

Relationship of water and leaf litter variability to insects inhabiting treeholes

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Abstract. I surveyed treeholes in central Pennsylvania for 7 mo in 1995 to investigate relationships among insect communities and water and leaf litter resources. I used water volume, essential to growth of treehole larvae, as an indicator of habitat size. Leaf litter is the basal food resource in treehole communities, and litter volume is related to the amount of energy available. Insect species richness and larval mosquito (*Ochlerotatus triseriatus*) and ceratopogonid midge (*Culicoides guttipennis*) densities were higher in treeholes that maintained high water volumes than those with low volumes throughout the study. Treeholes with high litter volume, irrespective of water volume, had the highest densities of *C. guttipennis*, and higher total larval densities than those with lower litter volumes; however, litter volume did not affect insect species richness. Scirtid beetle larvae were common in all treeholes, although their densities were unaffected by both litter and water volume. Insect species richness was not related to litter volume, unlike some other studies of phytotelmata. However, my study supported earlier conclusions that both habitat size and resource availability influence structure of treehole communities and maintain species populations. The influence of each resource on particular species presence and density may be related to physical aspects of treeholes, biotic interactions, and natural history of individual species.

Key words: aquatic insects, treeholes, resource availability, habitat size, species richness, leaf litter, Culicidae, *Ochlerotatus triseriatus*, Scirtidae, Ceratopogonidae.

Resource availability and habitat size influence the organization of many communities (Schoener 1989, Warren and Spencer 1996, Paradise 1998, Sota 1998, Srivastava and Lawton 1998). Changes in abiotic resources, such as water volume within aquatic habitats, or food resources, such as leaf litter in detritus-based systems, may affect community structure by eliminating species or allowing their persistence only within small populations (Schoener 1989, Pimm et al. 1991, Reice 1994, Srivastava and Lawton 1998).

Treeholes are small, detritus-rich aquatic habitats in tree cavities that can be readily used to study the effects of variation in abiotic factors and resources on species richness and abundance. Phytotelmata, aquatic habitats in or on plants, include treeholes, pitcher plants, bamboo shoots, and bromeliad bracts, and have been studied to determine factors influencing structure of insect communities (Sota et al. 1994, Barrera 1996, Kitching 2000, Yanoviak 2001). Many factors including water volume, leaf litter and nutrient levels, and water chemistry are hetero-

geneous among phytotelmata (Sota et al. 1994, Kitching 2000). For example, water levels in temperate-deciduous forest treeholes are influenced by direct precipitation and stemflow, with precipitation being frequent during spring and early summer (Carpenter 1982, Walker et al. 1991). The size and angle of the opening determine, in part, the amount of water and leaf litter entering a treehole (Kitching 1987), with larger treeholes receiving and retaining greater litter (energy) and water inputs for longer periods than smaller treeholes (Sota et al. 1994, Sota 1996, 1998). Larger habitats with more stable resources may allow for larger and more stable populations of treehole residents. For instance, treeholes and bamboo stumps with standing water for longer periods were more likely to have mosquito populations than those containing water for shorter periods (Sota et al. 1994).

Precipitation, temperature, habitat size, and amount of organic detritus influence desiccation rates within treeholes (Sota et al. 1994, Aspbury and Juliano 1998). Treeholes in the warm southeastern United States often are affected by desiccation, with some resident insects being more desiccation-resistant than others (Bradshaw and Holzapfel 1988). As water volumes decline, tree-

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hole drying affects availability and breakdown of leaf litter (Aspbury and Juliano 1998), which can eliminate desiccation-intolerant species (Jenkins et al. 1992). Although treehole species may be eliminated as treeholes dry, these species may persist elsewhere (Kitching 1987, Bradshaw and Holzapfel 1988, Sota et al. 1994). Insect colonization rates may also be higher in treehole habitats with more water availability than in those with less (Paradise 1998). Therefore, water resource levels necessary for developing larvae may ultimately determine insect community structure in treeholes.

Within temperate treeholes, leaf fall occurs annually, and leaf litter is the major energy resource (Carpenter 1983, Walker et al. 1991). Positive correlations among leaf litter mass, species richness, and metazoan biomass and density have been reported, with each of these variables also correlating with total treehole volume (Sota 1996, Paradise 1998, Sota 1998, Daugherty and Juliano 2001). Increases in leaf litter quantity may increase habitat heterogeneity and abundance of rare species (Jenkins et al. 1992, Srivastava and Lawton 1998, Paradise 1998, Yanoviak 1999a, 2001). Thus, the quality and quantity of leaf litter may regulate treehole residents often by increasing individual growth rates (Fish and Carpenter 1982, Leonard and Juliano 1995, Walker et al. 1997, Paradise and Kuhn 1998). In addition, high litter availability may increase by-products of decomposition, which may attract ovipositing females (Wilton 1968, Beehler et al. 1992), and thus increase abundance by recruitment. Alternatively, low litter availability may promote competition or facilitation via resource partitioning (Hard et al. 1989, Heard 1994, Barrera 1996, Paradise 1999). For example, competition occurs among mosquito species and is resource dependent (Hard et al. 1989), but shredding activities by beetles can facilitate mosquito growth when resources are low (Paradise 1999).

Water and leaf litter volume vary among and within treeholes, but how do temporal changes in these resources affect community structure of residents? I investigated this question by determining the relationships among treehole water volume, leaf litter volume, and species richness and densities of common insects within Pennsylvania treeholes, based on repeated observations made over one season. By comparing communities among treeholes having different water and leaf litter regimes over time, I tested the

hypothesis that treeholes with higher volumes of water and leaf litter support higher richness and densities of common resident insects than treeholes with lower amounts of these resources.

