, lake and stream communities may also be subject to "bottom-up" control, whereby changes in inorganic nutrient (e.g., nitrogen and phosphorus) quantities alter primary productivity (e.g., Proulx et al. 1996; Spencer and Ellis 1998). Changes in productivity are then reflected by variation in abundance or diversity within consumer populations or assemblages (e.g., Hershey et al. 1988; Hart and Robinson 1990; Perrin and Richardson 1997). The quality and quantity of leaf-litter resources may similarly regulate detritivore populations and detritus-based assemblages in large aquatic systems (e.g., Gee 1988; Richardson 1991; Dobson 1994).

Top-down and bottom-up control of community structure are less studied in small aquatic habitats, such as phytotelmata. However, predators influence the diversity and abundance of some taxa (often other predators) living in the water held by pitcher plants (Addicott 1974; Cochran-Stafira and von Ende 1998), bromeliads (e.g., Lounibos et al. 1987), *Heliconia* spp. bracts (Naeem 1988), bamboo stumps (Sota and Mogi 1996), and tree holes (e.g., Bradshaw and Holzapfel 1983; Fincke et al. 1997; Nannini and Juliano 1998). Predation tends to reduce species richness and abundance in these systems (but see Louton et al. 1996), and these effects are partly attributed to small habitat size (Addicott 1974). Unlike predators in the intertidal zone (Paine 1966) and other relatively open systems, predators in phytotelmata can efficiently patrol the entire habitat. Thus, few temporal or spatial prey refugia exist, and the potential for strong top-down effects is great (but see Lounibos et al. 1997).

Fewer studies have addressed the role of resource availability in structuring phytotelm communities (e.g., Naeem 1990; Sota 1996). Plant detritus, especially leaf litter, forms the nutrient base for food webs in many types of phytotelmata, including most water-filled tree holes (see Snow 1949; Kitching 1971 for descriptions of this habitat). Macroorganisms in tree holes consume decaying litter directly (e.g., Paradise and Dunson 1997), or indirectly by grazing and filtering decomposer microbes from litter surfaces and the water column (e.g., Fish and Carpenter 1982; Walker and Merritt 1991). Litter quality and quantity influence growth rates and life history characteristics of some tree-hole macroinvertebrates (e.g., Carpenter 1982a; Hard et al. 1989; Lounibos et al. 1993; Léonard and Juliano 1995; Walker et al. 1997), and resource availability affects community parameters in experimental tree hole analogs (Jenkins et al. 1992; Srivastava and Lawton 1998; Yanoviak 1999a, 1999b).

Water-filled tree holes are common in lowland moist forests of Panama. Although *c*. 60 different species of macroorganisms are associated with this habitat, most individual holes contain fewer than ten species on any given wet season day (Yanoviak, in press). Detritivores and omnivores comprise the majority of the fauna, but most holes also contain one or more of seven top predator species, with larvae of giant damselflies (Odonata: Pseudostigmatidae) being the most common (Fincke 1999). In addition to supporting manageable and specialized macroorganism assemblages, tree holes are generally small, easy to sample, and can be replicated with simple materials (e.g., plastic containers). Thus, this is a particularly tractable system for community-level experiments.

I designed this study to test the hypothesis that macroorganism community structure (i.e., species richness, composition, and abundance) in water-filled tree holes of Panama is influenced by the presence or absence of top predators (odonates) and the availability of food resources (leaf litter). Based on qualitative surveys in Panama, and previous work on this system (Fincke et al. 1997), I predicted that macroorganism species richness and abundance would be lower in holes containing odonate larvae than in holes without odonates.

Because the number of consumer species and individuals in a habitat is often linked to resource availability (reviewed by Srivastava and Lawton 1998), I predicted that addition of leaf litter to tree holes would increase macroorganism species richness and abundance, and that removal of litter would have the opposite effect. I also predicted that: (1) litter effects would be short-lived, and community parameters would return to initial levels after termination of manipulations; (2) litter addition and removal would affect species distributions; and (3) species persistence times would be greater in litter addition holes than in litter removal holes.

Finally, Washburn et al. (1991) and Fincke et al. (1997) showed that parasite and predator effects on mosquito abundance differ when nutrient levels are relatively high or low in artificial tree holes. Based on these studies, I predicted that resource availability and predation would have interactive effects on community structure (i.e., the influence of odonates is respectively masked or enhanced when leaf litter abundance is high or low).

Materials and methods

This study was conducted in the seasonally moist lowland forest of Barro Colorado Island (BCI), Panama (see Leigh et al. 1996 for a site description). The fauna and abiotic characteristics of BCI tree holes are described elsewhere (Yanoviak 1999c, in press). To standardize potential effects of hole location and size on community structure, all holes used in this study were located in the understory (maximum height 1.5 m) and were ≤3 l in volume. I measured pH, height above the ground, total volume, and water surface area in each hole at the start of experiments (Tables 1, 2). Hydrion narrow- and broad-range colorimetric strips were used for all pH measurements.

