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Do local conditions trump spatial factors within a simulated treehole metacommunity?

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ABSTRACT

Metacommunity ecology is concerned with effects of dispersal and habitat conditions on the structure and dynamics of local communities. We tested the effects of distance between communities and habitat size (a proxy for local conditions) on structure and dynamics of communities in a metacommunity. Mesocosms of two sizes were placed at varying distances from known treehole habitats. We monitored communities for effects on colonization, occupation, abundances, and community similarity. Because treeholes vary in size, we predicted that habitat size would more strongly influence communities than distance. We predicted that species would differ in responses to distance and size because of variation in habitat requirements and dispersal abilities. Previous research suggested that the mosquito *Aedes triseriatus* would be unaffected by size or distance, whereas the midge *Culicoides guttipennis* would be affected by habitat size. The predator *Toxorhynchites rutilus* would be affected by habitat size, and its presence would affect local composition. Similarity would be greater in close communities of similar size. We found strong effects of habitat size on colonization, occupancy, and density of several species, including *C. guttipennis*, two syrphids and *Tx. rutilus*. *Toxorhynchites rutilus* densities were negatively correlated with prey densities. *Aedes triseriatus* was not affected by distance or habitat size. Densities were asynchronous across communities, regardless of distance or habitat size. Spatial and temporal turnover were high, but same size habitats were more similar than different size habitats. Community similarity increased as distance between habitats decreased. We conclude that local conditions in treeholes more strongly affected community structure than distance between habitats. However, composition is best explained by both the local and the regional.

KEYWORDS: colonization, dispersal, habitat patch, mesocosm, metacommunity dynamics, patch occupancy, predation, resources

INTRODUCTION

The composition and relative abundance of species in spatially-structured communities are strongly related to and affected by abiotic and biotic conditions within a local habitat [1-5], which are patches of distinct habitat type within a larger environmental matrix. At larger scales dissimilarity in community structure among local communities may arise from spatial processes, such as distance and degree of isolation between habitats or from dispersal ability of individual

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species [6-8]. Populations in these habitats may persist for a time or go locally extinct, or they may be rescued from extinction by colonization events [7]. The dynamics of metacommunities, sets of communities connected by dispersing species, in spatially structured habitats are thus affected by factors operating at different scales [7, 8]. Knowledge of the relative strengths of these factors should increase our understanding of community structure, diversity patterns, population biology, evolutionary adaptations, succession, and species interactions, and could lead to strategies or policies to better conserve biodiversity, manage invasive species, and make land use decisions.

Several related models are used to understand metacommunity dynamics. All make predictions about the relative influence of local and spatial factors, and integrate the factors to better understand community structure and dynamics. Predictions of the different models are not mutually exclusive, and several recent studies of various systems have found support for more than one model in describing metacommunity dynamics [5, 9-13]. Consequently, the relative importance of local and spatial factors is not fully understood.

Metacommunities, such as phytotelmata, ponds, decomposing logs, and rock pools are known to be affected by local conditions, where species are responding to environmental factors [5, 9-17]. The species sorting model predicts that local factors will have a large influence on community composition. Variation in resource availability and predation among patches causes differences in local demography, the outcome of interactions, and, ultimately, community composition [5, 10-12]. Different species perform better in some patch types than others [7, 9], and dispersal among patches is not so frequent that species regularly occur in sink, or suboptimal, patches [12]. Although regional factors have less influence than local factors in this model, some dispersal allows changes in local conditions to be tracked by species, resulting in temporal changes in species composition [7]. The neutral model also states that dispersal limitation structures meta-communities, but in contrast to the species sorting model, the neutral model predicts that species are equivalent in life history characteristics. Diversity then arises through local extinction and speciation [7].

As dispersal among local habitats increases or distance between them decreases, different dynamics in metacommunities are expected. With some amount of dispersal or intermediate distances between patches, the patch dynamics model predicts that resident populations undergo repeated extinction and colonization, species diversity in patches increases, and communities close together tend towards a high degree of similarity [9]. Species relative abundances will shift over time, but these shifts will not correlate to any temporal changes in environmental conditions [9]. Local populations may be eliminated in sink habitats, or by presence of predators or superior competitors. As dispersal increases or distance between habitats decreases further, the mass effects model predicts existence of populations of species in habitats where they could not exist otherwise [7, 8, 12]. In this model, spatial factors are strong relative to local factors, such that migration can rescue populations in suboptimal habitat. Community similarity among patches is predicted to be high in this model and will correlate to the distance between patches and depend upon the dispersal abilities of resident species [9].

Our objective was to better understand the relative importance of local and spatial factors in a model metacommunity, the treehole metacommunity. Ellis *et al*. [12] examined two decades of data on mosquitoes inhabiting Florida treeholes and Paradise *et al*. [13] examined three years of surveys of the entire insect community in North Carolina treeholes, both in unmanipulated field studies. Each concluded that the communities were strongly affected by local conditions, although distance effects were also evident, supporting both the species sorting and mass effects models. In order to test predictions of metacommunity theory, we used mesocosms to manipulate local conditions and distance between patches in a simulated treehole metacommunity. We then allowed for colonization to occur and determined the relative influence of local and spatial factors on local and regional diversity in a treehole metacommunity. Only a few other studies have attempted to manipulate metacommunities in the field [4, 18-19]. The study of metacommunities in

the field lags behind theoretical and laboratory studies, and is the only way to determine whether predicted patterns or patterns observed in the laboratory exist in natural metacommunities.

Treeholes are distinct water-filled container habitats in trees, often numerous in forests [13]. Treeholes in a forest form a metacommunity as they are a set of local communities linked by dispersal of multiple, potentially interacting species. Adult insects emerging from treeholes are the dispersal phase, while the larval communities represent a set of discrete communities within a metacommunity. The local patches, individual treeholes, vary in volume, shape and area of opening, and these factors are known to affect populations and communities within [15, 20]. The size and shape of a treehole also affects water chemistry parameters, local factors known to affect species [21]. Local community structure may be affected by predation and resources, which may also be affected by habitat size [13, 15, 22-25]. Seasonal changes in leaf litter resource availability and insect occupation and colonization also affect treehole communities [13, 15]. Individual treeholes are affected by regional dispersal patterns that are dependent upon the spatial pattern of treeholes within a forest [12, 13]. Knowledge of the dynamics of treehole metacommunities will lead to a better understanding of dynamics of species within metacommunities, including medically-important mosquitoes inhabiting containers around human populations.

The treehole fauna in North Carolina treeholes is well-known and is composed of a variety of insects, other invertebrates, and microbes [20, 26]. We studied the insects, most of which are dipterans. The most abundant dipterans are the culicid *Aedes triseriatus* (Say) and the ceratopogonid *Culicoides guttipennis* (Coquillet) [20, 26]. Other dipterans include the culicids *A. albopictus* (Skuse), *Orthopodomyia signifera* (Coquillet), *Toxorhynchites rutilus* (Coquillet), and *A. hendersoni* Cockerell, the syrphid *Mallota posticata* (Fabr.), and the psychodid *Telmatoscopus albipunctatus* (Williston) [27]. The lone coleopteran is the scirtid *Helodes pulchella* (Guerin) [26].

