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Concurrent effects of resource pulse amount, type, and frequency on community and population properties of consumers in detritus-based systems

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Abstract

Episodic resource inputs (i.e., pulses) can affect food web properties and community dynamics, but detailed mechanistic understanding of such effects remain elusive. Natural aquatic microsystems (e.g., tree holes, human-made containers) are colonized by invertebrates that form complex food webs dependent on episodic and sometimes sizeable inputs of allochthonous detritus from adjacent terrestrial environments. We investigated how variation in pulse frequency, amount, and resource type interacted to affect richness, abundance, composition, and population sizes of colonizing invertebrates in water-filled tires and tree hole analogs in a forest habitat. Different container types were used to assess the generality of effects across two environmental contexts. Containers received large infrequent or small frequent pulses of animal or leaf detritus of different cumulative amounts distributed over the same period. Invertebrates were sampled in June and September when cumulative detritus input was equal for the two pulse frequencies. Pulse frequency and detritus type interacted to affect the responses of richness and abundance in both months; pulse frequency alone in June affected the relationship between richness and abundance. Richness and abundance were also greater with more detritus regardless of detritus type. One group, the filter feeders, were most important in driving the response of abundance and richness to pulses, especially in June. This work highlights the potential complex nature of responses of communities and populations to resource pulses and implicates the ability of certain groups to exploit pulses of detrital resources as a key to understanding community-level responses to pulses.

Keywords

detritus; mosquitoes; oviposition; productivity; resource subsidies

Introduction

Resources pulses are unusually high inputs of ephemeral materials, which are then depleted by consumers (Ostfeld and Keesing 2000; Holt 2008). Understanding the effects of pulsed resources on communities presents multiple challenges to ecologists, who must integrate both bottom-up and top-down effects and concomitantly consider other factors, such as period and amplitude of the pulses (Holt 2008), behavior of species, species interactions, and trophic dynamics (Ostfeld and Keesing 2000). Examples of pulsed resource additions exist for recipient terrestrial (e.g., dead animal carcasses, Yang 2004; 2006; Schneider et al.

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2011; marine animals, Rose and Polis 1998; seeds, McShea 2000) and aquatic (mostly invertebrates, Kawaguchi et al. 2003; Zhang et al. 2003) communities. Although the majority of energy in many food webs passes through detrital pathways (O'Neill and Reichle 1980; Wetzel 1995; Moore et al. 2004) where it can have profound effects on community structure, food web dynamics, and stability (Hairston and Hairston 1993; Yang 2006; Yee and Juliano 2007), there has been little progress in quantifying the effects of resource pulses in detritus-based systems (Yang 2006).

In many freshwater systems terrestrial detritus is the primary resource for food webs. For example, terrestrial plant detritus accounts for up to 99% of the energy driving metabolism in headwater streams (Minshall 1967) where it can have profound effects on multiple trophic levels (Wallace et al. 1997). For systems where detritus is the main source of energy, inputs often occur in pulses, which can be both temporally and spatially variable (Polis and Hurd 1996, Moore et al. 2004, Nowlin et al. 2007). Little is known about how the size and frequency of pulsed detritus inputs (Holt 2008) affect recipient food webs compared to systems dominated by primary producers. For example, predictable changes in community dynamics often result from the response of primary producers to pulsed resources in terrestrial (Ostfeld and Keesing 2000) and aquatic (Sommer 2002) systems, whereas in detritus-based systems our ability to make such predictions is lower. Thus, there is a need for empirical tests of general theory and models for community responses to resource pulses (Yang et al. 2010) and quantification of the effects of pulsed resources for both detritus- and primary-production based systems.

Inter-habitat transfer of resource subsidies is common (Polis et al. 1997; 2004), and such subsidies can have strong effects on recipient food webs (e.g., Polis and Hurd 1996; Polis et al. 1997, Rose and Polis 1998, Henschel et al. 2001). Subsidies also have indirect effects on food webs, including in the alteration of trophic cascades (Nakano et al. 1999; Henschel et al. 2001). Models of such inter-habitat resource subsidies usually postulate constant inputs through time (Huxel and McCann 1998; Huxel et al. 2002), although it is clear that these resource subsidies usually occur as pulsed inputs varying in size and frequency (Yang 2004; Nowlin et al. 2007).

Species-energy theory postulates that patterns of richness can be explained by variation in resources over space or time (Preston 1962; Wright 1983), which can result in a positive relationship between abundances of individuals and richness, as both increase with resource abundance (Srivastava and Lawton 1998). Two of the most common mechanistic hypotheses for this positive relationship are the More Individuals hypothesis (Srivastava and Lawton 1998) and the Resource Specialization hypothesis (Keddy 1984; Abrams 1995; Hurlbert 2004). The More Individuals hypothesis suggests that greater resource supply (i.e., productivity) supports greater population densities, increasing the persistence of rare species and thus richness via decreasing extinction frequencies. For the Resource Specialization hypothesis, increasing resources leads to an increase in the availability of rare resources, which are required by some specialist species. The increase in quantity of rare resources may allow inferior competitors to persist in the presence of superior competitors. These two hypotheses make distinct predictions for how richness and abundance jointly respond to resource pulses (Fig. 1, Drever et al. 2009). The More Individuals hypothesis predicts that richness and abundance are positively related and both increase with pulse size, with larger pulses shifting both richness and abundance toward higher values along the same trend line (Fig. 1a). The Resource Specialization hypothesis predicts that large pulses increase richness, but not necessarily abundance (Fig. 1b) because large pulses increase the chance of adding sufficient rare resource types to enable new species specializing on those resources to persist in the community. Both of these predicted outcomes can occur simultaneously if both mechanisms operate (Fig. 1c). Tests of these predictions would lead to better theoretical

understanding of the relationships among species richness, abundance, and resource supply (Drever et al. 2009).