I censused the macrofauna of each hole by removing its contents with a turkey baster or siphon into a white pan. Macroorganisms were identified and counted, and subsamples were collected when species could not be determined in the field. After each census, the organisms, litter, and water were returned to the hole and the pan was rinsed. Additional methodological details for natural and artificial tree hole sampling are summarized elsewhere (Yanoviak 1999c).

Predation

I used a predator exclusion experiment to determine the effects of odonates on species richness and abundance of other macroorgan-

Table 1 Means (SD) of physicochemical properties, species richness, and abundance measured at the start of the predator exclusion experiment (December 1995). *Area* is estimated water surface area. *Exclusion* holes were covered with chicken wire to prevent odonate colonization. *Control* holes were not covered. Volume ranges in brackets (n=17 for each mean, df=32 for all t-tests). Volume, area, and abundance data were transformed prior to analysis

	Control	Exclusion	t_{obs}	P
Height (cm)	55 (42)	64 (44)	1.18	0.25
Volume (ml)	1075 (922) [20–3000]	583 (433) [17–1600]	0.60	0.55
Area (cm²)	111 (83)	62 (51)	1.66	0.11
pH	6.06 (0.95)	6.32 (0.63)	0.94	0.36
Richness	4.8 (2.4)	4.9 (2.0)	0.15	0.89
Abundance	48.7 (45.6)	29.7 (26.1)	0.56	0.58

Table 2 Means (SD) of physical characteristics, species richness, and abundance measured at the start of the nutrient addition/removal experiment (week 0). Volume ranges in brackets. Volume, area, and abundance data were transformed prior to analysis

	Litter added	Litter removed	Control	$F_{2,33}$	P
Height (cm)	62 (42)	51 (45)	41 (35)	0.77	0.47
Volume (ml)	801 (533) [200–2000]	833 (865) [200–3000]	662 (472) [250–2000]	0.21	0.82
Area (cm²)	138 (122)	110 (84)	134 (110)	0.11	0.89
Richness	4.6 (2.1)	5.2 (2.8)	5.6 (1.8)	0.70	0.51
Abundance	20.8 (19.0)	23.1 (18.4)	45.5 (47.0)	2.19	0.13

isms in tree holes. In December 1995, I censused the macrofauna of 40 natural tree holes in the forest understory. I removed odonates and other top predators from 20 of the holes, and placed a canopy of chicken wire (2- to 3-cm mesh) over the hole openings to prevent recolonization by odonates. Earlier experiments using artificial tree holes showed that chicken wire or netting deters oviposition by odonates, but permits colonization by other tree hole inhabitants (Fincke et al. 1997; Fincke 1998). I distributed variation in hole size between covered and uncovered holes as much as possible. Hereafter, I refer to uncovered holes as the *control* treatment and covered holes as the odonate *exclusion* treatment. All 40 holes were left untouched until the start of the following wet season.

In mid-May 1996, I surveyed all experimental holes for the presence of odonates and other top predators, and removed any odonate larvae found in exclusion holes (5 of 20 holes). Odonates present in these holes most likely originated from eggs deposited prior to installation of the chicken wire in December 1995; pseudostigmatid eggs are concealed in the woody margins of tree holes and require up to 196 days to hatch (Fincke 1998, 1999). Six of the holes (3 control and 3 exclusion) were dry or otherwise disturbed, and were removed from the experiment. I censused the remaining 34 holes every 14 days from 10 June until 29 July, 1996 (n=4 censuses per hole), and I measured pH in each hole during censuses 1, 2, and 4. Any leaf litter trapped by the chicken wire covering an exclusion hole was collected and added to the hole after each census.

Resource availability

In mid-August 1997, I divided 36 natural tree holes equally among three litter treatments: a control group, a litter removal group, and a litter addition group. I censused all holes 2 days before the start of experimental manipulations (hereafter, this initial census is identified as week 0). I assigned holes to treatment groups based in part on general shape, tree species, and initial macroorganism species richness to distribute potential sources of variance among groups as much as possible. Six control holes from the predator exclusion experiment were used again in this experiment, but none of the exclusion holes were reused.

I removed all macrodetritus (>1 cm²) from the 12 litter removal holes on week 0 and at least once each week thereafter until week 6. Care was taken to keep disturbance to a minimum during litter removal. Litter addition holes received 0.014 g leaf litter cm⁻² water surface area on week 0, and then 0.007 g cm⁻² on weeks 2 and 4. I based the litter addition quantities on the average oven dry weight of litter collected over a 30-day period in artificial tree holes (650-ml cups, 71-cm² opening) tied to trees 1.0 m above ground level (mean=0.007 g cm⁻² surface area, SD=0.33). Litter added to holes consisted of approximately equal proportions of leaves or leaflets of *Ceiba pentandra*, *Dipteryx panamensis*, *Ficus yoponensis*, and *Platypodium elegans* collected from tree crowns or recent branch falls (as described in Yanoviak 1999b). All litter was air-dried for ≥7 days and then oven-dried (70°C, ≥48 h) before weighing.