We hypothesized that local conditions would have greater effects than degree of isolation on local composition. Habitats with similar environmental conditions would have more similar communities than dissimilar habitats. Further, we predicted that local conditions and degree of isolation would affect species differently, as habitat preferences and dispersal abilities are known to differ among at least some of the species that have been more studied [20, 25, 28-31]. The most abundant species (*A. triseriatus* and *C. guttipennis*) would colonize all habitats and show no effect of distance. They should have high patch occupancy and colonization rates. Because mesocosms always had sufficient water *A. triseriatus* was not predicted to experience habitat size effects, whereas *C. guttipennis* was predicted to experience habitat size effects because it is known to favor smaller habitats [20]. Mosquito population dynamics would thus be synchronized among all treatments because of their dispersal ability and use of any container with sufficient water, and midge dynamics would be synchronized within habitat size treatments even across distances. Not much is known about the rare species, but we predicted that they may favor a certain size habitat, and degree of isolation should play a role in their dynamics due to smaller population sizes. These species should have low patch occupancy and colonization. Finally, we predicted presence of the predator *Tx. rutilus* would further increase community dissimilarity if predators themselves are affected by habitat size or degree of isolation. The presence of the predator in any one local community should increase the variation in structure between that community and communities without the predator; diversity of prey will increase and abundance of prey populations will decrease in presence of the predator [25].

MATERIALS AND METHODS

Experimental design

We created mesocosms with two diameters of PVC pipe cut to two different lengths (7.65 cm ID cut to 11.0 cm length and 10.15 cm ID cut to 19.7 cm length; hereafter small and large, respectively). We chose habitat size as the environmental condition variable because it is known to affect several other parameters, including dissolved oxygen and temperature and has strong effects on both patch occupancy and dynamics of individual treehole species [13, 15, 20]. The volumes

were 500 ml for small and 1,500 ml for large mesocosms. We inserted a lining of black fiberglass window screening, held in place at the top with a PVC pipe coupling and caulk. We used aquarium caulk to affix an end cap at the bottom. We attached each mesocosm to a 1.5 cm PVC pipe frame using expandable polyurethane foam as protection.

We deployed mesocosms in late spring 2006 in a hardwood second growth forest on the Davidson College Ecological Preserve (area centered on 35^{o} 30' 37''N, 80^{o} 49' 48''W). We tied frames to trees with clothesline and glued window screen to the top of each frame, 25 cm above the mesocosms, to reduce debris that entered mesocosms and better control resource availability. We wrapped frames and trees in chicken wire to protect them from disturbance by vertebrates.

We used a 2 x 3 design, with two to three replicates of each treatment. Habitat size (small and large) was crossed with distance to known treehole habitat (short, medium, and long). Short, medium, and long distance corresponded to low, medium, and high isolation and volume was held constant by adding water after weekly censuses. Sixteen mesocosms were established, arranged in three sets each beginning near a pre-established pair of mesocosms from other experiments performed in 2004 and 2005 (Figure 1). Within each set of mesocosms, we positioned one mesocosm of each habitat size 5-10 meters and 25 to 30 m from the sources, and we positioned one small and/or one large mesocosm at least 75 m from sources of dispersing adults. In addition to distance from those sources, we knew that experimental mesocosms were at least the nominal distance to other mesocosms or treeholes, the latter of which also served as sources of dispersing adults. When insects later emerged from experimental mesocosms, they also served as sources. Distances and placement was limited by proximity to known treeholes, leading to fewer replicates of long distance mesocosms; we did not have enough locations 75 m or more from other treehole habitats to have six long distance mesocosms.

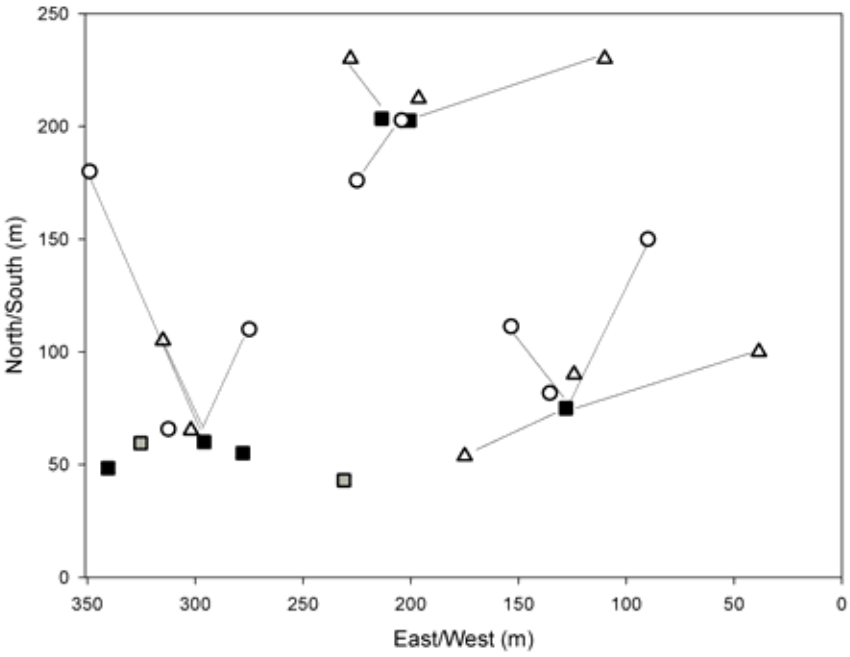

Figure 1. Positions of mesocosms in forest. Distances are in meters but axis labels do not reflect actual spatial coordinates. Open triangles and circles are small and large habitat size, respectively. Black squares are source mesocosms from a previous experiment and gray squares are treeholes. Short distance mesocosms are right next to sources on map. Lines connect source mesocosms to medium and long distance mesocosms to show original setup.

We searched the forest for treeholes and other breeding sites to ensure that no container habitats were closer to a mesocosm than the minimum distances we set. Because we have studied treeholes in this area for over 5 years, performing multiple searches during that time, we were confident that we knew where all treeholes were, as well as most other breeding sites such as discarded tires.

We recorded spatial coordinates for each mesocosm using GPS, and we determined distance between all mesocosm pairs, regardless of which set it was in or its distance to a source. While distances between replicates and source mesocosms were set, which led to three different degrees of isolation, it was also of interest to compare dynamics between all pairs of mesocosms. We validated distances for pairs that were within sight of one another using an infrared rangefinder (Bushnell Yardage Pro Sport 450, Overland Park, KS). Mesocosms were between 10 and 290 m apart. While the maximum distance could be travelled by dispersing adults of any of the study species, which we know because we have found all species in treeholes that were as isolated as our long distance mesocosms, we used the term "degree of isolation" to describe the relative differences among treatments. No treatment was completely isolated, and the distances between mesocosms fell within the range of distances apart for treeholes in the region (range = 7 to 404 m apart, median distance = 153.2 m) [13].

We conducted three trials beginning in May 2006 and ending in July 2007 to examine short term colonization patterns. The first trial lasted 10 weeks from May 2006 through July 2006, the second trial for six weeks from August 2006 to September 2006, and the third trial for 16 weeks from March 2007 through July 2007. To begin a trial, we filled each mesocosm with distilled water and 7 grams of dried oak leaf litter (*Quercus* spp.), a common genus of tree in our forest, per liter. For the second and third trials, mesocosms were completely emptied and refilled with fresh water and leaf litter.