We investigated effects of detritus pulse frequency, amount, and type on communities of invertebrates colonizing aquatic containers (tree holes, tires). Tree holes are cavities in trees that collect water and detritus and are colonized by a diverse assemblage of specialized aquatic invertebrates (Kitching 2000). Water-filled vehicle tires also are colonized by aquatic invertebrates, although these systems contain many more generalists (Yee, D.A., personal observation). Communities in both container types develop via sequential colonization, which contrasts with previous studies of effects of resources pulses that emphasize population and community responses within established communities (Yang 2006; Nowlin et al. 2007, Yang et al. 2011). Containers are donor-controlled (Moore et al. 2004), as their food webs receive energy almost exclusively from allochthonous detritus inputs from adjacent terrestrial habitat. Algae can be found in tires (Carpenter 1983), but detritus is more important for consumers (Kling et al. 2007; Yee et al. 2010). Inputs of detritus into tires and tree holes can be episodic and seasonal (Lounibos et al. 1992; Yee et al. 2007a), and can affect populations and community composition of heterotrophic microorganisms (Verdonschot et al. 2008), which in turn affect invertebrate consumers (Yee et al. 2007b; Yee and Juliano 2007). Major detritus inputs into containers are senescent leaves (Kitching 2001) and terrestrial invertebrate carcasses (hereafter, animal detritus, Yee et al. 2007a), both of which may be substantial, brief, and sporadic. In our study area there are multiple inputs of detritus, with ~75% of annual leaf additions during October–November and peak animal detritus inputs during July–August (Yee et al. 2007a). Effects of leaf (e.g., Léonard and Juliano 1995; Srivastava and Lawton 1998; Kaufman et al. 1999) and animal (Yee and Juliano 2006; 2007; Yee et al. 2007b; Murrell and Juliano 2008) detritus on populations and communities in tree holes and tires are well known. Containers are ideal model systems for manipulative tests of predictions about the effect of detritus on community organization (Srivastava and Lawton 1998; Kneitel and Chase 2004; Yee and Juliano 2007; Yee et al. 2007b).

We manipulated pulse frequency (small, frequent pulses versus large, infrequent pulses) and amount of animal and leaf detritus in simulated tree holes and vehicle tires and determined the population and community responses of colonizing invertebrates. Because the life span of most invertebrates in tires and tree holes is short compared to the growing season (Yee, D.A., personal observation), we expected that variation in pulse frequency would affect communities through changes in richness, abundance, and community composition (Yang et al. 2008; Drever et al. 2009). We had four general predictions irrespective of container type: 1) regardless of pulse frequency, animal detritus would support greater richness and abundance than leaf detritus, 2) regardless of type or frequency, increasing detritus amount would increase abundance and richness and change community composition (i.e., relative abundances of particular species), 3) pulse frequency would affect richness and abundance and their relationship to one another, and 4) changes in communities with pulse frequency would be a result of changes in abundances of functional feeding groups.

Prediction 1 arises because animal detritus typically contains more nitrogen than plant detritus (Yee and Juliano 2006) and is more directly available to some consumers (Yee et al. 2007c). Because nitrogen is often limiting in container systems (Carpenter 1982; Walker et al., 1997; Kaufman et al. 2002) we expect additions of high-nitrogen animal detritus to have a greater positive effect on communities of invertebrates compared to low-nitrogen plant detritus (Yee and Juliano 2006; 2007). Using different detritus types also permits us to test the Resource Specialization hypothesis outlined above (Fig. 1b), because as we add more of one type of detritus, we increase the chance of persistence for new species specialized on that detritus type. If this occurs, we predict that richness-abundance relationships will differ

for animal vs. plant detritus, especially with frequent vs. infrequent pulses (Drever et al. 2009). Prediction 2 arises because nutrients often are limiting in containers, and containers with more detritus are colonized by more species and often support more individuals (Srivastava and Lawton 1998; Kitching 2000; 2001; Yee et al. 2007a; Yee and Juliano 2007). Prediction 3 results from the postulate that pulse frequency affects richness and abundance (Holt 2008; Sommer 2002; Grover 1988; 1997). Richness is sometimes maximized at an intermediate pulse frequency, with inter-pulse intervals of ~3 times the mean generation time of the target organisms (Sommer 2002; Holt 2008, but see Robinson and Sandgren 1983). Models (Hsu 1980) and chemostat studies (Grover 1988; 1997) suggest that intermediate pulse frequency and amplitude can lead to stable coexistence, or to prolonged non-equilibrium coexistence of competitors. In contrast, for competing container mosquitoes, small, steady resource inputs may be more likely to yield coexistence, compared to infrequent, large pulses (Bevins 2007). And finally, Prediction 4 is based on the observation that abundances of detritivores respond to detrital pulses (Yang 2006). In our system, food webs are dominated by detritivores, with no herbivores and few predators. Thus, we focus on how pulses affect abundances of three functional feeding groups that differ in spatial and trophic proximity to detritus and feeding mode (Yee et al. 2007, Yee and Juliano 2007): deposit feeders live in and ingest detritus (closest proximity to detritus), filter feeders primarily ingest microorganisms suspended in the water column or growing on detrital surfaces (intermediate proximity to detritus), and predators consume other invertebrates (furthest from detritus). Given these categories, we anticipate that large, infrequent pulses may increase populations of consumers that would directly benefit from large influxes of material (deposit feeders), but have less effect on groups that rely on microorganism processing of detritus (filter feeders). In contrast, small, frequent pulses may benefit filter feeders over deposit feeders if pulse frequency was sufficient to maintain microorganism populations in the face of consumption by filter feeders. In either case, predators would likely benefit from more detritivores, but deposit feeders, residing within the detritus, may be less vulnerable and valuable to predators. Consumers at higher trophic levels may generally be less responsive to pulses if they feed on multiple functional feeding groups (Anderson and Polis 2004, Yang et al. 2010).

As we were interested in testing the generality of these predictions, we used tires and tree holes that share many species, but differ in opening size and depth and relative abundances of generalist species. These differences may affect community responses to our manipulations in ways that are difficult to predict.

Methods

Tree hole analogs (hereafter, “holes”), designed to mimic natural tree holes, and tires were located within ParkLands Foundation Merwin Preserve, Lexington, Illinois (40° 39' 10 N, 88° 52' 21 W). This site is dominated by mature oak, hickory, elm, and maple trees, and contain natural tree holes and discarded vehicle tires that provided a source of invertebrate colonists.

Holes were constructed out of 10 cm diameter PVC pipe cut into 25 cm segments, and sealed at the bottom with a plastic cover and rubber cap to make them water tight (Yee and Juliano 2007). Hole had lids with a 4 cm opening to decrease evaporation and uncontrolled additions of detritus. Holes were placed in wire mesh cages (1.3 × 1.3 cm openings) attached to trees (< 30 cm diameter), approximately 1 m off the ground and 10 m apart. Cages minimized uncontrolled additions of detritus and disturbance by vertebrates.

Golf cart tires were 45.7 cm high × 21.6 cm wide and free of invertebrate eggs. Each tire was attached upright to the base of a mature tree (< 30 cm dbh) using wire. Wire mesh (1.3

× 1.3 cm openings) was affixed over both openings to minimize uncontrolled additions of detritus and disturbance by vertebrates. A 30 m buffer zone separated areas where tires and holes (collectively, containers) were located.