I recorded the number of macroorganism species present and their abundance in each hole on weeks 2–6. I censused all holes again on week 10 (i.e., after ≥5 weeks without litter addition or removal) to determine if the macrofauna had recovered from the manipulations. One of the control holes dried out during the experiment and was not included in analyses.

Predator×resource interaction

On 1 October 1997, I tied 30 artificial tree holes (650-ml black plastic cups) to trees separated by 5–10 m in the forest understory. I evenly divided the cups into three resource availability treatments based on the quantity of initial litter inputs: *high*=4.00 g (±0.001), *medium*=0.40 g (±0.001), and *low*=0.04 g (±0.0005). The composition, origin, and treatment of litter was the same as described above. I filled the cups with filtered (0.25 mm mesh) rain water and left them undisturbed for 3 weeks to allow communities to develop.

At the end of the third week (hereafter, day 0), I censused the contents of all artificial tree holes and added one mid-size *Megaloprepus coerulatus* larva (Odonata: Pseudostigmatidae; 10–18 mm body length excluding caudal lamellae) to half of the cups in the experiment. The initial body length of odonates did not differ among treatments ($F_{2,12}$=1.32, P=0.30). I censused the macrofauna of all cups on days 4, 8, 16, and 32. Odonates were not counted in censuses. I checked the cups every 3 days for the presence of *M. coerulatus* larvae and removed any macrodetritus (>0.25 cm²) foreign to the experiment. I collected all experimental detritus remaining in the cups on day 32. Some litter fragments were lost from two cups that were disturbed between days 16 and 32, so these data were excluded from the analysis of remaining litter mass.

I measured the body length of the *M. coerulatus* larvae on days 8, 16 and 32. One larva was missing from the high litter treatment on day 8, and one was missing from the medium litter treatment on day 16. I replaced the missing individuals with new mid-size larvae, but excluded these replicates from the analysis of predator growth. *Toxorhynchites theobaldi*, another top predator in BCI tree holes, was occasionally found in non-predator holes. I included this species in census data, but consistently removed individuals when they occurred to reduce confounding of odonate effects. I analyzed species richness and abundance data from day 4–32 censuses with a 2×3 factorial repeated-measures ANOVA using presence or absence of *M. coerulatus* and litter quantity as main effects.

Data were tested for normality and homogeneity of variance with normal probability plots and *F*-tests prior to analysis. Ryan-Einot-Gabriel-Welsch multiple range tests (SAS 1989) were used to compare means when ANOVA results were significant. All *G*-tests had *df*=1 unless otherwise noted, and *G* values were adjusted with Williams' correction (Sokal and Rohlf 1981). Data used in *G*-tests were pooled across time within a hole to maintain statistical independence. Bonferroni-adjusted α values were used to correct for multiplicity and are noted in the text. Proportional data were arcsine square-root transformed before analysis, and the log(x+1) transformation was used to improve normality for all abundance data and for other data where noted. Means shown in the results were calculated from untransformed data.

Results

Tree hole physicochemical properties, macroorganism species richness, and macroorganism abundance did not differ between controls and treatments at the start of the predator exclusion (Table 1) and resource availability (Table 2) experiments. Average pH was similar between control and predator exclusion holes during the 1996 censuses (repeated-measures ANOVA: $F_{1,32}$=0.98, P=0.33; time×treatment P=0.095).

Predation

I predicted that macroorganism species richness and abundance would be lower in tree holes containing odonates than in holes without these top predators. The timing of the experiment (early wet season) was problematic because odonates had not colonized 5 of the 17 control holes by the second census date. Moreover, many of the holes that were colonized contained only small odonate larvae (<14 mm in body length), which have relatively
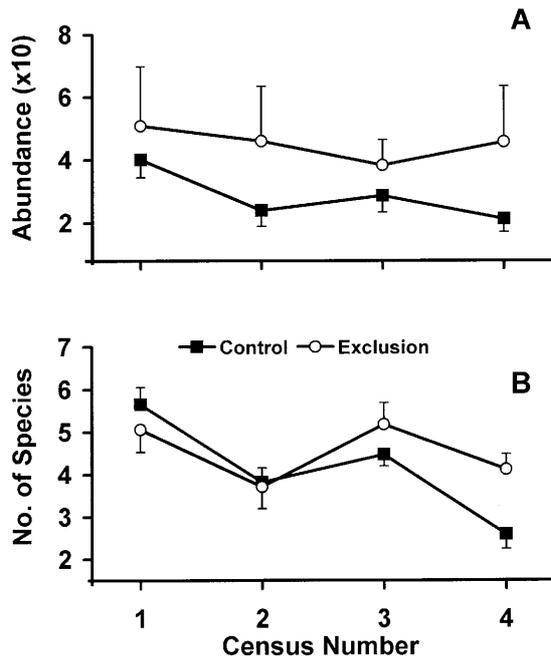
Fig. 1 Mean (±SE) **A** abundance and **B** species richness of non-odonate macroorganisms in *control* holes (odonates present) and odonate *exclusion* holes; n=17 for each mean
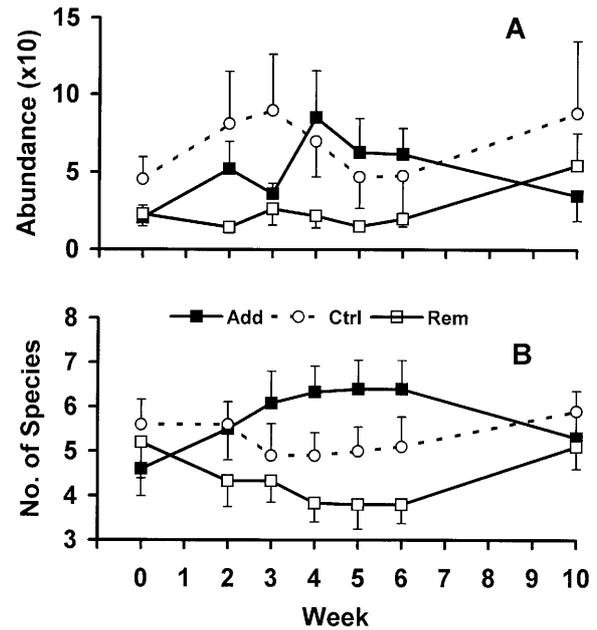