Censuses and monitoring

Each week, we removed all water from each mesocosm by light suction and placed it into pans. We extracted leaf litter, placed it into a tared beaker, and determined mass using a PocketPro digital balance (Acculab, Edgewood, NY). We counted larvae by species and size class in the field because we wanted to monitor the development of the community over time. We counted early instar mosquitoes as one species, as we could not distinguish them in the field. We know from previous studies and from larvae reared to adults that >90% of treehole mosquitoes in the study area are *A. triseriatus*. We carefully replaced the contents after each weekly sampling in the reverse order from which it was extracted. Water was added to maintain constant volume.

We monitored dissolved oxygen concentration at depth, specific conductance, temperature and pH to determine if they differed between habitat sizes. For the first three variables we used a YSI 85 dissolved oxygen and conductivity meter (YSI, Yellow Springs, OH). For pH, we used an Orion 290A pH meter (Thermo Scientific, Beverly, MA). We began by measuring these values weekly, but once we determined that the values stabilized and did not change dramatically in a container from week to week, we only monitored the values once every two to three weeks.

Analysis

Habitat differences

For each environmental variable we tested the effect of habitat size with a 2 sample randomization test using RT: A Program for Randomization Testing (v. 2.1) [32]. Because we analyzed data collected over time from the same unit, randomization statistics were used, as they do not assume a normal distribution. Randomization strategies for statistical analysis are based on repeatedly drawing thousands of new subsamples from the original sample. We determined significance based on 10,000 randomizations. We pooled data for each variable across all trials to conduct these tests. Observations with these variables [21] and examination of Trial 1 data led to the conclusion that the variables were fairly consistent within a habitat size. We used the results to characterize differences between the two habitat sizes.

Responses of species density over time

To test predictions about effects of habitat size and degree of isolation, we examined densities

and species diversity. Because each mesocosm was sampled repeatedly, we used profile analysis, a multivariate equivalent of repeated measures analysis of variance. This allowed us to test for effects of habitat size and degree of isolation over time without violating assumptions of ANOVA. In profile analysis, differences and averages at consecutive time points become transformed variables in two-way MANOVAs, where habitat size and isolation were fixed effects factors [33] to tests for interactions and main effects, respectively. The experiment-wise α of 0.05 was adjusted by dividing it by the number of profile analyses within a trial. All data were tested for univariate normality and homoscedasticity, and densities (number per liter) were log-transformed.

The measure of diversity used was e (base of the natural logarithm) raised to the power of the Shannon diversity [34]. All insect species were included in diversity measures, but only *C. guttipennis*, *A. triseriatus*, *Myiolepta* sp., *M. posticata* (Trials 1 and 3 only), and *Te. albipunctatus* (Trial 3 only) were analyzed for effects on their presence/absence and abundance. Other species were not observed in a trial or were not common enough to analyze, due to rarity or seasonal variation in abundance. Data from multiple consecutive weeks when a species was not observed were eliminated. Colonization in Trial 3 primarily occurred after the 6^{th} or 7^{th} week in Trial 3, so we ran profile analyses for all variables from week 7 to week 17.

Patch occupancy and colonization

We calculated occupancy as the proportion of mesocosms occupied by a species during each census [12] and calculated bootstrap means with 1,000 resamplings to examine mean proportion occupancy for a species within a trial and also within habitat size and degree of isolation. Weeks prior to the first colonization event or after the point at which no more larvae of a species were observed were not used in calculating occupancy.

Censuses allowed us to record colonization events based on appearance of first instar larvae. For *C. guttipennis*, *A. triseriatus*, *H. pulchella*, and *Tx. rutilus* we calculated the proportion of treeholes colonized each week. For species not counted by size we defined colonization as the appearance of larvae or when densities increased from one week to the next.

To determine whether proportion occupancy or colonization varied across degree of isolation, habitat size, or trial, we analyzed time-averaged variables using a nested ANOVA, with trial as the main effect and habitat size and degree of isolation nested within trial.

Effects of predation

We tested for a relationship between densities of all prey species, except *H. pulchella*, and the density of *Tx. rutilus*. We performed randomization regressions on log-transformed densities of the prey in any mesocosm in which we found the prey or *Tx. rutilus* or both, using log-transformed *Tx. rutilus* densities as the independent variable. In addition, we performed a randomization two-sample test on diversity in treeholes where *Tx. rutilus* was present *vs.* treeholes where it was absent, with significance calculated using 10,000 randomizations.

Spatial synchrony

We examined fluctuations of the density of each of six species across pairs of mesocosms by calculating correlations of log-transformed densities between each pair of mesocosms. Asynchrony, or low correlation, between pairs suggests local dynamics [12]. Synchrony between same size pairs suggests habitat size preference. We also used analysis of covariance (ANCOVA), with trial as the main effect, the habitat size comparison (small *vs.* small, large *vs.* small, or large *vs.* large) nested within trial, and distance between pairs as the covariate. Because synchrony values were not independent of one another, we interpret results cautiously, and we also used randomized linear regressions (10,000 randomizations) to examine the relationship between synchrony for a pair of treeholes against distance between pairs [32].

Species composition and turnover

We calculated spatial turnover as $[(A_{obs} + B_{obs})/(S_A + S_B)] \times 100$, where A_{obs} is the number of species found in site A but not in B, B_{obs} is the number of species found in site B but not in A, S_A is the species richness in site A, and S_B is the species richness in B [12]. We calculated this for all pairs that contained at least one species in one

of the mesocosms at a particular time. Bootstrap means of all within-trial pairs (1,000 resamplings) were calculated.

We calculated temporal turnover for each mesocosm by comparing data from one week to data from four weeks later using $[(X_{obs} + Y_{obs}) / (S_X + S_Y)] \times 100$, where X_{obs} is the number of species found in a mesocosm in week X but not in week Y (where $Y = X + 4$), Y_{obs} is the number of species found in a mesocosm in week Y but not in week X, S_X is the species richness in week X, and S_Y is the species richness in week Y [12, 35]. We calculated bootstrap means of temporal turnover (1,000 resamplings) for each mesocosm.

We performed a nested ANCOVA for mean spatial turnover with trial as the main effect, the habitat size comparison nested within trial, and distance between pairs of treeholes as the covariate. We performed a nested ANOVA on temporal turnover, with trial as the main effect, but with habitat size and degree of isolation as factors nested within trial. Finally, we also used randomization regression to examine the effect of distance on spatial turnover, and randomization ANOVA to test the effect of habitat size and degree of isolation on turnover.

RESULTS

Habitat differences

Dissolved oxygen concentrations were significantly higher in small than in large mesocosms (2 sample randomization test; 1.36 $\pm$ 0.09 SE *vs.* 1.04 $\pm$ 0.08 SE, $P = 0.003$, d.f. = 140). pH was significantly higher in small than in large mesocosms (2 sample randomization test; 6.21 $\pm$ 0.05 SE vs. 6.02 $\pm$ 0.06 SE, $P = 0.016$, d.f. = 142). Specific conductance did not differ between the two habitats. The mean difference between habitats was very small, only -0.45 µS (2 sample randomization test; $P = 0.47$; d.f. = 125). Temperature differed between the two habitats by only 0.08°C and was not significant (2 sample randomization test; $P = 0.47$; d.f. = 110).