Methods

Study sites

I conducted the study in 1995 within Centre County, Pennsylvania, USA, where I established 3 sites in each of the following 3 regions: 1) Plateau sites, in Pennsylvania State Gamelands #60 along the eastern edge of the Allegheny Front (lat 40°45'N, long 78°17'W); 2) Valley sites, in Pennsylvania State Gamelands #176 (lat 40°47'N, long 77°56'W), and 3) Ridge sites, in Rothrock State Forest, east of Valley sites (40°44'N, 77°44'W). Woody vegetation in all 3 forests consisted of 2nd-growth oak-maple forests, with red oak (*Quercus rubra* L.) and white oak (*Q. alba* L.) being the dominant species. The Gamelands and State Forest are managed for game and timber; study sites were mature forest stands more likely to include old trees containing treeholes. The 3 regions show differences in annual precipitation and chemistry, as Plateau sites experience slightly more rainfall at a lower pH (1995 rainfall for NADP [National Atmospheric Deposition Program] and PADCNr [Pennsylvania Department of Conservation and Natural Resources] sites = 95–102 cm, mean pH = 4.18; Lynch et al. 1996) than Valley and Ridge sites (1995 rainfall for NADP and PADCNr sites = 89–96 cm, mean pH = 4.31; Lynch et al. 1996). Statistical analyses of treehole water chemistry revealed regional differences in pH, similar to trends in rainfall pH, but most other water chemistry parameters revealed more variation among treeholes within than among regions (Paradise and Dunson 1998).

The treehole community

Diptera and Coleoptera larvae numerically dominate macroinvertebrate communities in treeholes of central Pennsylvania. Dipterans include 5 species of Culicidae, 2 species of Ceratopogonidae, and others (Barrera 1996). The most common dipterans in Pennsylvania treeholes are the culicid *Ochlerotatus triseriatus* (Say), ceratopogonid *Culicoides guttipennis* (Coquillett),

and the syrphid *Mallota posticata* (Fabr.) (Barrera 1996, Paradise 1998). Larvae of *O. triseriatus* primarily are filter feeders and browsers, consuming fine particulate organic matter (FPOM) and microbes (Merritt et al. 1992). *Culicoides guttipennis* and *M. posticata* larvae are deposit feeders and *C. guttipennis* also is a facultative predator (Barrera 1996, CJP, personal observation). Less-common dipterans include the psychodid deposit feeder *TelmatoSCOPEUS albipunctatus* (Williston), other culicids, a predaceous tipulid (*Limon-ia* sp.) and a predaceous dolichopodid (*Systemus* sp.) (Barrera 1996).

Larvae of the scirtid beetles *Helodes pulchella* (Guerin) and *Prionocyphon discoideus* (Say) also are common in Pennsylvania treeholes (Barrera 1996, Paradise and Dunson 1997). Scirtids are shredders and facilitate other treehole inhabitants because shredding increases leaf litter breakdown (Paradise and Dunson 1997, Paradise 1999). Shredder density may interact with litter quantity to affect community structure by increasing FPOM availability to insects consuming that resource (Heard and Richardson 1995).

Sample collection

At each site, I selected 3 basal treeholes between 1 to 5 L in total volume ($n = 27$) from red oaks or white oaks from a large set of treeholes, which I determined in 1994 to be within the desired size range and that held water throughout the year. I recorded total treehole depth and volume of all treehole components (i.e., water, leaf litter, coarse particulate matter <1 cm in diameter [hereafter called sediment]) initially in April 1995, and thereafter quantified these components monthly until October 1995. Each month, I removed all water by suction from each treehole, poured extracted water into pans, and then quantified volume. I extracted all pieces of leaf litter, bark, and twigs >1 cm², and placed them into a graduated beaker. Once there, I gently compressed the material to avoid harming insects in the sample, and then measured volume. This procedure gave a consistent approximation of relative litter volume leaf per treehole. However, it is important to note that this method did not accurately measure leaf mass; dry mass determination was not possible because I returned leaves to treeholes after each sampling.

I determined volume of sediment in April by

excavating the entire treehole and measuring volume in beakers. In remaining months, I collected subsamples (~100 mL) to estimate larval insect densities within the sediment. For each subsample, I homogenized the sediment with a ladle, withdrew a sample, leveled it off, and placed it in an enamel pan. I then added a small amount of water to disperse the sediment, and enumerated insects. I carefully replaced all sediment, litter, and water, in that order, after each monthly sampling.

I counted insect larvae by species and instar or size class (i.e., where instars could not be determined reliably, such as for scirtid beetles) in each treehole component. For analyses, I lumped different instars or size classes for each species, and quantified the total number of larvae and species for each treehole and month. It was difficult to distinguish between the scirtid beetle species in early instars, so I lumped these taxa for analysis.

Because of high inter-treehole variation in size and resources, I quantified temporal changes in resources and the community by monitoring the same treeholes rather than sequentially sampling new ones. I took care to minimize disturbance by excavating the entire treehole only once and using only sediment subsamples for subsequent measurements.

Statistics

I analyzed the data 3 ways to test the hypotheses that water volume and leaf litter volume affect treehole community structure. First, I used water and leaf litter volumes as covariates, month as a fixed factor, and individual treeholes as a repeatedly measured factor nested within month, in a repeated-measures multivariate analysis of covariance (MANCOVA). In this procedure, I used densities of *O. triseriatus*, *C. guttipennis*, densities of scirtid beetles (*H. pulchella* and *P. discoideus* combined), and species richness as dependent variables. I log-transformed water and litter volumes, and their interaction, as covariates in the analysis. I also conducted separate ANCOVAs, using the same statistical model as the MANCOVA, on each of the 4 dependent variables. These analyses tested hypotheses regarding the relationship between insect community dependent variables and water and litter volume independent variables.