Fig. 2 Mean (±SE) **A** macroorganism abundance and **B** species richness in natural tree holes to which leaf litter was added on weeks 0, 2, and 4 (*Add*), removed at least weekly until week 6 (*Rem*), or unmanipulated (*Ctrl*); n=11 for control means, n=12 for all others

slow feeding and growth rates (Fincke 1992a; Fincke et al. 1997). These problems were resolved by the third census date, when all control holes contained at least one large (>19 mm) odonate larva or at least two mid-size (14–18 mm) larvae.

Analyses of data from the third and fourth censuses showed that the abundance of macroorganisms, and the abundance of mosquitoes alone (for comparison with Fincke et al. 1997), were unaffected by the presence of odonates (repeated-measures ANOVAs: $F_{1,32}$ <1.70, P>0.20, α=0.025; time×treatment P>0.11 for both tests; Fig. 1A). Although they had no effect on macroorganism abundance, large odonate larvae reduced species richness relative to exclusion holes by an average of 1.12 taxa overall ($F_{1,32}$=5.65, P=0.024; time×treatment P=0.13; Fig. 1B).

Of 13 potential prey taxa (i.e., relatively common species with active larvae living in the water), the presence of the mosquito *Culex urichii* and the ceratopogonid midge *Bezzia snowi* were negatively associated with the presence of large odonate larvae in control holes (G>4.72, P<0.05 in both tests). The presence of *Aedes terrens*, the commonest mosquito species in natural tree holes on BCI (Fincke et al. 1997; Yanoviak, in press), was not associated with the presence or absence of odonates (G=0.23, P>0.50).

Resource availability

I predicted that addition and removal of leaf litter would respectively increase and decrease macroorganism spe-

cies richness and abundance relative to control holes. Differences in macroorganism abundance among all three treatments were non-significant during weeks 2–6 (repeated-measures ANOVA: $F_{2,32}$=2.82, P=0.074; Fig. 2A), but litter addition holes contained more macroorganisms than litter removal holes ($F_{1,22}$ =7.12, P=0.014, α=0.025). Addition of leaf litter to tree holes increased the average number of species present (pooled across time) by 1.04 over controls, whereas litter removal reduced richness by 1.08 species (Fig. 2B). These differences were significant during weeks 2–6 ($F_{2,32}$=5.00, P=0.013), and there were no time×treatment interactions for abundance or species richness (P>0.23 for all tests).

Because soluble nutrients are rapidly leached from leaf litter in tree holes (e.g., Carpenter 1982b), I predicted that experimental effects would disappear shortly after termination of litter manipulations. By week 10 (5 weeks after manipulations were terminated), average macroorganism species richness and average abundance had converged near initial (week 0) values and no longer differed among treatments (richness: $F_{2,33}$=0.08, P=0.92; abundance: $F_{2,33}$=0.13, P=0.88; Fig. 2).

The cumulative number of species found in each treatment of this experiment was similar (litter addition=26, litter removal=30, control=27), and all holes contained one or more top predators. The odonates *Megaloprepus coerulatus*, *Mecistogaster* spp., and Aeshnidae occupied 60%, 68.6%, and 20% of the holes, respectively. *Dendrobates auratus* tadpoles and larvae of the mosquito *Toxorhynchites theobaldi* occupied 5.7% and 28.6% of the holes, respectively. Tadpoles of *D. au-*

ratus were found only in litter removal holes, but all other top predators occurred in all treatments and were evenly distributed among treatments ($G<2.3$, $df=2$, $P>0.10$ in all tests; aeshnids and *T. theobaldi* were pooled to meet statistical assumptions).

