

DISTURBANCE, PREDATOR, AND RESOURCE INTERACTIONS ALTER CONTAINER COMMUNITY COMPOSITION

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Abstract. Species diversity at the local-community scale can be altered by numerous factors, including disturbances, predators, and resource levels. Intermediate levels of these three factors are predicted to enhance coexistence and diversity. However, no study has examined how these factors may interact to alter community composition. The protozoan and rotifer community that colonized containers set in a forest was used to examine the interactions between these local community processes. We conducted a fully factorial microcosm experiment that manipulated disturbance frequency, predator density, and resource levels to examine protozoan and rotifer richness, community composition, and species abundance. Species richness was significantly altered by disturbances and predators, while predator densities interacted with disturbances and resources. Total abundance was significantly affected by each treatment, as well as a disturbance and predator interaction. We found that community composition was altered by each of the treatments and their interactions, indicating that different groups of species were present depending on the treatments. These results indicate that strong species sorting occurs in this community. Understanding these factors alone and in concert can provide insight to the potential complexities that underlie community structure and species composition.

Key words: *Aedes albopictus*; container community; desiccation; disturbance; diversity; phytoplankton; predation; protozoa; resource addition; species composition.

INTRODUCTION

Community ecologists strive to understand the mechanisms that influence the patterns of species diversity in communities. Local coexistence among species is most commonly assumed to be facilitated by species-specific responses to variation in biotic and abiotic factors (Kneitel and Chase 2004). Three of the most commonly discussed factors that influence species diversity are disturbances (e.g., Connell 1978, Petraitis et al. 1989), predation (e.g., Paine 1966, Leibold 1996), and resources (e.g., Tilman 1982). A hump-shaped relationship between each of these factors and diversity (diversity first increases and then declines) is often predicted, but seldom found (Proulx and Mazumder 1998, Waide et al. 1999, Mackey and Currie 2001, Mittlebach et al. 2001).

Although the effects of disturbance, predation, and resources on species diversity are typically examined in isolation, both theoretical and empirical evidence suggest that these factors can strongly interact. Theoretically, the presence of a second factor may shift a hump-shaped relationship to the left or right in response to the first factor (Worm et al. 2002), or may dampen or increase the magnitude of the relationship

(Wootton 1998, Wilson and Tilman 2002). Empirical evidence supports this idea that interactions between two of these factors can influence species diversity. For example, studies on the interaction between resources and predation have found different effects of predators on diversity at low and high resource levels (Proulx and Mazumder 1998, Kneitel and Miller 2002). In studies on the interaction between disturbance and resources, Wilson and Tilman (2002) showed that high resources can dampen the hump-shaped relationship between disturbances and diversity of old-field herbaceous plants, whereas Warren and Spencer (1996) found no interaction between disturbance and resources on the composition of an aquatic insect community. Finally, studies on the interaction between disturbance and predation found that predation increased prey diversity in aquatic communities with low disturbance, but had no effects in high disturbance (Wootton et al. 1996; J. M. Chase, *unpublished data*).

No theoretical or empirical studies have yet explored the separate and interactive effects of all three factors—disturbances, resources, and predators—on species diversity. While neither theory nor empirical evidence are available to make any specific predictions, we expect some general responses to the interactions among these factors. Specifically, the trade-offs that influence patterns of coexistence and species diversity in response to resources, disturbances, and predation are orthogonal to each other; species trade off in their abilities to compete for low vs. high resources (Grover

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1997), to compete for resources or resist predators (Paine 1966, Leibold 1996), to compete for resources and tolerate disturbance (Petraitis et al. 1989), and to resist predators and tolerate disturbance (Wootton et al. 1996). In general, we expect that the effects of one factor on diversity will be greatest when the intensities of the other factors are lowest. For example, the effects of resources will be strongest when both predators and disturbances are infrequent, whereas the effects of resources will be reduced if either predation or disturbances are more common.

Here we describe an experiment that examines the combined effects of disturbances, predators, and resources on the natural protozoan and rotifer community found in small-container analogues of phytotelmata such as tree holes (Kitching 2000). We factorially manipulated disturbance by drying, predation by mosquito larvae, and resource levels by adding dried leaves, and examined the resulting protozoan and rotifer community (species richness and total abundance). We also examined whether community composition differed among treatments by using nonmetric multidimensional scaling. Our results indicate that the main effects of resources, predators, and disturbances, as well as their interaction, dramatically alter the composition, diversity, and relative abundance of the protozoan and rotifer community.