Overall community

Between 0 and 6 species were found in any one mesocosm at any one time (median = 2 species per mesocosm per census, mean = 2.12 $\pm$ 0.05 (SE)). Spring/summer trials (1 and 3) had the most active insect communities (median = 2 species per mesocosm for both trials, Trial 1 mean = 2.46 $\pm$ 0.08 (SE) and Trial 3 mean = 2.15 $\pm$ 0.07 (SE)). Trial 2 in autumn 2006 had lower densities and fewer active insect species (median = 1 species per mesocosm, mean = 1.51 $\pm$ 0.12 (SE)). A total of nine species of insect were found during the study.

Mosquitoes were the most common and abundant taxa (68.9% of all individuals and found in 89.2% of censuses). The midge *C. guttipennis* was the second most abundant (16.6% of all individuals in 49.6% of censuses). The syrphids *Myiolepta* sp. and *M. posticata* were not as common (7.4% and 1.6% of individuals), nor were *Tx. rutilus*, the top predator (2.0% of individuals over time) or *Te. albipunctatus*, *H. pulchella*, and a dolichopodid, *Systenus* sp., (each < 2.0% of individuals). The top predator typically exists in low abundance, and the presence of just one individual *Tx. rutilus* individual can deplete populations of all prey species [25].

Profile analysis

Culicoides guttipennis and *Myiolepta* sp. were affected by habitat size. Densities of *C. guttipennis* were significantly higher in small habitats in Trial 2 (Wilk's $\lambda_{4,7} = 0.14$, $P = 0.004$; Figure 2), and were consistently higher in small mesocosms in all trials (Figures 2a-c). *Myiolepta* densities were significantly higher in large habitats in Trial 1 (Trial 1 Wilk's $\lambda_{5,6} = 0.09$, $P = 0.004$; Figure 2d), with a habitat size by time interaction in Trial 3 (Wilk's $\lambda_{8,3} = 0.0077$, $P = 0.004$; Figure 2f). No other species tested were significantly affected by habitat size or degree of isolation according to profile analysis (Table 1). Diversity was not affected by either variable.

Patch occupancy and colonization

Each week about half the mesocosms contained first instar mosquitoes (Figure 3). Occupancy by mosquitoes was much higher than for any other species, regardless of treatment. Occupancy for *C. guttipennis* was second highest, although it had low proportion colonization, at about 15%. *Mallota posticata* and *Te. albipunctatus* had occupancy and colonization between 25-33% (Figure 3). *Myiolepta* sp., a species that we do not

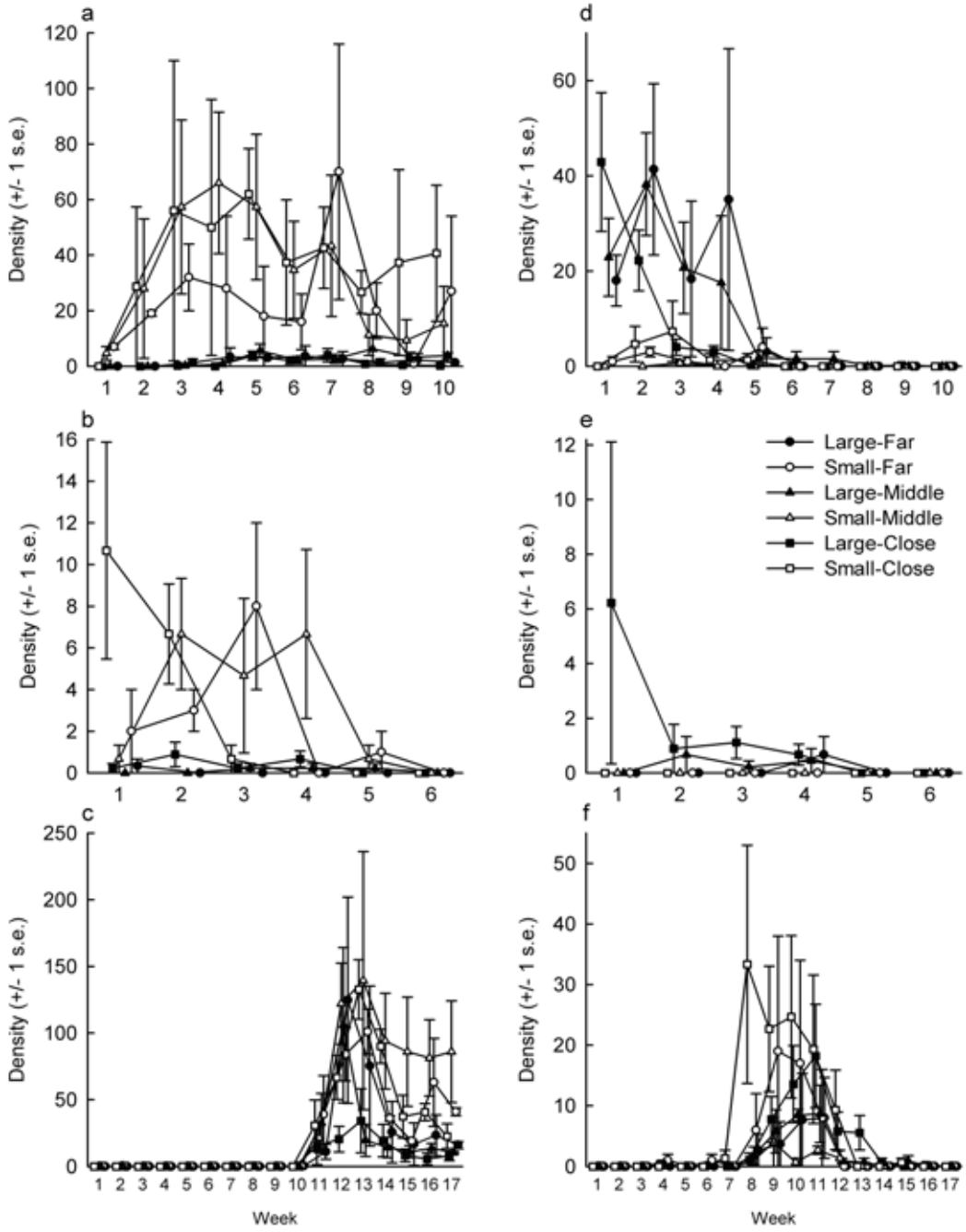

Figure 2. Densities over time for *C. guttipennis* and *Myiolepta* sp., both of whose densities were significantly affected by the habitat size of the mesocosm. Graphs a, b, and c are densities of *C. guttipennis* for Trials 1, 2, and 3, respectively. Graphs d, e, and f are densities of *Myiolepta* sp. for Trials 1, 2, and 3, respectively.

normally find in treeholes, colonized and occupied large mesocosms. Colonization for *T. rutilus* is only about 10%, although occupancy is close to 20%, suggesting that mortality or ovipositioning is low or longevity is high in mesocosms.