I predicted that differences in leaf litter availability would be reflected by differences in distribution of species among treatments. Specifically, I expected that relatively short-lived species (those completing larval development in <6 weeks) would respond to short-term changes in resource availability. Six taxa found in this experiment occurred often enough for quantitative analysis (i.e., in >5 holes of each treatment) and qualified as relatively short-lived: the mosquitoes *Aedes terrens*, *Anopheles eiseni*, *Culex corrigani*, and *Haemagogus* (*H.*) spp.; the midge *Bezzia snowi*; and the annelid *Dero* sp. Where they occurred, these taxa colonized a larger proportion of litter addition holes (68%) than control holes (41%) only after the start of manipulations ($t=3.62$, $df=10$, $P=0.005$). All of these species also disappeared from ≥50% of the same litter addition holes after manipulations were terminated (i.e., between weeks 6 and 10). The opposite pattern did not occur in the litter removal treatment; the proportion of litter removal holes from which these six species became locally extinct after week 0 did not differ from controls ($t=0.82$, $df=7$, $P=0.44$; test assumed unequal variance).

Finally, I predicted that the greater energy supply provided by litter addition would lead to greater species persistence (e.g., Srivastava and Lawton 1998) relative to litter removal. The mean persistence time (number of consecutive censuses that a species was present in a hole) did not differ between litter removal holes and litter addition holes (Kruskal-Wallis $\chi^2=0.17$, $P=0.68$). However, the average (±SE) number of species present for ≥2 consecutive censuses was marginally greater in litter addition holes (6.75±0.75) than in litter removal holes (4.33±0.47; Kruskal-Wallis $\chi^2=4.84$, $P=0.027$, $\alpha=0.025$).

Predator×resource interaction

I predicted that predation and initial resource (leaf litter) quantity would have interactive effects on macroorganism species richness and abundance within the physically standardized confines of artificial tree holes. As expected, there were no predator×resource interactions for richness or abundance on day 0, when odonates were first added to the experiment ($F_{2,24}<2.67$, $P>0.09$ in both tests). Although richness and abundance on day 0 were similar between holes that received odonates and those that did not ($F_{1,24}<1.76$, $P>0.20$; Fig. 3), these community parameters were significantly influenced by initial nutrient quantity. Macroorganism abundance and richness were greatest in the high litter quantity treatment on day 0 ($F_{2,24}>4.57$, $P<0.021$), but did not differ between low and medium litter quantity treatments (Fig. 4).

As the experiment progressed, predation and resource availability did not interact to shape macroorganism
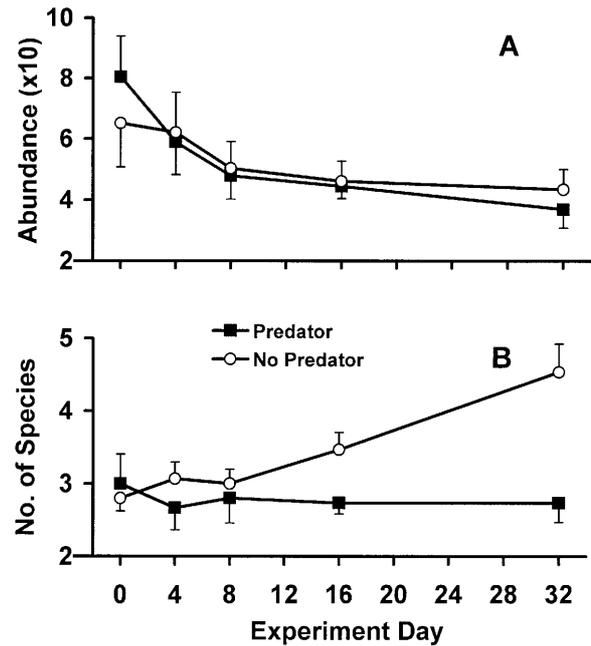

Fig. 3 Mean (±SE) **A** macroorganism abundance and **B** species richness in artificial tree holes with (■) and without (○) the odonate *Megaloprepus coerulatus*; $n=15$ for each mean
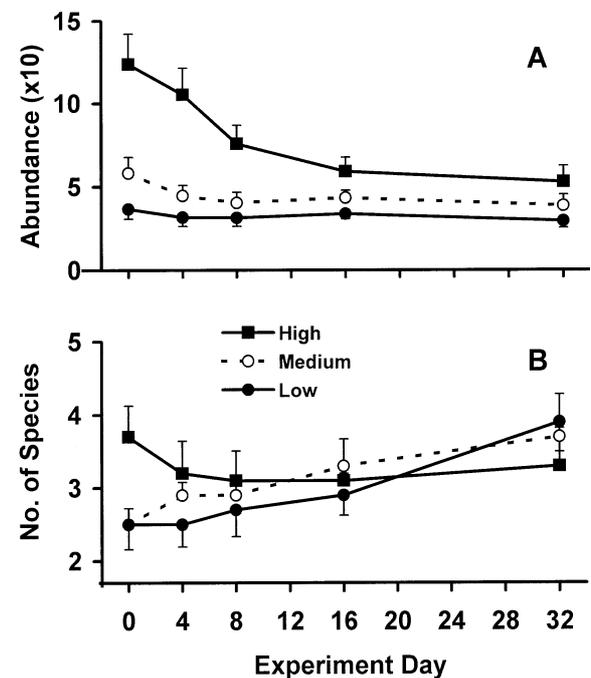