We used two types of detritus: leaves and dead crickets. Leaves were a mix of equal parts of senescent leaves of white oak (*Quercus alba*), sugar maple (*Acer saccharum*), and American elm (*Ulmus americana*), collected during the preceding autumn from the site and stored dry at room temperature. Leaves were cut into approximately 1.25 cm² pieces after the petioles were removed. Decorated crickets (*Grylloides sigillatus*) from colonies at the School of Biological Sciences, ISU, were used as a representative large-bodied terrestrial arthropod, similar in size to those collected as arthropod detritus from natural tree holes (Yee, D.A., unpublished data). Whenever possible, the mass of detritus needed for a treatment was comprised of whole crickets. Crickets were cold-killed and dried at 50°C for 48 hrs before being added to containers.

Cumulative detritus amount and pulse frequency were manipulated independently. We used three levels of leaf (1.00, 4.00, and 24.00 g) and two levels of animal (0.25 and 1.00 g) cumulative detritus additions. These amounts were consistent with amounts used in a previous experiment that yielded significant effects of detritus amount on richness and abundance of species colonizing similar containers (Yee and Juliano 2007). Because both container types were of standard size and volume (maintained at 1800 ml), water volume necessarily decreased as detritus amount increased. The decision to confound these two factors was motivated to create a realistic experiment representative of the relationship between water volume and detritus in nature. For all detritus amounts, we added detritus in either small infrequent pulses (hereafter, Frequent; 10% of total detritus added at container establishment and every two weeks at 9 additional times) or in two equal large infrequent pulses (hereafter, Infrequent; 50% total detritus added at container establishment and 50% added eight weeks later). Cumulative detritus added to each container under the two pulse frequencies was the same at two times: weeks 8 and 18 after establishment (hereafter June and September). We randomly assigned each detritus amount, type, and frequency combination to three containers, for a total of 30 tires and 30 holes.

Containers were established with detritus on 24-Apr-2004, approximately one month before invertebrate oviposition begins at ParkLands (Yee, D.A., personal observation). We sampled containers four times (20-May, 16-Jun, 23-Jul, and 17-Sept-2004) although we analyze only those dates when detritus amount was equal for the two pulse frequencies (i.e., June, Sept). Our sampling intervals were short enough to capture population dynamics of the most common mosquito in natural tree holes and tires (*Aedes triseriatus*, development times 20–40 d in tires in central Illinois, Léonard and Juliano 1995; Yee 2008). Because of time constraints in enumerating and identifying individuals in containers, half of the containers of each container type were sampled randomly on each of two consecutive days. During each day, we sampled at least one replicate of each frequency-detritus type-amount combination for each container type. We counted and identified all invertebrates to species or morphospecies, and then all fluid, detritus, and invertebrates were returned to the field within 24 hrs of collection.

Statistical Analyses

We tested for differences in richness and total abundance in June and September using MANCOVA (SAS Institute Inc., 2004) with detritus type (animal, leaf), frequency (frequent, infrequent), and container type (hole, tire) as factors, and log-transformed total detritus amount as the covariate. This analysis tests for the direct effects of pulse frequency, detritus type, and container type, on richness and abundance with detritus amount held constant statistically (Prediction 1–3). We $\log_{10}+1$ transformed invertebrate abundances to

meet assumptions of normality and homogeneity of variances. Significant effects analyzed further by multivariate contrasts. We tested the More Individuals and Resources Specialization hypotheses (Fig. 1) via regression of richness versus abundance with pulse frequency as a class variable (Prediction 3). Differences in community composition between pulse frequencies total amounts and kind of detritus, and container types across all time periods, (testing aspects of Prediction 2) were tested using permutation MANOVA using distance matrices (ADONIS - McArdle and Anderson 2001) with R (<http://www.r-project.org>). We tested for effects of our manipulations on functional feeding groups (Prediction 4) by MANCOVA, with detritus type (animal, leaf), pulse frequency (frequent, infrequent), and container type (hole, tire), as factors, and $\log_{10}+1$ transformed total detritus amounts as a covariate. Dependent variables were abundances of deposit feeders, filter feeders, and predators (see Table 1 for species). Significant effects were analyzed further using multivariate contrasts. For all contrasts, experiment wise α was controlled by Bonferroni adjustment of comparison wise α .

Results

Containers with the lowest amount of either detritus type were colonization by few individuals, suggesting insufficient detritus to attract or to support invertebrates; containers with greater amounts of detritus were consistently colonized by species representative of those containers at this site (Yee et al. 2007b; Kling et al. 2007; Yee and Juliano 2007). Mosquitoes dominated in holes, comprising 31% of all individuals. The most common taxa were the mosquitoes *Aedes triseriatus* and *Orthopodomyia signifera*, and the moth fly *Telmatoscopus albipunctatus* (Table 1). There were seasonal differences in abundance, with most species decreasing from June to September (Table 1). Exceptions to this trend were *T. albipunctatus* and ceratopogonids (Table 1). For both months tires were colonized by approximately 71% more individuals than were holes. The relative abundance of mosquitoes (~32% of all individuals) was similar in both container types. *Telmatoscopus albipunctatus*, ceratopogonids, and the facultatively predaceous mosquito *Anopheles barberi* were numerically dominant in tires, representing 48, 19, and 15% of all individuals, respectively. Total species richness was similar in tires ($S = 9$) and holes ($S = 10$). Based on ADONIS, community composition differed significantly for detritus amount ($F_{1,44} = 9.63$, $P < 0.001$), pulse frequency ($F_{1,44} = 2.02$, $P = 0.037$), container type ($F_{1,44} = 11.81$, $P < 0.001$), and detritus type ($F_{1,44} = 2.35$, $P = 0.017$). Community composition also was affected by interactions of detritus amount and container type ($F_{1,44} = 4.58$, $P < 0.001$), and pulse frequency and detritus type ($F_{1,44} = 2.00$, $P = 0.036$).

Abundance and Richness

For June and September, MANCOVA identified significant effects of detritus amount, container type, and a pulse frequency by detritus type interaction (Table 2). In most cases, abundance contributed more than did richness to the significant effects (Standardized Canonical Coefficients, SCCs, Table 2). More individuals and species were present with greater amounts of detritus, and in tires, as opposed to holes, in June and September (Tables 1 and 2). For the pulse frequency by detritus type interaction in June, more individuals were supported with infrequent pulses of animal and leaf detritus and frequent pulses of animal detritus compared to frequent pulses of leaf detritus (Fig. 2a). For September, infrequent pulses of animal detritus supported more individuals and species compared to infrequent pulses of leaf detritus, with frequent pulses of both detritus types intermediate (Fig. 2b).