METHODS

Study system

The structure and food web constituents of artificial containers are similar to phytotelmata, such as bromeliads, leaf axils, and pitcher plants (Maguire 1971, Srivastava and Lawton 1998, Kitching 2001, Kneitel and Miller 2002, 2003). Artificial and natural container habitats can vary in all of the factors (resources, predators, and disturbances) discussed above (J. M. Kneitel, *unpublished data*), and this variation is usually driven by their size, position, and location (Bradshaw and Holzapfel 1988, Juliano et al. 2002). Fallen leaves and drowned insects are the primary source of resources in this system; that is, the food web is detritus based. This detritus is primarily decomposed by bacteria, which are in turn consumed by the middle trophic level, primarily protozoans and rotifers. Numerous species of insect larvae consume these protozoans and rotifers, as well as the bacteria itself (Kitching 2000, 2001). The insect community has been well studied, especially in regard to the effects of resources and disturbances (drying) on the most common top predators, mosquito larvae (Diptera: Culicidae; Bradshaw and Holzapfel 1988, Kitching 2001, Juliano et al. 2002). Less is known about the protozoan and rotifer community; all of the protozoan and rotifer species encountered in this study are presented in the Appendix.

Experimental design

A regional species pool was created by collecting water from 24 plastic bowls (500 mL) attached to trees

(Srivastava and Lawton 1998) at Washington University's Tyson Research Center. Each bowl had been inoculated with dead leaves from nearby trees, and communities were allowed to establish over a 60-day period. The entire amount of water was collected, and mosquito larvae and decomposing leaves were filtered out. The species composition of protozoans and rotifers in the artificial container communities was similar to a survey of natural tree holes at the same site (J. M. Kneitel, *unpublished data*). We established a laboratory experiment by inoculating 40 mL of this regional pool of protozoan and rotifer colonists into 90 petri dishes (100 × 15 mm). Petri dishes were placed on a laboratory countertop, which received ambient light; the temperature was ~20°C.

The experiment consisted of a 3 × 3 × 2 factorial design including 3 levels of disturbance frequency (none, low [drying every eight days], and high [drying every three days]), 3 levels of mosquito (*Aedes albopictus*) larval density (none, low [one larva], and high [five larvae]), and 2 resource levels (low and high). We manipulated resources by adding 0.1 g of dried ash leaves (*Fraxinus* sp.) to high-nutrient treatments; no leaves were added to low-nutrient treatments. Larvae (2nd–4th instar) were collected from the filtered artificial containers and were maintained in the laboratory after multiple washings to remove protozoans and rotifers; individuals were randomly chosen and added to the experiment. The water in this pool was periodically changed and checked for contamination. Over the course of the experiment, mosquito larvae pupated and were replaced with individuals from this larval pool. We manipulated disturbance by either allowing or not allowing evaporation in the communities. High-disturbance treatments were allowed to dry at their natural evaporation rates (every three days). In the low-disturbance treatments, we added ~8 mL of distilled water daily; this amount was enough to allow the dish to retain water for 8 days. After all dishes dried, they were left dry for two days, at which time they were refilled with 40 mL of distilled water; we also reintroduced mosquito larvae from the larval pool into the predator treatments after dishes were refilled. In the no-disturbance treatments, we added ~15 mL of distilled water to the dishes daily to exactly counterbalance the rate of evaporation.

Sampling

The experiment experienced four instances of high-frequency and two instances of low-frequency disturbances before a final sampling on day 23. Because of the rapid population dynamics of the organisms in this community, this time period was long enough for the communities to approach a steady state in response to the treatments (see also McGrady-Steed and Morin 1996, Kneitel and Miller 2002). Sampling was conducted by gently stirring and extracting 1 mL from each community and placing it into a Sedgewick-Rafter cell

(Wildlife Supply Company, Buffalo, New York, USA). Using a phase-contrast microscope, we identified individuals to species (or taxonomic unit) and counted the individuals of each species. In some cases, abundances were very high, so we subsampled the abundance of those species by counting along transects through the cell.

Abundance differences among treatments can artificially inflate species richness measurements (Gotelli and Graves 1996). To control for these differences, rarefaction was conducted to calculate protozoan and rotifer species richness (EcoSim, version 7; Gotelli and Entsminger 2001). Each replicate was resampled 1000 times, and the mean number of species on the final point of the curve was used as our species richness estimate. A recent review of all the studies testing disturbance–diversity relationships showed that 116 of them measured species richness, 53 species diversity, and 28 evenness (Mackey and Currie 2001).

Statistical analysis

Treatment effects of disturbance frequency, predator density, and resource density were used in a three-way ANOVA, using SYSTAT, version 10.2.01 (SYSTAT 2002), to test their main effects and interactions on species richness and total species abundances (cells per milliliter). The results from rarefaction were used for species richness, and species abundances were natural-log transformed to obtain homogeneity of variances. Bonferroni-adjusted post-hoc tests were conducted to test differences among individual treatments.