Fig. 4 Mean (±SE) **A** macroorganism abundance and **B** species richness in artificial tree holes containing different initial quantities of litter (*High* 4.0 g, *Medium* 0.4 g, *Low* 0.04 g); $n=10$ for each mean

community structure in the holes; interactions were non–significant for both abundance (repeated-measures ANOVA: $F_{2,24}=0.01$, $P=0.99$) and species richness ($F_{2,24}=0.78$, $P=0.47$) during the days 4–32 censuses (time×predator×litter $P>0.23$ in both tests). Total macro-

organism abundance and the abundance of mosquitoes alone did not differ between predator and non–predator treatments ($F_{1,24}<0.24$, $P>0.63$, $\alpha=0.025$, time×predator $P>0.35$ in both tests; Fig. 3A). However, overall mean species richness was greater by 0.59 taxa in cups lacking odonates ($F_{1,24}=9.91$, $P=0.004$; Fig. 3B). This effect was primarily caused by data from days 16 and 32 (time×predator $P=0.008$).

Of the 22 taxa found in this experiment, only larvae of the predatory mosquito *Toxorhynchites theobaldi* were more common (i.e., occurred in more cups) where odonates were absent ($G=4.76$, $P<0.05$). The presence of *T. theobaldi* did not confound the absence of odonates; richness and abundance results were unchanged when the three cups containing *T. theobaldi* on every census date were removed from the analysis. In low and medium litter quantity treatments combined, larvae of scirtid beetles and the mosquito *Culex urichii* were collectively more likely to decline in abundance when predators were present, and either increase or remain relatively constant in abundance when predators were absent (Fisher's exact two-tailed $P=0.005$, $n=20$ cups containing *C. urichii*, scirtids, or both). Changes in abundance of these taxa were not associated with the presence or absence of odonates in the high litter treatment (Fisher's $P=0.52$, $n=10$).

Initial litter quantity had a significant effect on macroorganism abundance over the course of the experiment. Mean abundance was consistently greater in the high litter quantity treatment ($F_{2,24}=10.06$, $P=0.0007$, time×treatment $P=0.11$; Fig. 4A). Species composition also differed among litter treatments and over time. The dytiscid beetle *Copelatus* sp. occurred only in the medium litter treatment. The syrphid fly *Copestylum rafaelanum*, the tipulid fly *Sigmatomera* spp., the psychodid fly *Telmatoscopus* spp., and the mosquitoes *Culex mollis* and *Trichoprosopon digitatum* occurred only in the high litter treatment. *Copestylum rafaelanum* and *C. mollis* were found only on day 0 and day 4 censuses, whereas *Sigmatomera* spp. occurred only on day 16 and day 32 censuses. Despite the unequal distributions of these taxa among treatments and census dates, resource availability had no effect on mean species richness ($F_{2,24}=0.26$, $P=0.78$, time×treatment=0.49; Fig. 4B) in this experiment.

Litter resources influenced predator growth in the experimental tree holes. The average length of *M. coerulatus* larvae increased with initial litter quantity over time ($F_{2,10}=9.03$, $P=0.006$; time×treatment $P=0.03$) and mean lengths differed among all treatments on day 32 (Fig. 5). Predation and litter quantity had interactive effects on the degradation rate of leaf material (measured as the proportion of litter remaining at the end of the experiment; $F_{2,22}=4.03$, $P=0.032$). A larger fraction of litter remained when predators were present, but only when initial litter quantities were at low and medium levels (Fig. 6). The proportion of litter remaining in cups with predators was correlated with the log of initial litter mass (Pearson $r=0.618$, $n=14$, $P=0.019$). The same was true in cups without predators ($r=0.898$, $n=14$, $P=0.0001$).
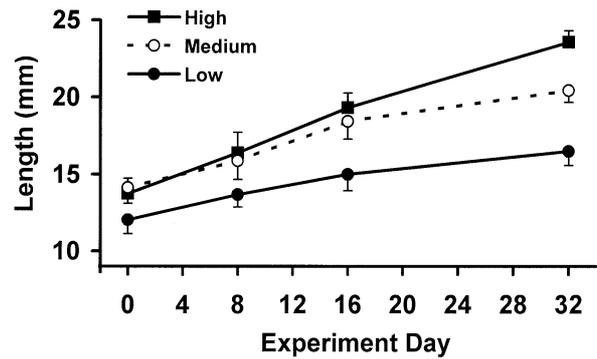