Regression analysis

In June, richness was affected by significant interactions of pulse frequency, detritus type, and abundance ($F_{1,44} = 4.49$, $P = 0.039$), and container type, pulse frequency, and

abundance ($F_{1,44} = 12.22$, $P = 0.001$). The relationship of richness to abundance increased significantly faster in containers with large, infrequent animal pulses versus small, frequent animal pulses or either frequency of leaves (Fig. 3a). Pulse frequency in both container types affected the richness-abundance relationship in a similar positive fashion (slopes not significantly different), although richness and abundance were generally greater for large, infrequent versus small, frequent pulses (Fig. 3b). Pulse frequency was not significant as both a main effect and as part of interactions in September, although richness again increased with abundance and was affected by container type ($F_{1,51} = 22.05$, $P < 0.001$), with holes having greater adjusted mean species than did tires.

Functional feeding groups

In both months there were significant effects of detritus amount and detritus type on abundance of functional feeding groups, with filter feeders often contributing most to the significant effects (Table 3). In June, the container type by detritus type interaction was significant with deposit feeders and predators contributing most to this effect (Table 3). Multivariate contrasts yielded significant differences between container types for leaf detritus (Pillai's $\text{Trace}_{3,49} = 0.273$, $P = 0.001$), with leaf detritus in tires supporting more deposit feeders ($\text{SCC} = 0.735$) and predators ($\text{SCC} = 0.910$), whereas leaf detritus in holes supporting more filter feeders ($\text{SCC} = -0.675$) (Fig. 4a). The difference between leaf and animal detritus appeared large (Fig. 4a) but was marginally not significant after Bonferroni adjustment (comparison wise $\alpha = 0.05/4 = 0.0125$, Pillai's $\text{Trace}_{3,49} = 0.186$, $P = 0.017$). Contrasts between detritus types within tires, and animal detritus between container types were not significant ($P > 0.05$).

In June, there was a significant pulse frequency by detritus type interaction that was largely explained by the abundance of filter feeders (Table 3). Multivariate contrasts yielded one significant difference among the frequency-detritus type combinations: between animal versus leaf detritus in frequent pulse containers (Pillai's $\text{Trace}_{3,49} = 0.238$, $P = 0.004$), which was mainly attributable to filter feeders ($\text{SCC} = 1.264$). Filter feeders were generally more common in animal versus leaf based containers (Fig. 4b).

In September (Table 3), filter feeders increased with cumulative detritus amount ($R^2 = 0.356$) and were more abundant with animal (mean \pm SE, $N = 62.4 \pm 3.3$) versus leaf detritus ($N = 24.7 \pm 15.3$). Predators were more abundant in tires compared to holes (hole $N = 1.1 \pm 0.5$ vs. tire $N = 22.9 \pm 6.6$).

Discussion

Magnitude, frequency, and composition of pulsed detritus inputs affected these container communities, a general result that has been observed across habitat types (Yang et al. 2008, 2010). Our hypothesis that detritus pulse frequency would affect richness, abundance, and community composition was supported, although effects of pulse frequency were mostly interactions with detritus amount and composition, and effects changed over time. We found strong support for the prediction that animal detritus supports more species and individuals compared to leaf detritus (Prediction 1) and that increasing detritus amount increases abundance, richness, and composition of invertebrates (Prediction 2). We also found some support, at least in June, for our predictions that community effects of pulse frequency are a result of differential effects on functional feeding groups (Prediction 4) and that pulse frequencies affect the relationship of richness and abundance, as these predictions were only accurate in June (Prediction 3). Pulse frequency had a similar effect in both container types (no container by frequency interactions); the apparent similarity of responses to many aspects of our manipulations of resource pulses suggests that communities in aquatic microsystems may show similar responses despite differences among container types in

water depth, container opening size, and species composition (see Table 1). Consistent responses to pulses across many systems have previously been documented empirically (Nowlin et al. 2008) and predicted theoretically (Holt 2008). Moreover, the response of particular functional feeding groups, especially filter feeders, in both container types to our treatments suggests the responses of particularly influential species that exploit detritus pulses could be a means to understand the complex responses of whole communities to resource pulses (Yang 2006).

Although pulses affected communities in both June and September, specific effects of pulse frequency were seasonal. In June, small frequent pulses of animal detritus supported more species and individuals than did other pulse frequencies or types of detritus (Fig. 2a). In September, large, infrequent pulses of animal detritus supported more species and individuals, although richness and abundance were generally higher for all treatment combinations and differences among container types were less dramatic (Fig. 2b). Different effects of pulse frequency on richness and abundance over time may be due to large-scale seasonal trends in abundance and richness of invertebrates. For example, differences in abundance among treatment levels were large in June, and abundance was a more prominent factor in driving differences among treatments (Fig. 2a, Table 2), whereas abundance and richness in September were both more similar among pulse frequencies and detritus types, and contributed more equally to the significant effects (Table 2). In September, about twice as many invertebrates colonized containers (Table 1), and this increase may have contributed to seasonal differences in responses of communities to our treatments.

Large, infrequent pulses generally increased richness and abundance across container types and time periods (Fig. 2a), and tended to produce steep relationships between richness and abundance compared to small, frequent pulses (Fig. 3). Some resource-based theory postulates that progress toward competitive exclusion may be slowed by sporadic resource pulses compared to continuous inputs (Grover 1988; reviewed by Grover 1997). Small, frequent pulses are closer to continuous inputs, so that our results are consistent with this prediction, suggesting that infrequent pulses of detritus may help to maintain greater, non-equilibrium diversity by slowing competitive exclusion (Grover 1997). Empirical studies of pulses have shown both monotonic (Robinson and Sandgren 1983) and unimodal (Sommer 2002) relationships of diversity to increasing resource pulse size and interval. Because we used only two patterns of pulse sizes and intervals, we cannot distinguish between unimodal and monotonic relationships, although our results confirm the importance of pulse size and interval for communities. Sommer (2002) suggested that diversity was maximized when pulses of resources came at intervals of approximately three times mean generation time. Our infrequent pulses came at eight-week intervals, which roughly corresponds to two or three generations (depending on conditions) of mosquitoes, the dominant members of the community. Thus, we could interpret our results as representing only the increasing portion of a unimodal relationship between diversity and pulse size and interval, a pattern that echoes past discussions of observed relationships of diversity to productivity (Rosenzweig and Abramsky 1993). Clearly, effects of resource pulse size and interval must be investigated over a wider temporal scale to distinguish between these alternative relationships.