Second, I used multiple regression to describe

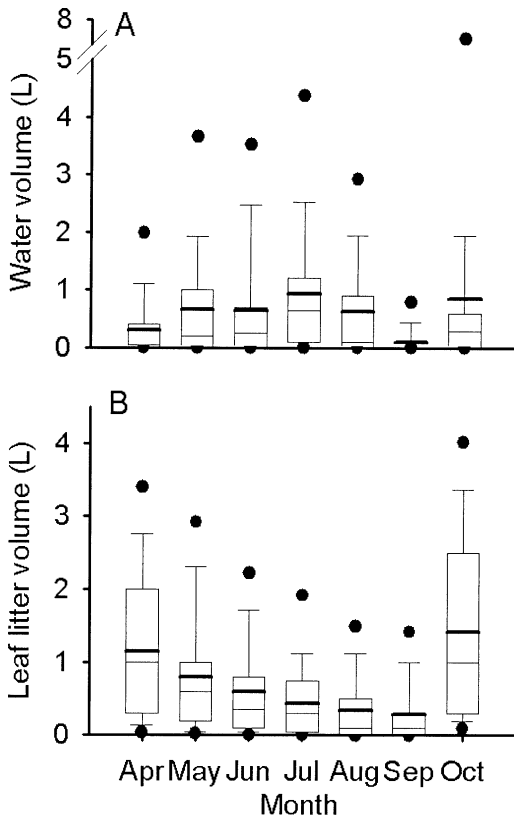


FIG. 1. Variability of water and leaf litter volume within 27 treeholes over time. A.—Box plots of water volume. B.—Box plots of leaf litter volume. The thin line within the box is the median, the thick line is the mean, boundaries of the box are the 25th and 75th percentiles, whiskers below and above each box are the 10th and 90th percentiles, respectively, and dots below and above whiskers are the 5th and 95th percentiles, respectively.

the relationships between independent variables (water and litter volumes, averaged for each treehole across the 7-mo study), and the maximum species richness, total insect density, and densities of *O. triseriatus*, *C. guttipennis*, and scirtid beetles. I reasoned that the maximum value for each dependent variable would be related to long-term conditions within treeholes. Although this approach caused a loss of temporal information, it indicated how average conditions in available resources can be used to predict individual treehole populations and community structure. These tests were similar to the MANCOVA, but the MANCOVA examined all the resource variables as repeated measures over time,

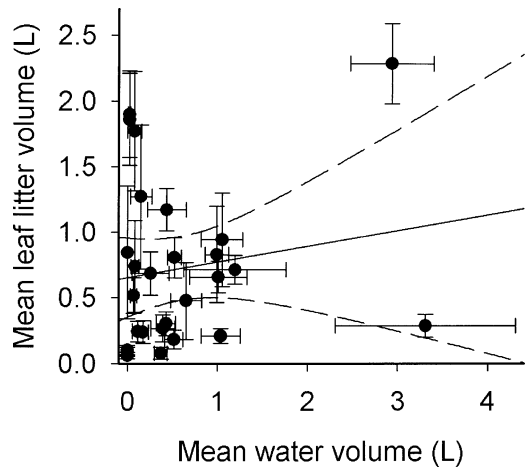


FIG. 2. Mean (+1 SE) water volume vs mean (+1 SE) leaf litter volume. Best fit regression line and 95% confidence belts (dashed lines) are also shown.

whereas the regression approach provided insight into how average resource conditions of treeholes related to structure of the insect community over the long term.

Third, for uncommon species not present in sufficient frequencies within treeholes to allow statistical analyses, I simply compared their individual monthly densities among treeholes with mean volumes of water and leaf litter, to assess relationships between density and water and litter volume.

I $\log_{10}(x + 1)$ -transformed all density and volume data to approximate normality, and then tested normality and heterogeneity of variance. To account for the number of tests of each type, I adjusted α ($= 0.05$) by dividing it by 5 (i.e., the number of tests of each type), such that adjusted $\alpha = 0.01$ for both the MANCOVA and regression analyses.

Results

Treehole size was related to water and litter volume, with individual treeholes exhibiting high variation in the quantity of litter and water resources (Figs 1, 2). Differences in these resources at least partially resulted from high seasonal variation in water and litter inputs, as rainfall was generally higher in spring than summer, and treeholes containing water in spring and early summer lost appreciable water in September (Fig. 1A).

TABLE 1. Repeated-measures MANCOVA, and univariate repeated-measures ANCOVA results for the 4 dependent variables (total insect species richness, and densities of the mosquito *Ochlerotatus triseriatus*, the ceratopogonid *Culicoides guttipennis*, and scirtid beetles) within treeholes tested in the ANCOVA. β = coefficient for the covariates, and SE = standard error of the coefficient. p -values < adjusted α of 0.01 were considered significant.

Variable/test	Covariate/factor	β	SE	df	F	p
MANCOVA	Log ₁₀ water volume			4,150	6.53	<0.0001
	Log ₁₀ leaf litter volume			4,150	2.04	0.09
	Log ₁₀ litter × Water volume			4,150	1.23	0.30
	Time			24,524	8.16	<0.0001
	Treehole			104,597	5.11	<0.0001
ANCOVA						
Richness	Log ₁₀ water volume	3.25	1.13	1,153	8.29	0.005
	Log ₁₀ leaf litter volume	2.23	1.00	1,153	4.92	0.028
	Log ₁₀ litter × Water volume	-5.74	3.60	1,153	2.53	0.11
	Time			6,153	4.44	<0.0001
	Treehole			26,153	6.90	<0.0001
<i>O. triseriatus</i>	Log ₁₀ water volume	2.39	0.67	1,153	12.93	<0.0001
	Log ₁₀ leaf litter volume	0.96	0.59	1,153	2.65	0.11
	Log ₁₀ litter × Water volume	-0.56	2.13	1,153	0.07	0.79
	Time			6,153	7.52	<0.0001
	Treehole			26,153	4.11	<0.0001
<i>C. guttipennis</i>	Log ₁₀ water volume	2.19	0.81	1,153	7.35	0.007
	Log ₁₀ leaf litter volume	1.44	0.72	1,153	4.01	0.047
	Log ₁₀ litter × Water volume	-5.13	2.58	1,153	3.96	0.049
	Time			6,153	17.47	<0.0001
	Treehole			26,153	2.87	<0.0001
Scirtidae	Log ₁₀ water volume	-0.17	0.57	1,153	0.09	0.76
	Log ₁₀ leaf litter volume	0.47	0.51	1,153	0.85	0.36
	Log ₁₀ litter × Water volume	-1.15	1.82	1,153	0.40	0.53
	Time			6,153	10.35	<0.0001
	Treehole			26,153	14.65	<0.0001

Litter predictably declined in most treeholes throughout the year (Fig. 1B), although it remained high in large treeholes. Increased precipitation and leaf fall in October increased treehole water and litter volume, respectively, especially in large-diameter treeholes that could easily collect stemflow and falling litter.