Fig. 5 Mean (±SE) body length (mm) of larval *M. coerulatus* added (on day 0) to artificial tree holes containing different initial quantities of litter (*High* 4.0 g, *Medium* 0.4 g, *Low* 0.04 g); $n=4$ for high and medium treatment means, $n=5$ for low treatment means
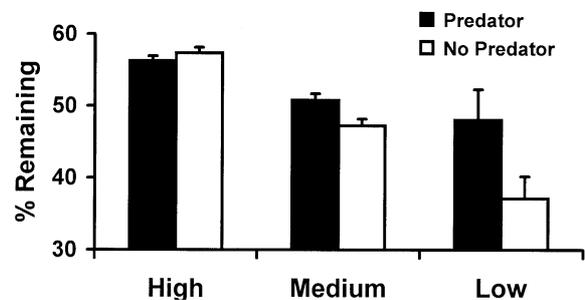

Fig. 6 Mean (+SE) percent litter mass remaining in artificial tree holes at the end of the predator–resource interaction experiment. *High*, *Medium* and *Low* refer to different initial quantities of litter in holes to which the predator *M. coerulatus* was (*filled bars*) or was not (*open bars*) added; $n=4$ for the high-no predator and low-predator means, $n=5$ for all other means

Discussion

Despite considerable work on the ecology of phytotelm communities, this study is the first to show that predation and resource availability influence the number of species present in natural water-filled tree holes. Specifically, my results show that tree holes contained fewer macroorganism species in the presence of large odonate larvae, and respectively contained more or fewer species when litter was added or removed. Because tree holes on BCI typically contain fewer than ten macroorganism species on any wet season day, the loss or addition of a single species reflects a large proportional change in assemblage structure.

Predation

Effects of odonates on community structure were similar in both natural and artificial holes: species richness was greater in the absence of odonates, but abundance did not differ. Results of this and related studies (Yanoviak 1999a) suggest that selective predation by odonates reduces macroorganism species richness by promoting lo-

cal prey extinctions in tree holes. In laboratory trials, most medium and large odonate larvae preferentially fed on larger mosquitoes when several sizes of the same prey species were available (Yanoviak 1999a). Most odonates also preferred *Culex* spp. larvae over *Aedes terrens* when similar-sized individuals of each were presented simultaneously.

In this study, the species that were negatively associated with large odonates in natural tree holes (*Bezzia snowi* and *Culex urichii*) were among the largest prey available (final instar body length >5 mm). *Toxorhynchites theobaldi*, the only species that occurred significantly less often when odonates were present in the artificial tree hole experiment, is one of the largest invertebrates in this system (Bradshaw and Holzapfel 1983). In addition, *T. theobaldi* is a potential competitor for mosquito prey with odonates, and its greater frequency in cups without odonates probably reflects the absence of intraguild predation and priority effects (Fincke 1999). Lounibos et al. (1987) found a similar negative association between *Toxorhynchites* and odonates in Venezuelan phytotelmata. The lack of association between the presence of *A. terrens* and odonates suggests that this species is not a preferred prey item in natural tree holes.

Lack of prey refugia is another mechanism potentially contributing to lower species richness in the presence of odonates. Although odonates appear to selectively feed on large prey, they will also take smaller organisms on occasion (Yanoviak 1999a), and probably pursue a broad range of prey types when food is limiting. Like other predacious aquatic insects (e.g., Formanowicz 1982), treehole odonates switch between sit-and-wait and active foraging tactics depending on their degree of starvation (author, personal observations). Some tree-hole mosquitoes alter their behavior in the presence of a predator (Grill and Juliano 1996), but most species must frequently move between the water surface and submerged detritus to obtain oxygen and food, respectively. Thus, they are especially vulnerable to attack by sit-and-wait predators.

An alternative explanation for reduced richness in the presence of odonates is that some prey species avoid colonizing holes containing predators (i.e., by detecting chemical or other cues). This is an unlikely mechanism because odonates are the most common top predators in tree holes (Fincke 1999), and most potential prey species are endemic to this habitat (Yanoviak, in press). Any species that depends on tree holes as a reproductive resource throughout the wet season would become extinct (on a regional scale) in an attempt to avoid odonates.

Resource availability

Manipulation of leaf litter quantity had significant effects on macroorganism species richness in natural tree holes. There are at least three possible mechanisms for this result. First, the greater energy supply in litter addition holes compared with litter removal holes may have increased the abundance and persistence of highly competi-

tive or rare species (e.g., Srivastava and Lawton 1998). Second, the presence or absence of litter may have influenced predator efficiency. Third, some species may have been differentially attracted to chemical or other cues (Bentley and Day 1989) specifically associated with the early stages of leaf decay in litter addition holes.