Nonmetric multidimensional scaling (NMS) was conducted, using SPSS, version 11.5 (SPSS 2002), to examine the differences in species composition relationships among the treatment replicates. A dissimilarity matrix using Euclidean distances was calculated from the species abundances in each treatment replicate. This nonlinear technique ranks points (treatment replicates) such that distance in ordination space represents community similarity (ter Braak 1995). The correspondence of the ordination diagram to the dissimilarity distances is described by a stress value where 0 is a perfect fit. The NMS analysis used two ordination axes. To better understand the treatment effects on species composition changes, we used the two dimension loading values for each treatment replicate as the dependent variables in a MANOVA.

RESULTS

Nineteen species were present in the regional pool (16 protozoans and 3 rotifers). Species richness in each of the replicates ranged from 0 to 12 (see the Appendix). In general, the presence of disturbances or predators significantly decreased species richness (Table 1, Fig. 1A, B). The interactions between these treatments also had important effects in this system. The disturbance \times predator interaction was significant (Table 1): disturbances decreased diversity more when predators

TABLE 1. Results from three-way ANOVA of treatment effects on species richness (rarefaction adjusted) and log-transformed total abundance.

Source	df	Species richness		Total abundance	
		F	P	F	P
Disturbance (D)	2	30.468	<0.001	9.170	<0.001
Predator (P)	2	31.180	<0.001	16.986	<0.001
Resource (R)	1	3.245	0.076	105.132	<0.001
D \times P	4	4.229	0.004	8.852	<0.001
D \times R	2	0.488	0.616	0.362	0.698
P \times R	2	3.690	0.030	1.242	0.295
D \times P \times R	4	1.298	0.279	2.288	0.068
Error	72				

were absent (predators absent, 49% vs. predators present, 13%). In contrast, predator effects on species richness were significant in both the presence ($P = 0.001$) and absence ($P < 0.001$) of disturbances, but the magnitude of the predator effects was somewhat greater in the absence (53% reduction) than in the presence of disturbance (27% reduction). A significant predator \times resource effect was exhibited in two ways. First, predators decreased species richness to a greater degree (51%) at low resource levels ($P < 0.001$) than at high resource levels (21% decrease; $P = 0.05$). Second, resources had no effect on species richness in the absence of predation ($P = 0.63$), but increased species richness by 59% in the presence of high predator densities ($P = 0.004$).

The total abundance of individuals (cells per milliliter) reflected a similar pattern as species richness (Fig. 1C, D). There were significant disturbance and predator effects in the same directions as the richness responses: disturbance and predation decreased abundance. Resource addition significantly increased protozoan and rotifer abundance (Table 1). A disturbance \times predator interaction also resulted from the lack of a disturbance effect when predator densities were high ($P = 0.42$; Table 1, Fig. 1C, D). In addition, predators reduced total abundance by 43% in the absence of disturbance ($P < 0.001$), but had little effect in the presence of disturbances ($P = 0.54$).

The NMS ordinations showed that the no-disturbance treatments were very different than the other treatments; community composition converged as disturbances increased (Fig. 2A, B). The two ordination axes explained much of the variance in the scaled data (ter Braak 1995): Kruskal's stress value (formula 1) was 0.064 and $R^2 = 0.995$.

A MANOVA was conducted on the dimension loadings to better understand treatment effects on the compositional differences. All treatments and their interactions had significant effects on the NMS dimension loadings (Table 2), indicating that all treatments and their interactions altered species composition significantly. The dominance of different species varied in different treatments. For example, *Colpoda* sp. and *Vorticella* sp. dominated disturbance treatments,