When averaged over time, the size of a treehole opening was correlated with time-averaged litter volume ($r = 0.42$, $df = 25$, $p = 0.0001$), but not with time-averaged water volume ($r = 0.001$, $df = 25$, $p = 0.99$). The total volume of treeholes (determined when full from water volume + litter volume + sediment volume), was highly correlated with area of the treehole opening ($r = 0.88$, $df = 25$, $p < 0.0001$), and there was no correlation between time-averaged litter and water volume ($r = 0.159$, $df = 25$, $p = 0.43$; Fig. 2).

All dependent variables varied seasonally and

among treeholes (Table 1). Water volume had a significant effect on insect species richness (Table 1). Treeholes with no water generally averaged <3 species (typically scirtid beetles and *C. guttipennis*), whereas those with as little as 0.25 L of water (but not dried out) averaged >3 and up to 6 species (Fig. 3A). Mean treehole water volume over the study also was a strong positive predictor of maximum species richness (Table 2). The relationship between richness and water volume was seasonal, as months with high volumes (averaged across treeholes) also showed high mean richness (Fig. 3B). Richness and larval densities declined between August and September, because of mortality or adult emergence (Figs 3B, 4B). Over the summer, litter declined and insect densities increased until September, a time when litter and densities were at their lowest levels (Fig. 4B). With the exception of 3 treeholes that had few insects and

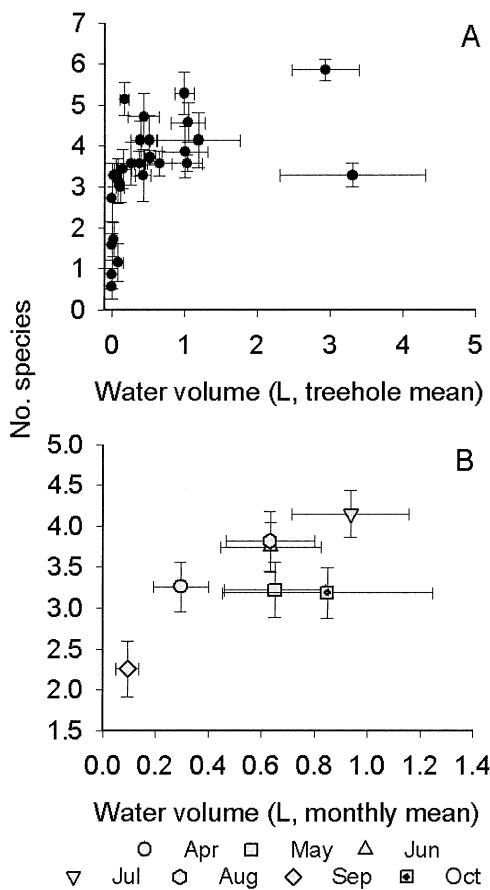


FIG. 3. Species richness vs water or leaf litter volume (mean +1 SE). A.—Richness vs mean water volume for each treehole, averaged over 7 mo. B.—Richness vs mean water volume for each month, averaged over all treeholes. Legend refers to B.

moderate to high litter volumes but unusually low water volumes (Fig. 2), there was a general, positive relationship between litter volume and insect density (Table 2, Fig. 4A). Richness was influenced by water volume through its effects on individual species, but treeholes with high litter supported high insect densities, at least during part of the season.

Density of *O. triseriatus* was affected by water volume because significantly higher numbers of larvae occurred in treeholes with more water, especially during May and June when treeholes were filled and eggs had hatched (Tables 1, 2, Fig. 5A, B). The effect of month on density was partially related to water volume because the extreme dry conditions in September eliminated

all mosquitoes (Fig. 5B). Density declines may have resulted from mortality and/or emergence because few larvae occurred in October, and treeholes with high water volume produced many pupae in June and July (Fig. 5B). Density was unrelated to litter volume (Tables 1, 2).

Densities of *C. guttipennis* were influenced by litter volume (Table 2). Larvae were found in 89.4% of censuses, although densities were highest when water volume was lowest, including one treehole that contained no standing water. *Culicoides guttipennis* was one of the few species found at high densities in treeholes with little water, often inhabiting sediment (Fig. 5C). Mean litter volume was a strong predictor of maximum *C. guttipennis* density (Table 2). The extremely high densities found in treeholes with low water and high litter in June and July were followed by comparatively low densities in August. Many individuals in July were late instars or pupae, and densities increased again in October after a 2nd generation of eggs hatched (Fig. 5D).

Densities of scirtid beetles were unaffected by water or litter volume (Tables 1, 2), contrary to my prediction. Scirtids were found in most treeholes sampled (84.6%). Most treeholes showed a similar pattern over time, with densities peaking in August when litter volume was lowest (Fig. 6A, B). Densities increased through August as litter decayed, with a sudden decline in September that remained low through October (Fig. 6B). Despite the apparent independence of scirtid densities from water volume and the different times of peak densities for scirtids and mosquitoes, mean densities of mosquitoes and scirtids were highly correlated ($r = 0.614$, $df = 25$, $p = 0.0003$). Both taxa favored large treeholes, which tended to have either high volumes of water or litter, or both. The pattern of scirtid densities was similar to total larval insect densities (Fig. 6A cf. Fig. 4A).