We also were interested in the underlying mechanisms explaining richness⁴⁰⁸ abundance relationships across pulse frequencies (Drever et al. 2009). Pulse frequency affected the richness-abundance relationship in both months, although the effects depended on other factors, and only in June did the slopes of the relationships differ between pulse frequencies (Fig. 3a). Results in both months were most consistent with a combination of the More Individuals and Resource Specialization hypotheses (Fig. 1c, Drever et al. 2009), wherein large infrequent pulses both shift the relationship of richness and abundance to greater

values, and also yield greater richness for the same abundances compared to smaller frequent pulses (Fig. 3a, b). This result suggests that with larger pulses, more species were maintained as a consequence of more individuals, but that some new, perhaps specialized species enhanced richness as well. Past work in containers has shown mixed support for the More Individuals hypothesis, although richness and abundance are strongly linked across changes in productivity (Srivastava and Lawton 1998; Yee and Juliano 2007; Yee et al. 2007b). Our observation that animal detritus supported more species and individuals than did leaf detritus, and that community composition differed between detritus types, are also consistent with the Resource Specialization hypothesis.

Consistent with predictions, increasing detritus amount (Prediction 2), and specifically high quality animal, as opposed to low quality plant detritus (Prediction 1), often supported more individuals and species in both container types (Fig. 2). The influence of animal detritus on container communities is well known (Yee and Juliano 2006; Yee et al. 2007a; Kaufman et al. 2010) and animal detritus also has important effects on terrestrial communities (Schneider et al. 2011) and cave communities (Schneider et al. 2011). Collectively, these results suggest that animal detritus may be a more influential energy source structuring recipient communities, even though pulse size and overall amount of animal detritus may be small compared to terrestrial plant detritus.

Behavioral responses are more important than reproductive response to pulses (Yang et al. 2010), especially when pulses occurs over short time scales that are insufficient for population growth responses (Yang 2006). In our study, large, infrequent pulses may have generally supported more individuals and species because these pulses attracted more ovipositing females. Behavioral aggregation is likely a typical response to systems dominated by ephemeral resource pulses (Yang et al. 2008), particularly those based on detritus, wherein a pulse may trigger a strong, rapid numerical responses via propagule input. This behavioral aggregation suggests that effects of resource pulses on diversity may be transient, non-equilibrium responses, and may contribute to diversity by further slowing progress toward competitive equilibrium (Grover 1997). Because most species that colonized our system have a terrestrial adult phase that we did not sample, it may be important to consider simultaneously external (i.e., behavioral aggregation involving oviposition) and internal (i.e., reproductive) responses to pulses (Ostfeld and Kessing 2000, Yang et al. 2010). It remains unclear whether observed community responses were solely the result of behavioral aggregation of oviposition responses, or also involved differential survival among treatment levels (Ostfeld and Kessing 2000, Yang et al. 2010).

Resource pulses may lead to or amplify indirect effects in communities, including bottom-up and top-down effects (Ostfeld and Kessing 2000; Yang et al. 2008). Top-down effects may follow strong responses to an initial bottom-up effect of a pulse (Jaksic et al. 1997). *Anopheles barberi*, the only important predator collected in this study, increased across time (Table 1), and was overall more abundant within large, infrequent- (mean \pm SE, June = 1.90 ± 1.2 , Sept = 15.33 ± 6.5) versus small, frequent-pulses (mean June = 1.10 ± 0.7 , Sept = 8.70 ± 2.7). Thus, it is possible that the differences in responses of communities to pulse frequency may depend strongly on these predators, but two observations suggest this is unlikely. First, though *A. barberi* preys on mosquito larvae, the intensity of predation by *A. barberi* on non-mosquitoes is unknown. Second, *A. barberi* abundance was greatest in September, but it did not appear to have any association with abundances of other species, given that overall richness and abundance was similar in June and September (Fig. 2a vs. b). Thus, even though top-down effects are possible, the absence of abundant, dominant obligate predators during this experiment suggests bottom-up effects are more likely. A recent meta-analysis of the effects of resource subsidies found that predators are less likely

to respond to resources than are lower trophic levels, including detritivores (Marczak et al. 2007).

Obligate specialists and opportunistic resident consumers are two groups that may disproportionately exploit detritus resource pulses (Ostfeld and Kessing 2000, Yang et al. 2008). Our system contains few if any true invertebrate residents (i.e., species that spend their entire life within a container), although both container types were colonized by specialists and generalists. We found strong overlap in composition of species between container types, but the numeric response of individual species to container type was considerable (Table 1). Overall, functional feeding groups were important in explaining responses of communities to pulses in June, when filter feeder abundance was significantly greater in containers with frequent pulses of animal versus leaf detritus (Fig. 4b), the same month wherein communities displayed greater abundance, and to a lesser degree, richness, in frequent-animal-pulse containers (Fig. 2a). Filter feeders represented about 84% of individuals encountered in June, but only about 61% of those encountered in September (Table 1) when there was no response of functional feeding groups to pulses (Table 3). Filter feeders were, in general, the most important functional group contributing to significant effects in our experiment in both months (Table 3). Filter feeders include several abundant species (Table 1). Most of these filter feeders are habitat generalists capable of colonizing a wide range of small bodies of water (Snow 1949; Barrera 1998), and thus their presence and strong numerical responses may suggest that some habitat generalists, especially those capable of quickly colonizing new locations, drive the community-level effects of resource pulses. The fact that animal detritus contains more nitrogen and phosphorus than plant detritus (Yee and Juliano 2006) and is more directly available to some consumers, especially filter feeders (Yee et al. 2007a; c), may also explain the strong effects of pulses of animal detritus on filter feeders.

Resource pulse theory remains incomplete (Holt 2008), in part due to a lack of a common vocabulary for resource pulses across different system types (Yang et al. 2008). Our understanding of pulses as an ecological driver of community structure and dynamics will improve as more systems are investigated under controlled conditions (Yang et al. 2010), including those based on detritus. Early work on pulses was limited to situations when particular events, both natural and anthropogenic, created pulses, yielding little potential to assess effects of pulse size, frequency, or resource type. We found that pulses produced strong, albeit interactive and complex effects on communities that were similar between the two systems considered here. Such complex effects are unexpected, given recent work suggesting that pulse-consumer interactions can be predicted from few parameters (Yang et al. 2010). The complex responses of invertebrate assemblages to our manipulations may indicate the typical result of pulsed resources, especially when other factors covary with pulse frequency.