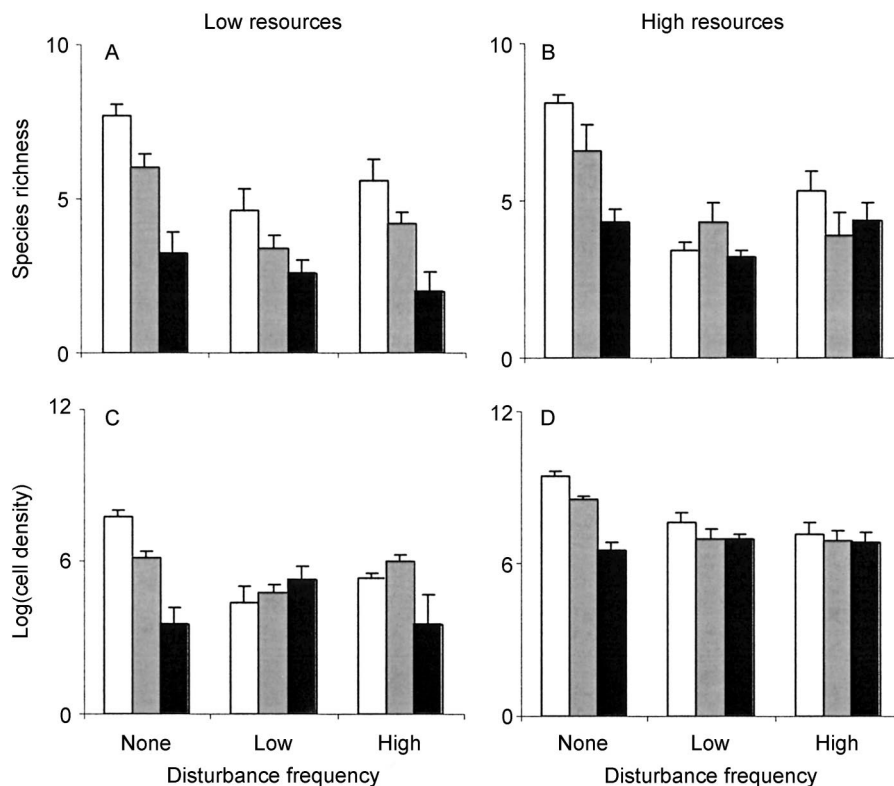


FIG. 1. Treatment effects on the means (± 1 SE) of (A, B) species richness (rarefaction adjusted) and (C, D) log-transformed total abundance (measured as no. cells/mL). Graphs A and C are at low resources and graphs B and D are at high resources. Open bars are no-predator treatments, gray bars are low-predator-density treatments, and solid bars are high-predator-density treatments.

whereas *Paramecium caudatum* and *Cyclidium* sp. dominated no-disturbance treatments (see the Appendix).

DISCUSSION

The protozoan and rotifer community of containers responded strongly to the disturbance, predator, and resource treatments and their interactions. We predicted that treatment effects would be greatest in the absence of the other treatments. This was true for disturbances and predators; however, this was not the case with the predation–resource interaction. In general, the presence of disturbances and predator density decreased species richness and total species abundance, while resources increased species abundances. Community composition was significantly altered by all treatments.

The presence of disturbances had a twofold effect on the protozoan community. First, it directly decreased diversity and altered composition of the protozoan community (Fig. 1A, B). This finding is consistent with numerous studies in a variety of other systems where a proportion of species can tolerate disturbance (e.g., Collins et al. 1995, McGrady-Steed and Morin 1996, Wilson and Tilman 2002). This common response suggests that a disturbance gradient (as found in the Intermediate Disturbance Hypothesis; Connell

1978) is unlikely to be important for altering community composition. Instead, the presence or absence of a disturbance and the differential response of species to this disturbance is likely more important (Chesson and Huntly 1997, Wootton 1998). Community composition in the presence of disturbances became more similar (Fig. 2; Chase 2003), indicating that there are some species in this community that can withstand drying by dormancy or resting cysts (e.g., *Colpoda*, *Vorticella*; see the Appendix). Those that dominated disturbed communities had very low abundance levels in the absence of disturbances (e.g., *Colpoda*, *Vorticella*) suggesting that there may be a trade-off between disturbance tolerance and competitive ability (Connell 1978, Petraitis et al. 1989, Kneitel and Chase 2004).

Second, disturbances interacted strongly with predator densities to affect protozoan diversity, composition, and abundance, a finding common in a variety of other taxa and communities (Sih et al. 1985, Schneider and Frost 1996, Wellborn et al. 1996, Spencer et al. 1999). In the absence of disturbances, predator consumption of lower trophic levels was likely unimpeded, which resulted in stronger effects. There were weaker effects of either treatment on species richness or abundance in the presence of the other, despite changes in species composition (Fig. 2B, Table 2). These results