Habitat size had a significant or nearly significant effect on occupancy of all species except *A. triseriatus* and *M. posticata* (Table 2). *Telmatoscopus albipunctatus* and *Myiolepta* sp. had significantly higher occupancy in large than in small mesocosms

Table 1. Results of profile analysis for densities of common species in each Trial. Trial 3 analyses are for weeks 7 - 17 except for *C. guttipennis*, which includes only weeks 10-17. The test statistic is Wilk's λ, and numbers in parentheses below Wilk's λ are degrees of freedom. All densities were log-transformed. T = Trial; H = habitat size effect; I = isolation effect; S = species richness.

Variable	Habitat size		Isolation		H x I		H x Time		I x Time		H x I x Time	
	Wilk's	P	Wilk's	P	Wilk's	P	Wilk's	P	Wilk's	P	Wilk's	P
C. guttipennis (T1)	0.018 (9, 2)	0.08	0.023 (18, 4)	0.47	0.025 (18, 4)	0.49	0.016 (9, 2)	0.07	0.018 (18, 4)	0.39	0.025 (18, 4)	0.49
C. guttipennis (T2)	0.14 (4, 7)	**0.004**	0.22 (8, 14)	0.12	0.22 (8, 14)	0.13	0.21 (4, 7)	**0.017**	0.15 (8, 14)	0.04	0.14 (8, 14)	0.037
C. guttipennis (T3)	0.18 (7, 4)	0.19	0.037 (14, 8)	0.11	0.51 (14, 8)	0.99	0.18 (7, 4)	0.18	0.034 (14, 8)	0.10	0.54 (14, 8)	0.99
mosquitoes (T1)	0.17 (9, 2)	0.56	0.065 (18, 4)	0.77	0.15 (18, 4)	0.94	0.36 (9, 2)	0.86	0.12 (18, 4)	0.92	0.066 (18, 4)	0.77
mosquitoes (T2)	0.44 (4, 7)	0.16	0.14 (8, 14)	0.04	0.26 (8, 14)	0.19	0.56 (4, 7)	0.34	0.47 (8, 14)	0.61	0.42 (8, 14)	0.51
mosquitoes (T3)	0.023 (10, 1)	0.36	0.025 (20, 2)	0.82	0.01 (20, 2)	0.65	0.048 (10, 1)	0.51	0.0005 (20, 2)	0.20	0.0028 (20, 2)	0.42
Myiolepta (T1)	0.09 (5, 6)	**0.004**	0.54 (10, 12)	0.90	0.42 (10, 12)	0.74	0.17 (5, 6)	0.03	0.43 (10, 12)	0.77	0.32 (10, 12)	0.54
Myiolepta (T2)	0.61 (3, 8)	0.24	0.61 (6, 16)	0.62	0.61 (6, 16)	0.62	0.83 (3, 8)	0.67	0.40 (6, 16)	0.22	0.40 (6, 16)	0.22
Myiolepta (T3)	0.0048 (9, 2)	0.02	0.017 (18, 4)	0.38	0.0013 (18, 4)	0.05	0.0077 (8, 3)	**0.004**	0.023 (16, 6)	0.18	0.0024 (16, 6)	**0.01**
M. posticata (T1)	0.37 (5, 6)	0.21	0.20 (10, 12)	0.26	0.16 (10, 12)	0.16	0.46 (5, 6)	0.35	0.26 (10, 12)	0.40	0.19 (10, 12)	0.24
M. posticata (T3)	0.51 (8, 3)	0.89	0.0057 (16, 6)	0.03	0.063 (16, 6)	0.48	0.56 (7, 4)	0.83	0.034 (14, 8)	0.10	0.15 (14, 8)	0.58
T. albipunctatus (T3)	0.25 (6, 5)	0.17	0.085 (12, 10)	0.14	0.062 (12, 10)	0.08	0.25 (6, 5)	0.17	0.077 (12, 10)	0.11	0.062 (12, 10)	0.08
S (T1)	0.22 (9, 2)	0.67	0.027 (18, 4)	0.50	0.019 (18, 4)	0.41	0.34 (9, 2)	0.85	0.001 (18, 4)	0.04	0.001 (18, 4)	0.04
S (T2)	0.54 (4, 7)	0.30	0.56 (8, 14)	0.77	0.44 (8, 14)	0.55	0.65 (4, 7)	0.49	0.50 (8, 14)	0.68	0.47 (8, 14)	0.61
S (T3)	0.13 (10, 1)	0.75	0.0063 (20, 2)	0.56	0.049 (20, 2)	0.92	0.11 (10, 1)	0.70	0.00087 (20, 2)	0.26	0.00077 (20, 2)	0.25

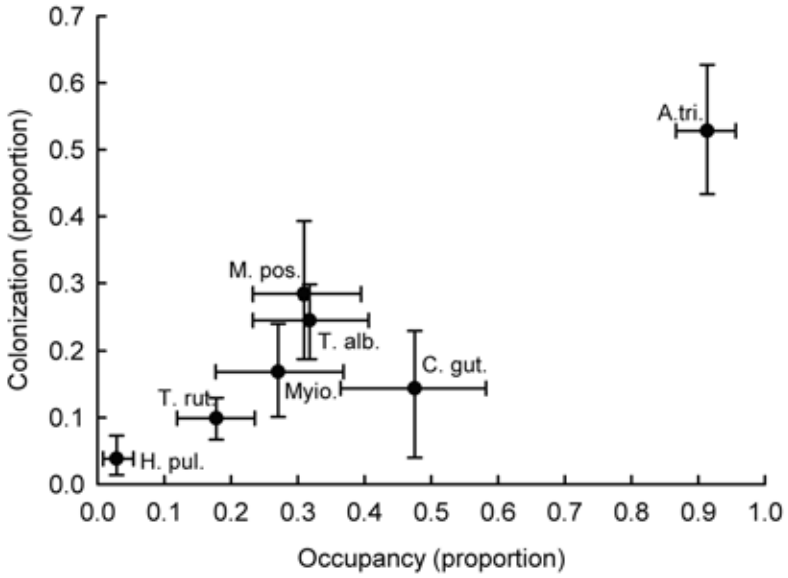

Figure 3. Proportion colonization vs. proportion occupancy. See text for methods of estimation. A. tri. = *A. triseriatus*, C. gut. = *C. guttipennis*, M. pos. = *M. posticata*, T. alb. = *T. albipunctatus*, Myio. = *Myiolepta* sp., T. rut. = *T. rutilus*, H. pul. = *H. pulchella*.

Table 2. Nested ANOVA results*. a. For proportion occupancy, across trial, habitat size and degree of isolation. b. For proportion colonization, across trial, habitat size and degree of isolation.

a.	Trial		Habitat size (trial)		Isolation (trial)	
	F	*P*	*F*	*P*	*F*	*P*
C. guttipennis	12.54	**0.007**†	10.64	**0.008**	0.45	0.82
A. triseriatus	0.90	0.46	2.42	0.16	1.23	0.40
M. posticata	0.13	0.74	1.92	0.26	1.65	0.32
T. albipunctatus	12.59	**0.007**	7.79	**0.016**	0.36	0.88
Myiolepta sp.	5.01	0.05	8.18	**0.015**	0.96	0.52
T. rutilus	0.19	0.69	8.80	0.03	1.00	0.50
b.	Trial		Habitat size (trial)		Isolation (trial)	
	F	*P*	*F*	*P*	*F*	*P*
C. guttipennis	38.15	**<0.0001**	7.79	**0.015**	3.60	0.07
A. triseriatus	5.89	0.04	0.47	0.72	1.39	0.35
M. posticata	47.25	**0.002**	13.83	**0.015**	2.96	0.16
T. albipunctatus	9.05	**0.015**	1.71	0.26	0.33	0.90
Myiolepta sp.	14.98	**0.005**	14.56	**0.004**	1.60	0.29
T. rutilus	0.00	0.99	5.00	0.08	2.96	0.16

*For both tables, Trial d.f. = 2, 6, habitat size (trial) d.f. = 3, 6, and isolation (trial) d.f. = 6, 6 for all species except *M. posticata* and *T. rutilus*, where they were1, 4; 2, 4; and 4, 4 respectively.
†*P* values in boldface are significant.