Uncommon treehole insects had variable relationships with water and litter volumes (Fig. 7), with many species being absent from treeholes during most censuses. Densities of *M. posticata*, when present, were highest in treeholes with relatively low water and high litter volumes (Fig. 7A, B). Similarly, *Systemus* sp. was most common in treeholes with low water and moderate litter volumes (Fig. 7C, D). The predatory culicid *Toxorhynchites rutilus* (Coquillett) was not found in treeholes until August, when

TABLE 2. Results of regression analysis between water and leaf litter volumes and insect species richness, total insect density, and densities of the mosquito *Ochlerotatus triseriatus*, the ceratopogonid *Culicoides guttipennis*, and scirtid beetles within treeholes. Water and litter volumes are in L, so regression equations can be constructed from the table using the coefficients (e.g., mean no. of species = $2.58 + [4.43(\log \text{ water volume})] + [0.38(\log \text{ leaf litter volume})]$). The *F* statistic is for the overall regression, and *t* statistics test whether coefficients were significantly different from 0. *df* = 2,24 for all regressions, and 24 for each *t*-test. * = significant overall regression, ** = significant coefficients (adjusted $\alpha = 0.01$).

Variable	Predictor	Coefficient	<i>F</i>	<i>t</i>	<i>p</i>
Richness	–	–	6.42	–	0.006*
	Y-intercept	2.58	–	6.23	0.0001**
	Log ₁₀ water volume	4.43	–	3.52	0.002**
	Log ₁₀ leaf litter volume	0.38	–	0.26	0.79
Log ₁₀ <i>O. triseriatus</i> density	–	–	10.19	–	0.001*
	Y-intercept	0.87	–	2.26	0.03
	Log ₁₀ water volume	5.26	–	4.50	0.0001**
	Log ₁₀ leaf litter volume	–1.24	–	0.90	0.38
Log ₁₀ scirtid density	–	–	3.78	–	0.04
	Y-intercept	2.04	–	7.16	0.0001**
	Log ₁₀ water volume	1.95	–	2.25	0.03
	Log ₁₀ leaf litter volume	1.36	–	1.32	0.20
Log ₁₀ <i>C. guttipennis</i> density	–	–	9.84	–	0.001*
	Y-intercept	1.84	–	8.28	0.0001**
	Log ₁₀ water volume	–0.756	–	1.12	0.27
	Log ₁₀ leaf litter volume	3.52	–	4.39	0.0001**
Log ₁₀ insect density	–	–	8.82	–	0.001*
	Y-intercept	2.45	–	14.28	0.0001**
	Log ₁₀ water volume	0.74	–	1.41	0.17
	Log ₁₀ leaf litter volume	2.33	–	3.77	0.001**

it occurred in only 6 of 27 treeholes and at densities <3 larvae/L. Similarly, *Telmatoscopus albipunctatus* was not found until August, when it occurred in only 4 treeholes, and usually at densities <3 larvae/L. Of the 5 other taxa found (i.e., the culicid *Orthopodomyia signifera* (Coquillett), the tipulid *Limonia* sp., the ceratopogonid *Dasyhelea* sp., unidentifiable Muscidae, and Chironomidae) densities never exceeded 5 larvae/L, nor were these taxa found in >10% of treeholes, or in any one treehole for 2 consecutive months.

Discussion

Environmental factors affecting insect community structure within treeholes and other phytotelmata include habitat size, water volume, and food availability, although these factors vary spatially and temporally (Kitching 1987, Jenkins et al. 1992, Sota et al. 1994, Barrera 1996, Paradise 1998, Yanoviak 1999b). My objective was to

examine temporal changes in food and water resources, to better understand insect species composition in a detritus-based community. I predicted that high volumes of water and/or leaf litter within treeholes would increase insect species richness and density of individual populations. In this context, effects of environmental fluctuations on insects depend, in part, on insect life-history traits, such as dispersal ability and phenology (Sota et al. 1994). For instance, mosquitoes overwinter as eggs whereas scirtids overwinter as larvae and then pupate in early spring (Barrera 1996). Thus, resources and physical characteristics of treeholes, as well as species adaptations, will influence composition (Paradise 1998).

Effects of water volume

Treeholes depend on direct precipitation and stemflow for water input (Carpenter 1982, Walker et al. 1991); thus, they collect and retain dif-

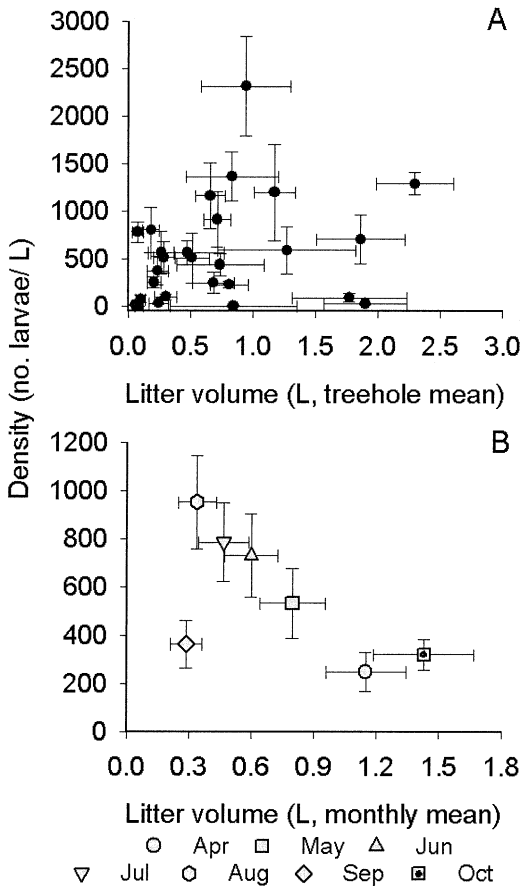


FIG. 4. Total larval densities vs water or leaf litter volume (mean +1 SE). A.—Mean total insect density vs mean leaf litter volume for each treehole, averaged over 7 mo. B.—Mean total insect density vs mean leaf litter volume for each month, averaged over all treeholes. Legend refers to B.