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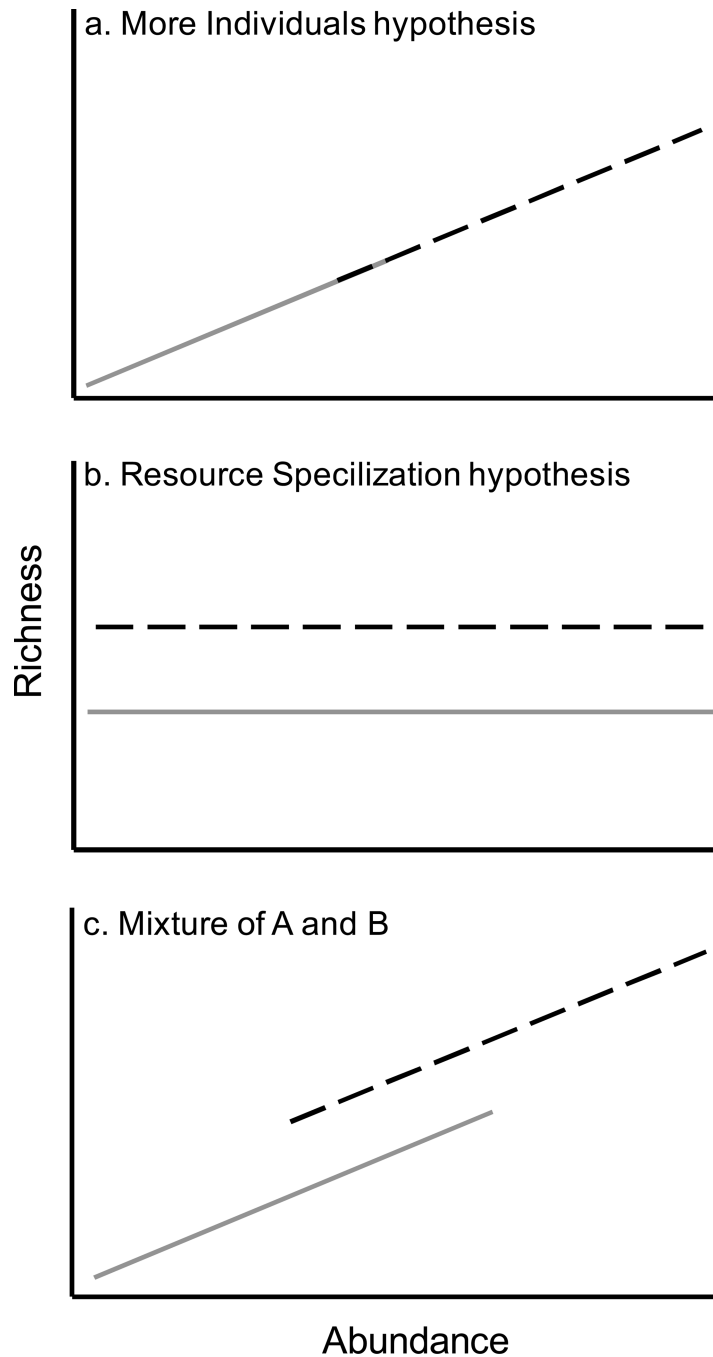


Fig. 1. Predicted effects of pulse frequency on the richness-abundance relationship. Lines represent different pulse frequencies (dashed = large, infrequent pulses, solid gray = small, frequent pulses). A) More individuals hypothesis predicts that large, infrequent pulses increase abundance and so increase richness, shifting the relationship up and to the right, B) Resource specialization hypothesis predicts that large, infrequent pulses enable specialist species exploiting those large resource pulses to persist, increasing richness without increasing overall abundance, and C) Contributions to the richness-abundance relationship from both hypothesized mechanisms (after Drever et al. 2009)

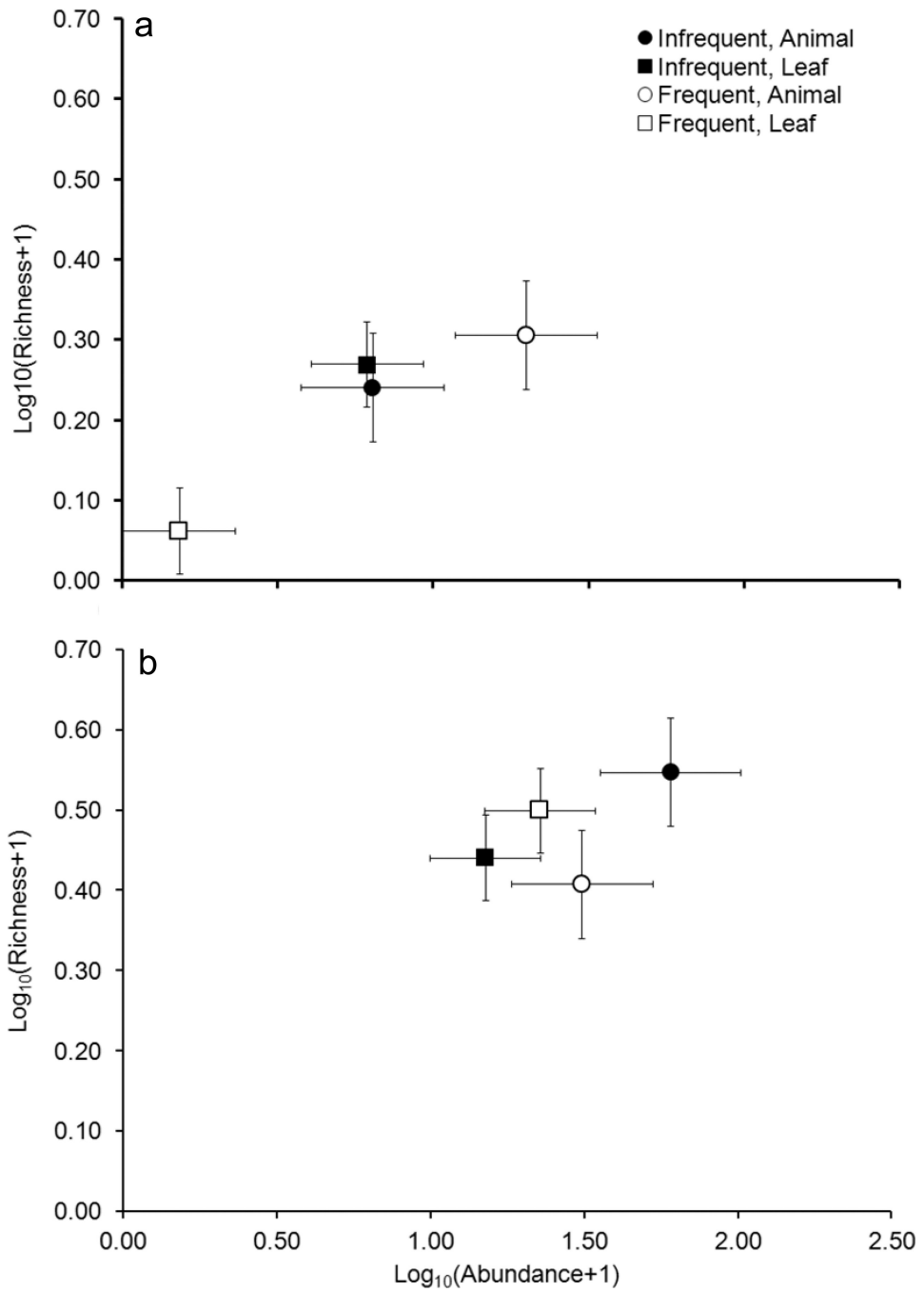


Fig. 2. Response of richness and abundance ($\text{log}_{10}+1$) of colonizing invertebrates for the significant effects of pulse frequency (closed symbols = infrequent pulses, open symbols = frequent pulses) and detritus type (circles = animal detritus, squares = leaf detritus) in a) June and b) September. Adjusted means (\pm SE) based on multivariate analysis of covariance (Table 2)