(Figure 4b). *Toxorhynchites rutilus* had higher occupancy in large than in small mesocosms (0.32 ± 0.04 SE vs. 0.11 ± 0.03 SE), although not statistically significant. The proportion colonization of *C. guttipennis* was higher in small containers than in large, and for the two syrphids it was higher in large containers than in small (Table 2b; Figure 4d). Degree of isolation did not affect the colonization or occupancy of any species (Table 2a). Colonization of *C. guttipennis*, *Te. albipunctatus*, *M. posticata*, and *Myiolepta* sp. was significantly different across trials (Table 2b; Figure 4c), and occupancy was different across trials for *C. guttipennis* and *Te. albipunctatus* (Table 2a, Figure 4a).

Effects of predation

The density of each prey species was negatively affected by the density of the predator *Tx. rutilus*, as evidenced by the highly statistically significant negative slopes of all regressions between the predator and each prey species (Table 3). Densities in the absence of *Tx. rutilus*, as evidenced by the y-intercepts of the regressions, were all highly significantly greater than 0. Diversity increased with increasing density of *Tx. rutilus*; the slope of diversity against density of the predator was significantly greater than 0. The average transformed diversity in the absence of predation was 1.53, and at maximum *Tx. rutilus* density it was 2.29.

Spatial turnover and synchrony

Spatial turnover was significantly affected by both habitat size and distance between pairs, and was also different across trials (Table 4). During Trials 1 and 2 spatial turnover was lower when comparing habitats of the same size (small vs. small and

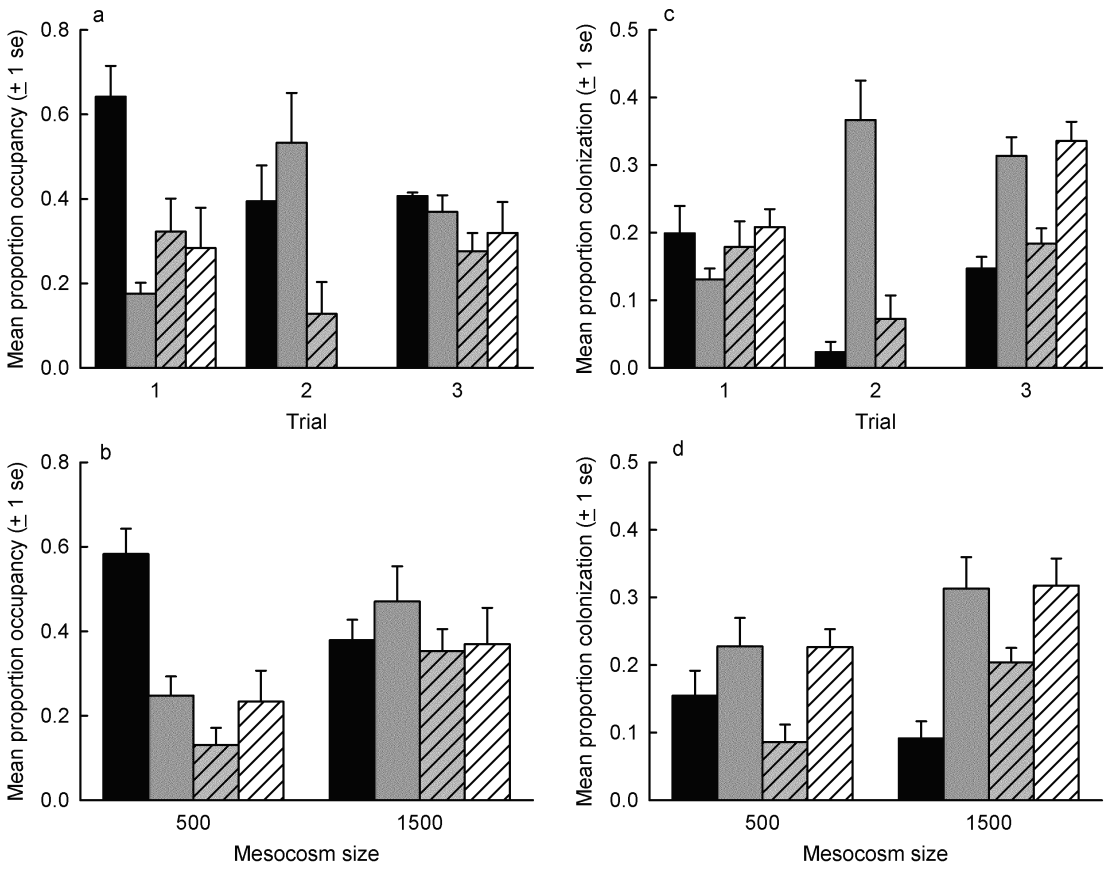

Figure 4. Occupancy and colonization for *C. guttipennis* (black), *Te. albipunctatus* (gray), *Myiolepta* sp. (gray with hatching), and *M. posticata* (hatched). a. Mean proportion occupancy across trial. b. Mean proportion colonization across trial. c. Mean proportion occupancy across mesocosm size. d. Mean proportion colonization across mesocosm size.

Table 3. Results of randomization regressions of prey densities vs. *T. rutilus* densities*.

Species	$N^{\dagger}$	$R^{2\ddagger}$	*F*	Parameter	Coeff.[§]	s.e.[¶]
C. guttipennis	256	11.7	34.79	Y-intercept	1.22	0.04
				T. rutilus density	-1.28	0.22
A. triseriatus	472	4.1	21.01	Y-intercept	1.51	0.03
				T. rutilus density	-0.86	0.19
Myiolepta sp.	178	39.9	118.46	Y-intercept	0.84	0.04
				T. rutilus density	-1.71	0.16
M. posticata	130	37.6	78.75	Y-intercept	0.61	0.04
				T. rutilus density	-1.18	0.13
T. albipunctatus	147	20.2	37.88	Y-intercept	0.59	0.03
				T. rutilus density	-0.79	0.12
Diversity	495	5.4	29.25	Y-intercept	1.53	0.03
				T. rutilus density	0.95	0.17

*All regression models and coefficients were significant at $P<0.001$.
[†]N = sample size,
[‡]R^2 = percentage of variation in prey density explained by predator density,
[§]Coeff. = the y-intercept or slope of the regression,
[¶]s.e. = standard error of the coefficient.

Table 4. Results of spatial turnover and synchrony analyses, with trial as a fixed effect, habitat size comparison nested within trial, and distance between pairs as a covariate.