ferent amounts of water depending on size, angle of opening, and total volume of the treehole (Kitching 1987, Sota et al. 1994). I determined that the size of the opening was uncorrelated with water volume, and I showed that species richness increased as water volume (i.e., treehole capacity), but not litter, increased. Larger treeholes may contain more species because they are easier to find by ovipositing females, and also because they may hold more water and, thus, are less susceptible to drying than smaller treeholes (Bradshaw and Holzapfel 1988, Sota et al. 1994). In experimental treehole mesocosms with high water to litter ratios, early oviposition led to higher species richness than in meso-

cosms with a low water to litter ratio (Paradise 1998). Water volume also affected species richness of microbial communities within rain pools, where richness declined as pools dried (McGrady-Steed and Morin 1996). In this sense, variability in abiotic resources such as water volume may affect community structure by either eliminating species or allowing their persistence as small populations (Schoener 1989, Pimm et al. 1991, Reice 1994). Treeholes with different water volumes and size characteristics often show contrasting susceptibility to desiccation (Barrera 1996). Barrera (1996) argued that north-eastern treeholes generally do not dry out as often as southern treeholes (see also Bradshaw and Holzapfel 1988). Desiccation may constitute an unpredictable disturbance in Pennsylvania treeholes, which may change community composition by eliminating populations at low densities or species not adapted to drying (Pimm 1982, Pimm et al. 1991, Jenkins et al. 1992). Thus, high water volumes maintained over the summer, may be critical for colonization, persistence of drought-intolerant species, and high species richness.

As predicted, high densities of *O. triseriatus* occurred in treeholes with high water volumes, irrespective of litter abundance. Preference of *O. triseriatus* for high water volume has been shown in simulated treeholes (Paradise 1998), and in natural treeholes larvae appear quickly after filling from rain as a result of hatching of drought-resistant eggs oviposited above the waterline (Bradshaw and Holzapfel 1983). In addition, *O. triseriatus* larvae disappeared in treeholes that dried up. However, absence of *O. triseriatus* in permanently inundated treeholes may have resulted from stochastic dispersal and colonization (Kitching and Beaver 1990) because some treeholes with water could have supported *O. triseriatus* populations but may not have been found by ovipositing females.

Effects of leaf litter

Leaves fall annually within temperate-deciduous systems, and often are the major energy resource in detritus-based aquatic habitats (Carpenter 1983, Walker et al. 1991, Wallace et al. 1997). The volume of litter in my study was correlated with the size of the treehole opening, and appeared to influence maximum total insect density and density of *C. guttipennis*. High

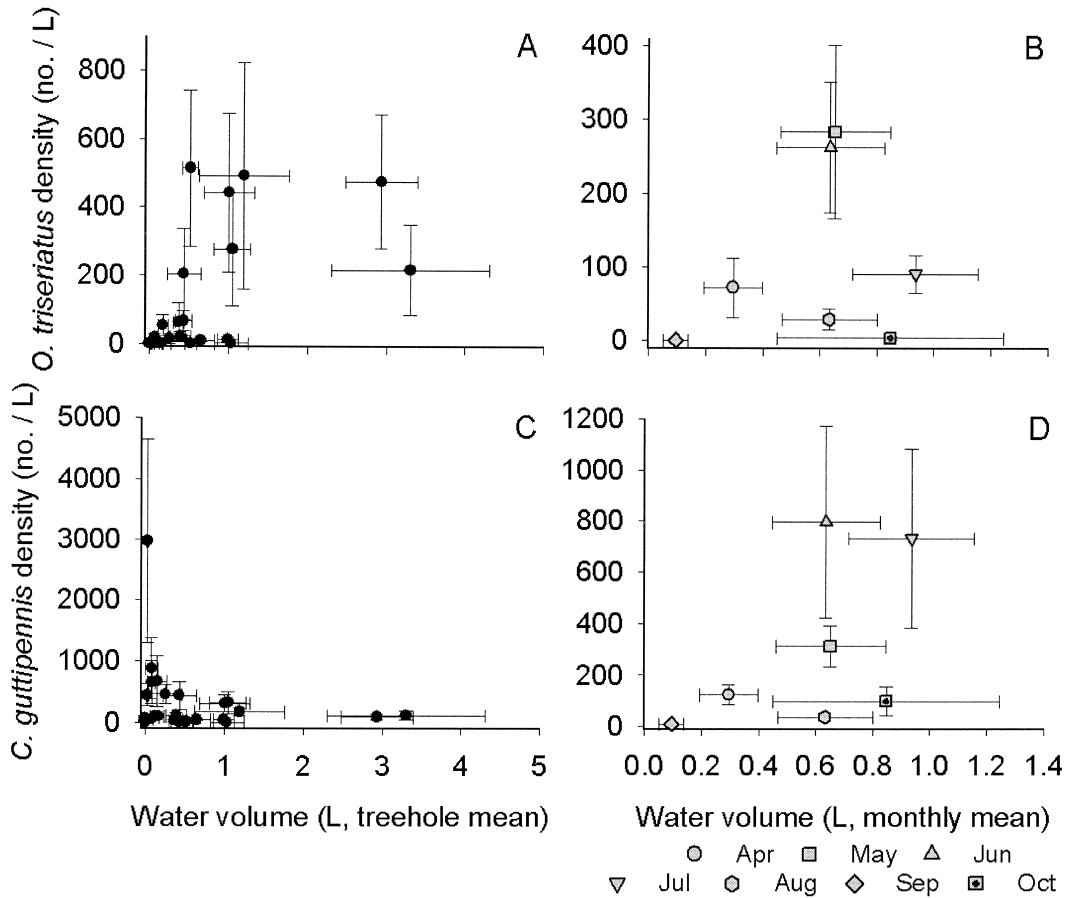


FIG. 5. Densities of common larvae of treehole insects vs treehole water volume (mean +1 SE). A.—*Ochlerotatus triseriatus* vs mean water volume for each treehole over the 7-mo study. B.—*O. triseriatus* vs mean monthly water volume. C.—*Culicoides guttipennis* vs mean water volume for each treehole over the 7-mo study. D.—*C. guttipennis* vs mean monthly water volume.

total densities were mostly attributable to *C. guttipennis* and scirtid beetles because these species composed 87% of larvae in treeholes averaging >0.5 L of litter. Treehole mosquitoes indirectly depend on leaf litter because they consume litter-associated microbes rather than litter directly. However, my data indicated that presence of standing water, rather than litter abundance, was a critical resource, likely because of the importance of water as a stable habitat (Sota et al. 1994, Paradise 1998).