These mechanisms are not mutually exclusive, and are sensitive to hole-specific conditions (e.g., nutrient inputs from stemflow; Carpenter 1982a) and characteristics of prey assemblages (e.g., size-structure) that were not measured in this study. However, lower macroorganism abundance in litter removal holes than in litter addition holes suggests that increased predator efficiency or nutrient limitation caused local extinctions. Leaf litter is functionally important as a source of both energy and structural heterogeneity in many aquatic habitats (e.g., Richardson 1992). In spatially limited systems such as tree holes, litter potentially restricts the movements of predators and can serve as refugia for prey. Thus, the quantity of litter present in a hole presumably affected predator-prey encounter rates.

The lack of difference in species persistence times shows that turnover was similar among treatments, but the larger number of persistent species in litter addition holes suggests that the added energy enabled a larger number of potentially competing species to coexist. Six taxa colonized holes proportionally more often after litter addition, and then disappeared from most of the same holes after litter manipulations were terminated. This effect is unlikely to be the result of differential colonization because these six species were not unique to litter addition holes. Intensive laboratory and field studies are needed to more thoroughly address each of these possible mechanisms.

In the artificial tree hole experiment, the most dramatic effects of initial litter quantity on macroorganism abundance were found during the first few censuses (up to day 16, 5 weeks after the experiment was set up; Fig. 4A). This pattern suggests that the major effects of litter resources on community structure occur only during the early stages of leaf degradation, when most soluble compounds are leached into the water (e.g., Carpenter 1982b; Gillon et al. 1994). Results of the litter manipulation experiment in natural holes (Fig. 2; week 10) also support this conclusion.

Predator×resource interaction

The lack of interaction between predator and resource effects on community structure in the artificial tree hole experiment, and the lack of a predator effect on mosquito abundance, differ from the findings of Fincke et al. (1997). Differences between results of these two studies are partly attributed to the type of data gathered in each, and to the relatively short duration of the experiment in this study. Fincke and coworkers showed that odonates can reduce the abundance of certain size classes or stages (e.g., pupae) of mosquitoes without significantly reducing total abundance. Such an effect may have oc-

curred in this study, but macroorganism abundance was not quantified by size or life stage.

Some taxa (*C. urichii* and scirtid beetles) indicated a trend toward development of a predator×resource interaction, and odonates grew faster in the high litter quantity treatment (cf. Fincke et al. 1997). However, total macroorganism abundance had barely stabilized by the last two censuses (Fig. 4A). Fincke and coworkers censused artificial tree holes over a much longer period of time (up to 10 weeks after mosquito abundance became relatively stable) and included fallen fruit as a nutrient source. Thus, the comparatively short experimental time span and the lack of prolonged nutrient availability precluded an interaction in this study. A replicate experiment run for a longer time period, and with repeated litter inputs (as in the resource availability experiment discussed above), will provide more conclusive evidence regarding predator×resource interactions in this system.

Given that the leaf material used in each artificial tree hole was of similar composition, the difference in litter degradation rates among treatments was unexpected. Individual leaf fragments were progressively smaller from the high quantity treatment to the low quantity treatment. Because the decomposition rate of a leaf is associated with its physical characteristics, such as permeability and thickness (e.g., Gillon et al. 1994), the correlation of percent litter remaining with initial litter mass is partly attributed to the greater relative surface area of leaf fragments in the low and medium litter treatments. An alternative explanation is that water in cups containing high litter quantities became saturated with soluble compounds, thereby slowing the rate of leaching. This is unlikely because the experiment was conducted in the wet season, and fresh water in the form of rain and stemflow frequently entered all cups.

My results showed a significant interaction between predation and litter quantity effects on litter degradation rate (Fig. 6). Mosquito larvae and other organisms facilitate the degradation of leaf litter in tree holes (e.g., Carpenter 1982b; Fish and Carpenter 1982; Yanoviak 1999b,1999d), and the significant interaction indicates that predation by odonates can reduce facilitation effects when resources are limiting (i.e., a trophic cascade). Odonates did not have an indirect effect on litter degradation when resources were abundant because they were swamped with prey. Faster odonate growth in the high litter quantity treatment indicates that a greater absolute amount of prey biomass was consumed. However, the biomass consumed represents a relatively small fraction of the total prey abundance in this treatment. The greater frequency with which *C. urichii* and scirtid beetle larvae declined in abundance in low and medium litter cups containing odonates further explains the interaction. Both taxa are potential prey for odonates, and both function as grazing omnivores or detritivores in tree holes (Yanoviak, in press). A trophic cascade was not detected in a separate tree hole microcosm experiment (Yanoviak 1999d), probably because that study employed a less voracious predator and only a single grazer species.

Conclusion

My results show that predation and resource availability influence community structure in water-filled tree holes, and that these factors operate at different time scales. Leaf litter inputs affect community parameters over a period of weeks, whereas predation may act over many months (i.e., as long as large odonates are present). On BCI, fresh litter tends to be most abundant in the early wet season (e.g., Foster 1996), when hole occupancy by odonates is relatively low (Fincke 1992b). Thus, examination of predation and nutrient effects on community structure in a seasonal context would be an appropriate extension of this work.

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