	Trial		Mesocosm size comparison		Distance	
	F	*P*	*F*	*P*	*F*	*P*
Spatial turnover - entire community* (350)[†]	77.79	**<0.001**[§]	5.86	**<0.001**	16.03	**<0.001**
Spatial synchrony						
C. guttipennis density* (321)	147.93	**<0.001**	5.42	**<0.001**	0.03	0.86
A. triseriatus density* (349)	75.23	**<0.001**	4.87	**<0.001**	18.98	**<0.001**
Te. albipunctatus density* (264)	11.69	**<0.001**	1.47	0.19	10.15	**0.002**
M. posticata density[‡] (164)	1.93	0.17	2.47	0.05	6.75	**0.01**
Myiolepta sp. density[‡] (176)	0.32	0.57	12.28	**<0.001**	0.03	0.86
T. rutilus density[‡] (74)	1.95	0.17	1.85	0.13	1.71	0.20

*Numerator d.f. for factors: trial = 2; habitat size = 6; distance = 1
[†]Denominator d.f. in parentheses
[‡]Numerator d.f. for factors: trial = 1; habitat size = 4; distance = 1
[§]*P* values in boldface are significant.

large vs. large) than when comparing habitats of different size (Figure 5). Spatial turnover was lowest in Trial 3 and highest in Trial 2. Spatial turnover increased significantly as the distance between mesocosm pairs increased (β = 0.00045 ± 0.00011 (se); Table 4). Spatial turnover at distance 0 was significantly greater than 0, indicating lack of similarity (y-intercept = 0.30 ± 0.017 (se), t = 17.55, P < 0.001), and at 300 m, near the maximum distance apart, the estimated spatial turnover was 0.44.

Spatial synchrony varied across trial for three species, *A. triseriatus*, *C. guttipennis*, and *Te. albipunctatus* (Table 4). Spatial synchrony for the first two species along with *Myiolepta* sp. was also significantly affected by habitat size. *Aedes triseriatus* and *Myiolepta* sp. showed higher synchrony when comparing large to large mesocosms (Figure 5b). Distance between pairs significantly affected spatial synchrony for *A. triseriatus*, *Te. albipunctatus*, and *M. posticata* (Table 4). Distance had a negative effect on synchrony of these three species (*A. triseriatus*: β = -0.00098; *Te. albipunctatus*: β = -0.0011; and *M. posticata*: β = -0.0012; significance values in Table 4). The randomization regressions examining the effects of distance between pairs on spatial synchrony yielded the same results as the ANCOVA and are not shown.

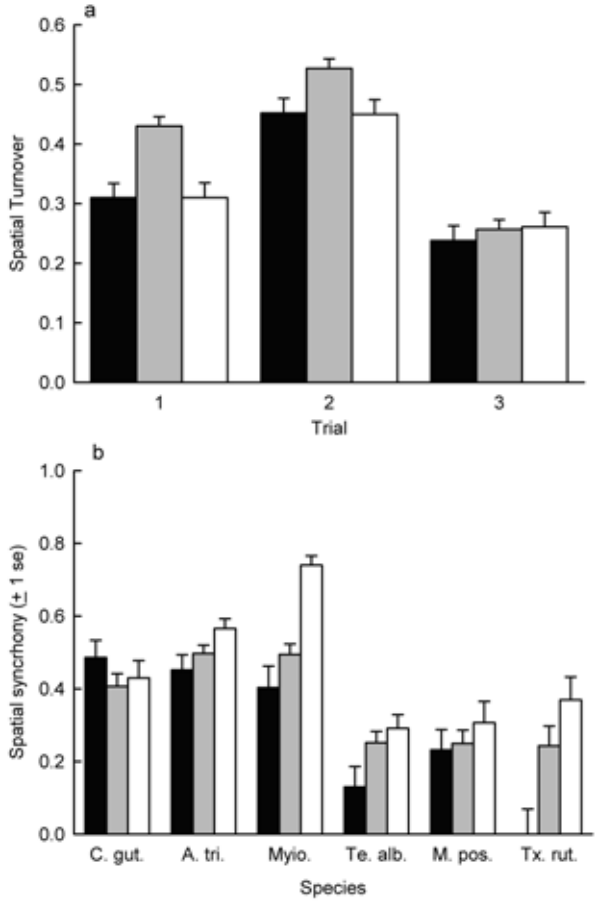

Figure 5. Spatial effects. a. Mean spatial turnover (± 1 se) for comparisons between small and small mesocosms (black bars), small vs. large mesocosms (gray), and large vs. large mesocosms (white). b. Spatial synchrony for six treehole species averaged across three trials. Shading as in (a). The three leftmost species had spatial synchronies that were significantly affected by the size comparison.

Temporal turnover

Temporal turnover over a four week time span, which will be high when a community is dissimilar from one time point to another, was significantly affected only by habitat size (nested ANOVA: Isolation: $F_{6,308}$ = 1.80, P = 0.10; Habitat size $F_{3,308}$ = 4.85, P = 0.003; Trial: $F_{2,308}$ = 2.50, P = 0.08). The 1-way randomization ANOVAs examining the effects of degree of isolation and habitat size were qualitatively similar, with a marginally significant effect of isolation and a highly significant effect of habitat size (Isolation: $F_{2,317}$ = 3.89, P = 0.02; Habitat size $F_{1,318}$ = 9.24, P = 0.003). Temporal turnover was significantly higher in large habitats than in small (0.56 ± 0.04 vs. 0.35 ± 0.04 (Trial 1); 0.38 ± 0.10 vs. 0.30 ± 0.10 (Trial 2); 0.40 ± 0.02 vs. 0.35 ± 0.03 (Trial 3)).

DISCUSSION

Local habitat effects

We directly manipulated mesocosm size, which we used as a proxy for variation in local conditions. Containers of different size had differences in volume, depth, and surface area, all of which can affect insect communities differently [21]. We were interested in achieving large differences in local conditions, not in testing the individual effects of volume, depth, and surface area, which have been tested elsewhere [21]. Habitat size treatments led to large differences in environmental conditions. Our mesocosms were significantly and

consistently different in dissolved oxygen concentrations and pH, consistent with other studies in treeholes and mesocosms [15, 21]. Deep containers tend to have lower dissolved oxygen, which leads to differences in the community [21]. Both habitat sizes had conditions well within the range of conditions observed in treeholes [15, 21], and colonization and occupancy of most species were similar to those in treeholes [13].

Aedes triseriatus, the numerically dominant taxon, was not affected by the habitat sizes tested, as predicted, and, as in treeholes [13], it was the most dominant taxon across time and treatment. Colonization by mosquitoes was equivalent to that of natural treeholes, and occupancy was higher. This was perhaps due to the higher frequency of sampling than in previous studies [13], which was shorter than larval development time, the short length of each trial during which larvae were active, or the physical conditions of the containers. The simulated habitats with high and constant levels of water were conducive to dominance by mosquitoes [21, 36]. In treeholes with little standing water, mosquito dominance decreases [15]. This and the synchronization of mosquito populations in the large habitat size treatment (relative to the lower synchrony for small habitat size containers) suggest that mosquitoes do have habitat preferences. The habitat size treatments used here were within the range preferred by ovipositing females and favorable to larvae, which helps explains why colonization and occupancy were similar in both habitat size treatments. At least for the container sizes tested here, mosquitoes in treeholes seem to undergo repeated colonization, with either local extinction due to predation or mass adult emergence, suggestive of the patch dynamics model of metacommunities.