I also predicted that densities of *C. guttipennis* would be high in treeholes with high litter volume. These midges generally occur in sediment below litter (Barrera 1996), where they consume decaying leaves. The positive relationship between litter volume and *C. guttipennis* density

may, thus, result from increased habitat complexity or productivity because treeholes with higher litter also are likely to have higher rates of litter decay and potentially more food for midges than treeholes with less litter (Paradise and Dunson 1997). Treeholes accumulate litter and sediment over time, and large treeholes filling with litter and sediment may become limited in the amount of water they can hold, although such treeholes may support large populations of desiccation-resistant *C. guttipennis* (Barrera 1996).

I also predicted that scirtid beetle densities would be positively correlated with litter volume, based on relationships reported between container sizes, litter amount, and scirtid density from other studies (Sota 1996, Paradise

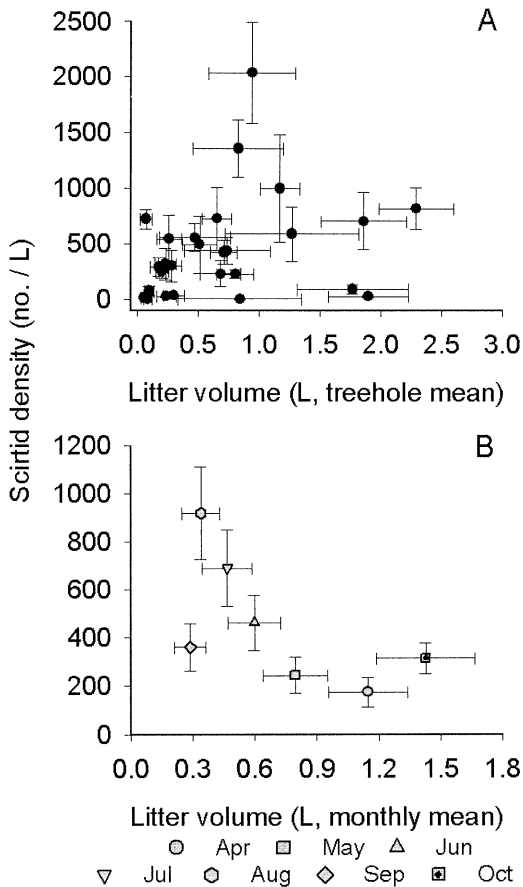


FIG. 6. Combined scirtid beetle (*Prionocyphon discoideus* and *Helodes pulchella*) densities vs treehole leaf litter volumes (mean +1 SE). A.—Mean litter volume for each treehole, averaged over 7 mo. B.—Mean litter volume for each month, averaged over all treeholes. Legend refers to B.

1998, Daugherty and Juliano 2001). Scirtids are primarily shredders, and their feeding directly increases leaf breakdown and, thus, indirectly increases growth of *C. guttipennis* and *O. triseriatus* (Paradise and Dunson 1997, Paradise 1999). In this context, scirtid density and its effects on litter breakdown may be important in determining treehole community structure by regulating FPOM concentrations for deposit and filter feeders, or by providing oviposition cues for females of other species (Wilton 1968, Beehler et al. 1992). Shredding by scirtids, however, did not increase total species richness in my study, as reported elsewhere (Sota 1998, Daugherty and Juliano 2001), although their activity

may have produced the strong relationship between litter quantity and total insect density. If true, then scirtids may accelerate initial leaf decomposition in autumn, which in turn may support increased microbial productivity and increased *C. guttipennis* and *O. triseriatus* populations, possibly by the following spring. The decline in scirtid densities seen in September and October could have been caused by desiccation and could decelerate leaf decomposition and, thus, disrupt the processing chain in treeholes.

It is possible that the presence of scirtids and midges in nearly every treehole, combined with the low overall number of species in the pool, may have diminished richness differences in treeholes with contrasting litter levels and, thus, led to no apparent relationship between richness and litter level. Positive correlations in other studies have been found among litter abundance, richness, total metazoan biomass, and treehole capacity (Sota 1998, Daugherty and Juliano 2001). In those studies, total treehole capacity led to increased litter volume, and these 2 variables were positively correlated in my study ($r = 0.616$, $df = 25$, $p = 0.001$). Large treeholes with wide openings likely accumulated substantial litter, which in turn may have led to high insect densities. Treehole insect species partition litter by particle size and also consume microbes and protozoans (Walker et al. 1991, Barrera 1996), thus promoting high densities and richness during times of high food availability, such as in late spring when litter decay is rapid. Contrary to the poor correspondence between litter and richness I observed, richness and food web complexity in detrital systems often are influenced by the amount of energy available, with several experimental studies reporting direct relationships in energy and richness (Jenkins et al. 1992, Warren and Spencer 1996, Srivastava and Lawton 1998). Increased litter may increase occurrence and abundance of rare species (Jenkins et al. 1992), although I did not observe this result, possibly because of the overriding effects of water volume on richness.