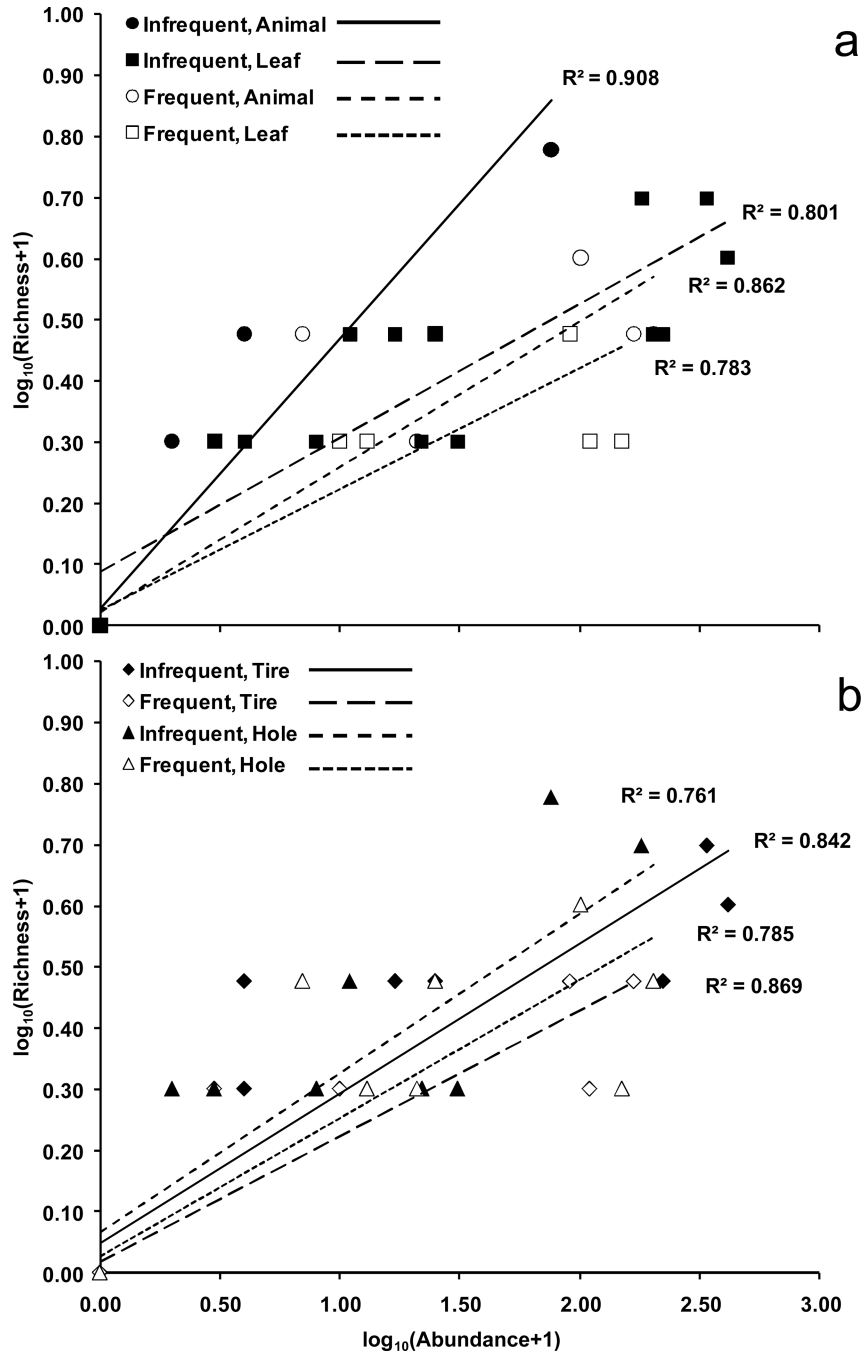


Fig. 3. Significant effects of a) pulse frequency by detritus type and b) pulse frequency by container type on the relationship between richness and abundance of invertebrates in June