Strong preferences for containers of different habitat sizes were exhibited by several species. Oviposition preferences or differential survival of larvae could explain greater densities in one habitat over another [21, 25, 28]. For *C. guttipennis* and syrphids, greater colonization in preferred habitats indicates oviposition preferences. Syrphid larvae are air-breathers, so low oxygen at depth may not affect them as adversely as larvae of *C. guttipennis*, which breathe cutaneously. *Culicoides guttipennis* is often found in shallow treeholes with high sediment and leaf litter content [15]. *Myiolepta* sp., as a facultative resident of mesocosms, whose densities were more synchronized in large habitats, may tend to breed more in larger bodies of water, and females may be more attracted to the greater surface area of large mesocosms. Different habitat preferences among species will result in dissimilarity among local communities, which is a prediction of the species sorting model. Species sorting is observed when different species have higher survival and densities in some patch types than others [7, 9], and thus local conditions can strongly affect metacommunity dynamics [5, 9-13, 16, 17]. The presence of each species in sink habitats suggests dispersal and colonization are occurring at a high enough rate, which is in line with patch dynamics predictions, but not as high as predicted by mass effects models.

Densities of other species were not affected by habitat size, but preferences were observed in colonization, occupancy, and synchrony. *Telmatoscopus albipunctatus* and *Tx. rutilus* had higher occupancy in large mesocosms than in small mesocosms. Populations of the two mosquito species, *A. triseriatus* and *Tx. rutilus* were more synchronized in large habitat size mesocosms than in small or small *vs.* large mesocosms. These and other indicators of habitat preferences translate to communities of the same size being more similar than communities of different size. These findings again support a primacy of local conditions over spatial effects, as predicted in species sorting metacommunity models [7, 8].

Local communities were strongly affected by habitat size, which had a significant effect on temporal turnover. The species sorting model predicts temporal changes as a low rate of dispersal causes species composition to change over time. Further, seasonal effects on synchrony and turnover, such that synchrony was low and turnover was high in Trial 2 may be caused by lower larval activity in autumn [15]. Because of seasonal changes in abundance or presence of species, spatial turnover (community dissimilarity) also changed with time of year. While temporal turnover was highest in Trial 2, larger habitats still changed more rapidly than smaller, suggesting higher colonization in large habitats or less predation or competition in smaller habitats. The high

temporal and spatial turnover is consistent with the patch dynamics model of metacommunities [12]. Containers that were the same size exhibited more similarity than containers of different size, as predicted, due to preferences of different species. The dynamics in local community composition are thus affected by habitat size and changes in environmental conditions associated with volume and container shape differences. There is enough dispersal and colonization that species are routinely found in lower densities in less preferred habitat, as suggested by patch dynamics, but the strong effect of local conditions also agrees with species sorting predictions [7].

Isolation and distance

Degree of isolation did not affect density, colonization, or occupancy of any species, contrary to predictions. The occurrence of all species at some time in all mesocosms, regardless of degree of isolation, suggests that all species could disperse within the range of distances examined, well within the ranges known for treehole metacommunities [13]. If all species can reach all patches in a forest, yet dispersal is still low to moderate, environmental factors may still predominate [37]. The strong habitat size effects suggest that habitat factors are more significant in colonization and abundance of species, which suggests the species sorting or patch dynamics model, depending upon the level of dispersal of individual species.

Distance between local communities had a significant effect on community similarity, as observed in treeholes [12-13]. However, even at close distances spatial turnover was greater than zero suggesting dissimilarity between neighboring containers. Studies in other systems have found community dissimilarity to be associated with environmental heterogeneity and distance [8, 38]. Densities of individual species were not synchronized across habitat, and most synchrony estimates were well below 0.5, suggesting asynchrony. Further, synchrony decreased for three species, *A. triseriatus*, *Te. albipunctatus*, and *M. posticata*, as pairs of mesocosms became further apart. While dispersal appears to be global within the range of distances examined here for one forest, populations of treehole species are not generally synchronized, which reduces similarity between habitats. Dispersal and colonization may be mostly confined to smaller spatial ranges. The high spatial turnover and low synchrony appear to be influenced by distance between habitats, suggesting the patch dynamics model, but dissimilarity between very close habitats suggests an influence of local conditions, suggesting the species sorting model.

Predation effects

Since occupancy for *Tx. rutilus* is slightly lower in mesocosms as compared to treeholes [13], and colonization of mesocosms is about a third of what it is in treeholes (29%), we suggest that oviposition is lower, but more larvae survive in mesocosms. This is likely due to the large and constant volume of water as well as the high colonization of various prey species. Occupancy and density of the predator were higher in large mesocosms than small, and *Tx. rutilus* is known to oviposit more in habitats with larger surface area [39]. Our data also suggest a preference of *Tx. rutilus* for large habitat size mesocosms and this has implications for further increasing heterogeneity among local habitats. Thus, differences in habitat sizes can indirectly cause greater differences in local communities.

The presence and increasing density of *Tx. rutilus* correlated with declining populations of all species and increasing local diversity. Variation in predation among patches causes differences in local demography of prey, the outcome of interactions, and, ultimately, community composition [5, 10-12]. Decreasing prey densities or survivorship is known to occur in the presence of this predator [25, 40-42]. The presence of the predator in large habitat sizes and its absence in small habitats would cause greater dissimilarity between the communities in those two habitats. The increase in diversity suggests a keystone role of *Tx. rutilus*. However, the correlation of this predator with higher species richness is likely caused by a correlation in habitat preferences of prey and predator [25]. More species preferred large habitat to small, if they had any preference at all, and while we did not find a significant effect of habitat size on diversity, an overall habitat size effect could be diminished by variable presence of

the predator. Prey populations might tend to be higher in large mesocosms except when those habitats are occupied by predators. Dispersal is frequent enough that species regularly occur in sink habitats and can recolonize preferred habitats quickly after predators have completed development. This scenario suggests both the species sorting model, in the strong effects of species interactions, and the patch dynamics model, in the high spatial and temporal turnover that results from variable presence of the predator [5, 7, 10].

CONCLUSIONS

Treehole metacommunity dynamics are affected by both local habitat conditions and spatial attributes. Habitat conditions, which led to variable preferences and species sorting, more dramatically affected the dynamics of the communities than distance between habitats or degree of isolation of a habitat, a finding in line with other studies [5]. All species and community measures were affected to some degree by habitat size, whereas not all variables revealed distance or isolation effects. This is as we predicted, as was the result that communities within habitats of similar size were more similar to each than to habitats of different habitat size. Those similarities and differences appeared to be related to environmental conditions and the preference of several prey species and the top predator for large habitats. Environmental conditions, directly or indirectly, may be the most important variable in colonization and dispersal of species living in metacommunities [8, 43]. Both the species sorting and the patch dynamics models of metacommunities were supported by the data, and local environmental conditions and distance between habitats affected species differently. The influence of both environmental conditions and spatial structure highlights the need for integration of these factors in determining composition of local and regional communities.

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