Resource interactions

The water volume and litter (energy) content of the treehole habitat may separately affect species richness, or both may covary, such that large habitats holding more water have higher litter abundance. In addition, such treeholes tended to

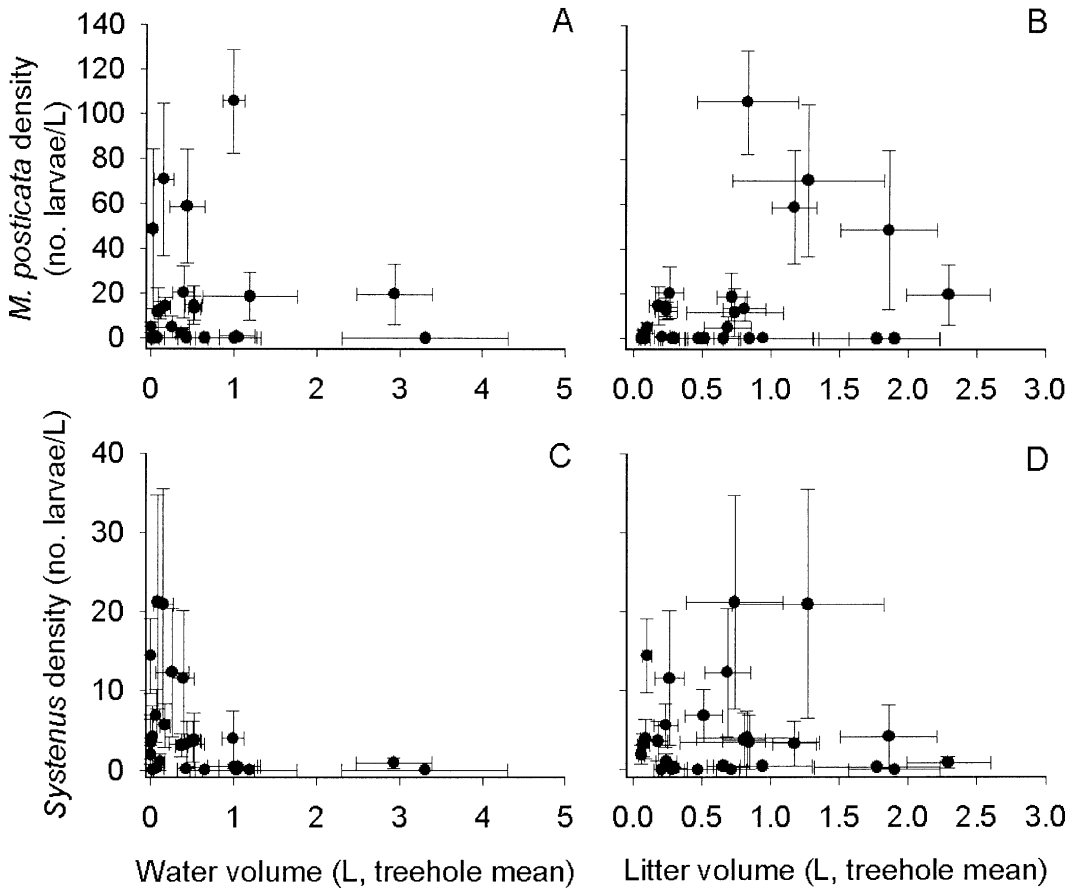


FIG. 7. Larval densities of 2 less-common insect species within treeholes vs treehole water or litter volume (mean +1 SE). A.—*Mallota posticata* vs mean treehole water volume. B.—*M. posticata* vs mean treehole leaf litter volume. C.—*Systemus* sp. vs mean treehole water volume. D.—*Systemus* sp. vs mean treehole leaf litter volume.

have high densities of both *O. triseriatus* and scirtid larvae. Large treeholes often have higher habitat heterogeneity than small treeholes, possibly allowing greater habitat partitioning by treehole residents (Bradshaw and Holzapfel 1983, Kitching 1987, Sota et al. 1994, Barrera 1996) and potentially increasing refuge from predation or desiccation. As treeholes dry, both water volume and leaf decay decrease (Aspbury and Juliano 1998), resulting in a potentially strong water-volume effect that is indirectly related to food availability. Leaf litter plays a major role in determining insect density or biomass (Sota 1998, Daugherty and Juliano 2001). Where water volume is more variable, such as in my study, it likely has a stronger role in determining species richness by regulating presence or absence of desiccation-intolerant species. Occur-

rence of less-common treehole species indicates that many of these species prefer either high water volumes or high litter volumes, although more species overall occurred in treeholes with high water volumes. Small changes in the number of insect species in communities often cause disproportionately large changes in richness when the species pool is small (Yanoviak 2001). Rare species in my study, apparently sensitive to treehole water volume, revealed a relationship between volume and richness because these species occurred only in treeholes with high water volumes.

Variability of resources within detritus-based aquatic communities affects the productivity and stability of the habitat. The fact that water volume was a better predictor of species richness in Pennsylvania treeholes than was leaf lit-

ter volume is counter to evidence indicating a positive relationship between productivity and richness (Jenkins et al. 1992, Warren and Spencer 1996), suggesting an interactive role between water volume and litter availability. Both resources are important in determining treehole habitat characteristics, which ultimately are determined by morphology of the treehole itself. In phytotelmata and other detrital aquatic habitats, total consumer productivity, productivity of individual species, and community structure all depend on input of water and litter resources, which in turn are affected by environmental variation of the habitat. Controversy exists regarding the relative importance of water vs litter resources, yet it is clear that both resources relate to habitat size and, thus, are important determinants of population sizes and community structure in treeholes.

Acknowledgements

I thank N. Aldredge, J. Bermel, K. Lentz, E. A. McGraw, J. Whalen, J. York, and S. Paradise for field assistance, Bill Dunson and 2 anonymous reviewers for helpful comments and discussion, the Pennsylvania Game Commission for permission to work on State Game Lands, and the Pennsylvania Department of Environmental Resources for permission to work in Rothrock State Forest. This research was funded by the US Environmental Protection Agency (EPA) through award #R-822298-01-0 to W. A. Dunson. The research has not been subjected to EPA review and, therefore, does not necessarily reflect the views of the Agency.

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Received: 27 June 2002

Accepted: 2 September 2004