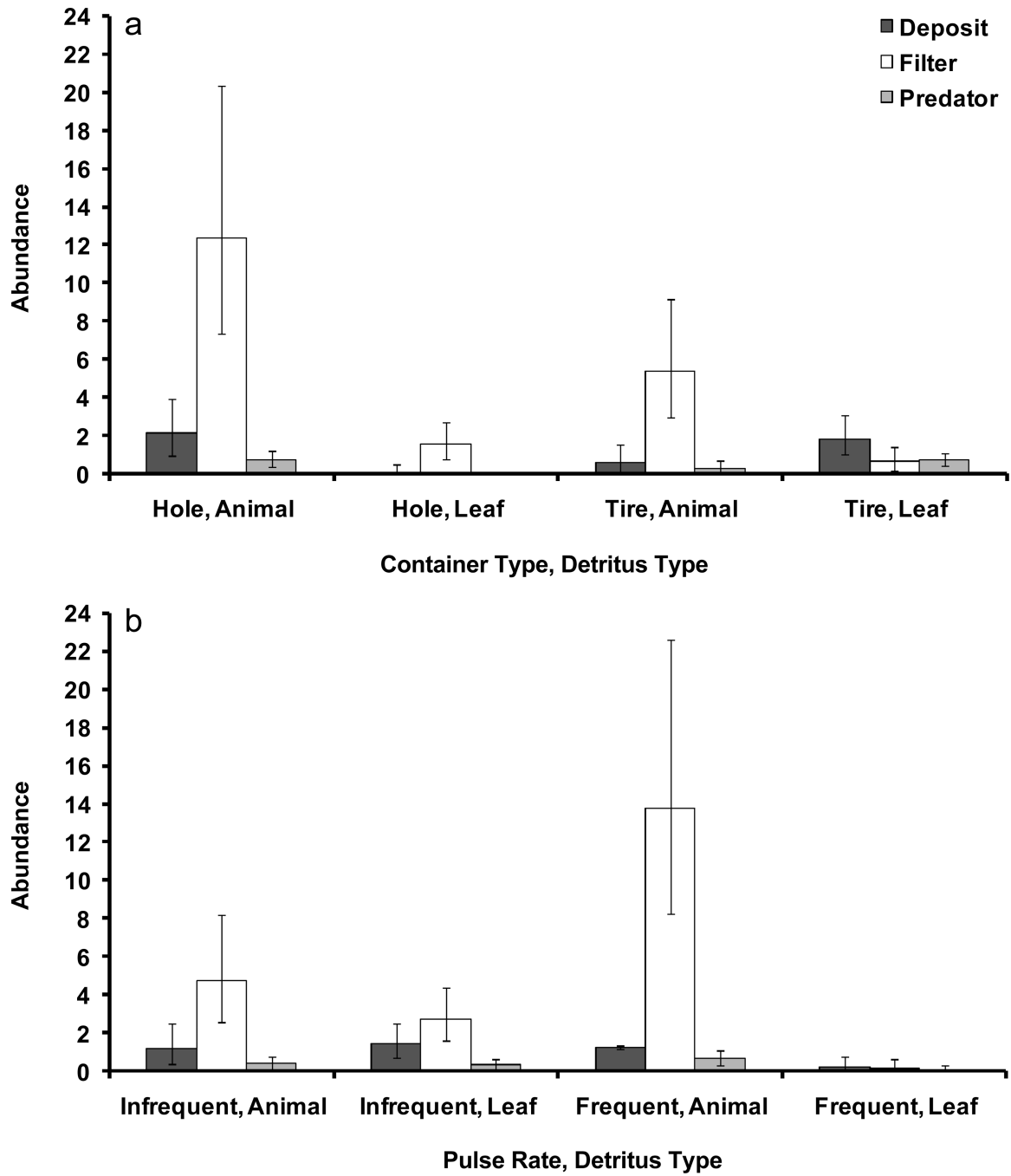


Fig. 4. Response (back transformed means \pm SE) of functional feeding groups (deposit feeders, filter feeders, predators) for the significant interactions in June for a) container type by detritus type, and b) pulse frequency by detritus type. Note that back transforming means resulted in nonsymmetrical error bars

Table 1

Invertebrates colonizing tree hole analogs and tires during 2004. Numbers of individuals during each of the two surveys when cumulative amounts of detritus were equal regardless of pulse frequency (June and September) and cumulative numbers in all months and treatments (n = 30). Functional feeding groups include filter feeders (F), deposit feeders (D), facultative predators (P), or undetermined (U).

Family or group	Species	Feeding group	Holes			Tires		
			June	Sept	Total	June	Sept	Total
Culicidae	<i>Aedes triseriatus</i>	F	46	224	270	0	49	49
	<i>Aedes hendersoni</i>	F	0	5	5	0	0	0
	<i>Anopheles barberi</i>	F, P	16	34	50	75	687	762
	<i>Culex restuans</i>	F	118	16	134	367	0	367
	<i>Orthopodomyia signifera</i>	F	83	167	250	0	95	95
Phoridae	<i>Megaselia immitriz</i>	F	498	95	593	20	1	21
Syrphidae	<i>Mallota posticata</i>	D	215	12	227	138	25	136
Ceratopogonidae	<i>Culicoides</i> sp.	D	30	8	38	536	71	607
Psychodidae	<i>Telmatoctopus albipunctatus</i>	F	37	641	678	332	1552	1884
Stratiomyidae	Morphospecies 1	D	0	62	62	0	0	0
Nematomorpha	Horsehair worm	U	0	0	0	1	0	1
	Total		1043	1264	2307	1469	2480	3949

Table 2

Results of multivariate analysis of covariance (\log_{10} detritus amount) on species richness (S) and abundance (N) of invertebrates colonizing artificial containers during June and September. Large standardized canonical coefficients for significant effects are represented in bold. Degrees of freedom for all analysis are the same (2, 50)

Source	Pillai's Trace	P-value	Standardized canonical coefficients		
			Log S	Log N	Log N
June					
Detritus Amount (D)	0.382	< 0.001	-0.801	1.951	
Detritus Type (T)	0.039	0.368	1.380	-0.293	
Pulse Frequency (R)	0.080	0.133	-2.225	1.915	
Container (C)	0.099	0.073	-0.859	1.990	
C × R	0.006	0.849	-0.695	1.872	
C × T	0.050	0.280	0.862	0.367	
R × T	0.149	0.018	-0.070	1.341	
C × R × T	0.013	0.722	1.326	-0.220	
September					
D	0.383	< 0.001	-0.191	1.357	
T	0.322	< 0.001	1.351	-1.008	
R	0.019	0.615	1.213	-0.053	
C	0.117	0.044	-0.648	1.470	
C × R	0.031	0.423	-0.633	1.469	
C × T	0.016	0.676	0.919	0.445	
R × T	0.118	0.043	0.870	0.510	
C × R × T	0.038	0.380	1.095	0.177	

Table 3

Results of multivariate analysis of covariance (log₁₀ detritus amount) on log₁₀+1 abundance of functional feeding groups of invertebrate larvae during June and September in artificial containers. Large standardized canonical coefficients for significant effects are represented in bold. Degrees of freedom for all analysis are the same (3, 49).

Source	Pillai's Trace	P-value	Standardized canonical coefficients			
			Deposit	Filters	Predator	
June						
Detritus Amount (D)	0.432	< 0.001	0.125	1.224	0.195	0.195
Detritus Type (T)	0.137	0.063	0.000	1.305	0.078	0.078
Pulse Frequency (R)	0.018	0.824	1.013	0.136	0.238	0.238
Container (C)	0.097	0.169	0.476	-1.185	0.747	0.747
C × R	0.026	0.727	0.603	-0.220	1.011	1.011
C × T	0.215	0.008	0.795	-0.261	0.881	0.881
R × T	0.143	0.054	0.203	1.193	0.195	0.195
C × R × T	0.004	0.980	-0.105	1.344	0.469	0.469
September						
D	0.442	< 0.001	0.055	1.270	0.340	0.340
T	0.205	0.010	-0.154	1.172	-0.462	-0.462
R	0.072	0.296	1.210	-0.146	-0.658	-0.658
C	0.548	< 0.001	-0.788	0.485	1.405	1.405
C × R	0.071	0.300	1.033	0.342	1.011	1.011
C × T	0.081	0.242	-0.400	0.125	1.500	1.500
R × T	0.110	0.126	-0.441	1.260	0.562	0.562
C × R × T	0.032	0.662	-0.290	1.120	0.930	0.930