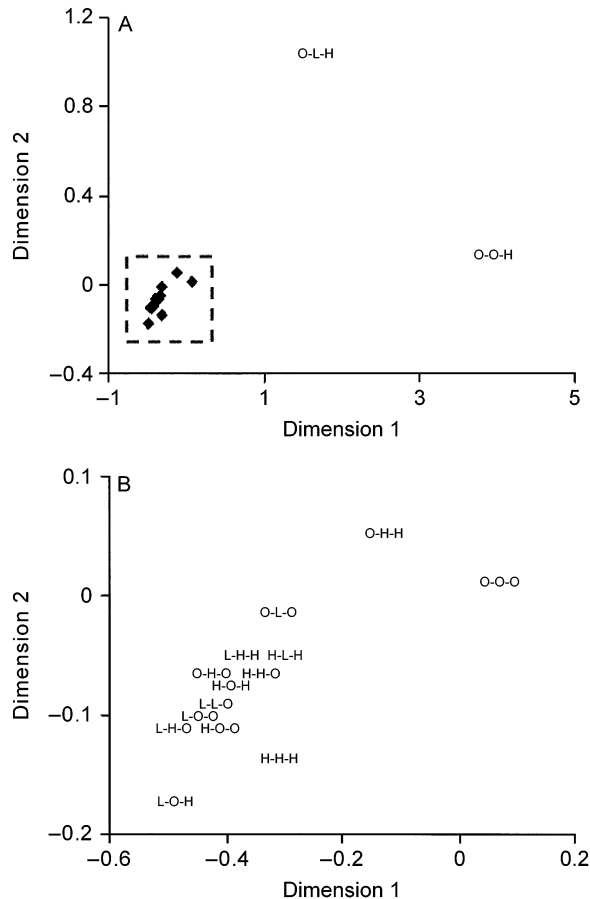


FIG. 2. Biplot graphs of two-dimensional ordination results from nonmetric multidimensional scaling. A coarse view of the biplots is shown in panel (A); details of the contents of the box enclosed by dashes are enlarged in panel (B). Labels for treatments are as follows: the first letter refers to the disturbance treatment (O = none, L = low, H = high), the second letter refers to predator density (O = none, L = low, H = high), and the third letter refers to the resource treatment (O = none added, H = addition).

show that the interactions between these local processes and species-specific responses are important for local community dynamics, although neither facilitated coexistence among the protozoan and rotifer species (Wootton 1998). The presence of other local community processes may interact with disturbances resulting in deviations from the predictions of the Intermediate Disturbance Hypothesis (Connell 1978, Wootton 1998).

The effects of the interaction between predators and resources have received much attention recently (Proulx and Mazumder 1998, Chase et al. 2002, Worm et al. 2002). The results of this study were consistent with previous work that found decreased diversity with increasing predator densities at low resource levels (Proulx and Mazumder 1998, Kneitel and Miller 2002, Worm et al. 2002). While meta-analyses (Proulx and Mazumder 1998, Worm et al. 2002) have found consistent increases in diversity with increasing predator

TABLE 2. Results of treatment effects on nonmetric multidimensional scaling (NMS) dimension loadings (two values) using MANOVA.

Source	Wilks' lambda	F	df	P
Disturbance (D)	0.431	18.596	4, 142	<0.001
Predator (P)	0.783	4.625	4, 142	0.002
Resource (R)	0.677	16.936	2, 71	<0.001
D × P	0.609	4.988	8, 142	<0.001
D × R	0.532	13.157	4, 142	<0.001
P × R	0.857	2.836	4, 142	0.027
D × P × R	0.716	3.233	8, 142	0.002

levels at high resources, we still found decreased effects on diversity. We also found no resource effect on richness in the absence of predators, but diversity increased by 59% with resource addition at high predator levels, another finding that differed from the meta-analysis conducted in Worm et al. (2002). One explanation for this pattern is that competition for resources dominates in the absence of predators, whereas species that are weaker competitors, but tolerant of predators, are facilitated by the presence of predators and resources (Leibold 1996).

In this study, we found that the effects of disturbances, predators, and resources affected species richness, abundance, and species composition. Changes in species composition indicated that different sets of species inhabited the different communities altered by the treatments. It appears that trade-offs (in response to disturbances, predators, and resources) among these protozoan and rotifer species facilitate coexistence in this system (Kneitel and Chase 2004). For example, the presence of disturbances is likely to maintain certain species in the regional pool that would otherwise be driven to extinction (e.g., *Colpoda*, *Vorticella*; see the Appendix). Compositional differences among treatments also imply that β diversity (the difference in species composition among local sites) is likely higher when there is spatial and temporal variation in disturbances (as well as predators and resources), and therefore may maintain higher levels of regional diversity (Kneitel and Chase 2004). We conclude that patterns of diversity, composition, and abundance respond to multiple limiting factors and their interactions. We suggest that progress in community ecology, with particular reference to understanding the factors that influence patterns of species diversity, abundance, and composition, will require a more general empirical and theoretical framework that explicitly recognizes and predicts responses of communities to multiple factors and their interactions.

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APPENDIX

A table of mean species abundances in each of the 18 treatments in this study is available in ESA's Electronic Data Archive: *Ecological Archives* E085-059-A1.