Oecologia (2007) 154:377–385
DOI 10.1007/s00442-007-0837-5

COMMUNITY ECOLOGY

Richness–productivity relationships between trophic levels in a detritus-based system: significance of abundance and trophic linkage

Donald A. Yee · Susan Harrell Yee · Jamie M. Kneitel · Steven A. Juliano

Received: 7 April 2007 / Accepted: 25 July 2007 / Published online: 23 August 2007

Abstract Most theoretical and empirical studies of productivity–species richness relationships fail to consider linkages among trophic levels. We quantified productivity–richness relationships in detritus-based, water-filled tree-hole communities for two trophic levels: invertebrate consumers and the protozoans on which they feed. By analogy to theory for biomass partitioning among trophic levels, we predicted that consumer control would result in richness of protozoans in the lower trophic level being unaffected by increases in productivity, whereas richness of invertebrate consumers would increase with productivity. Our data were consistent with this prediction: consumer richness increased linearly, but protozoan richness was unrelated to changes in productivity. The productivity–richness relationships for all taxa combined were not necessarily consistent with relationships within each trophic level. We used path analysis to investigate the mechanisms that may produce the observed responses of trophic levels to changes in productivity. We tested the importance of the direct effect of productivity on richness and the indirect effect of productivity mediated by effects on total abundance. For protozoans, only direct effects of productivity on richness were important, but both direct and indirect effects of productivity on richness were important for invertebrates. Protozoan richness was strongly affected by top-down impacts of abundance of invertebrates. These results are consistent with theory on biomass partitioning among trophic levels and suggest a strong link between richness and abundance within and between trophic levels. Understanding how trophic level interactions determine productivity–richness relationships will likely be necessary in order for us to achieve a comprehensive understanding of the determinants of diversity.

Keywords Bacteria · Consumer · Invertebrate · Productivity · Protozoans · Tree hole · Trophic structure

Communicated by Andrew Gonzales.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0837-5) contains supplementary material, which is available to authorized users.

D. A. Yee (✉)
Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB Canada, T2N 1N4
e-mail: dyee@ucalgary.ca

D. A. Yee · S. A. Juliano
Department of Biological Sciences, Behavior, Ecology, Evolution, and Systematics Section, Illinois State University, Normal, IL, USA
e-mail: sajulian@ilstu.edu

S. H. Yee
Department of Ecology and Evolution, University of Chicago, Chicago, IL, USA
e-mail: yee.susan@epa.gov

Present Address:
S. H. Yee
Gulf Ecology Division, United States Environmental Protection Agency, Gulf Breeze, FL 32561, USA

J. M. Kneitel
Department of Biological Sciences, California State University, Sacramento, CA 95819-6077, USA
e-mail: kneitel@csus.edu

Introduction

Productivity is perhaps the most widely studied ecological factor postulated to explain global patterns of species diversity (Abrams 1995; Rosenzweig 1995; Waide et al. 1999;

Mittelbach et al. 2001). Current theory for food web dynamics, trophic regulation, and productivity–richness relationships typically focuses on gross primary productivity (GPP, grams carbon per square meter per year, Rosenzweig 1995) or a surrogate of GPP (Dodson et al. 2000; Mittelbach et al. 2001), even though the majority of energy in many food webs passes through detrital pathways (O'Neill and Reichle 1980; Wetzel 1995; Moore et al. 2004). Detritus can support higher diversity, larger predator biomass, and longer food chains than would be supported by primary productivity alone (Hairston and Hairston 1993), and it can stabilize the dynamics of consumer populations, alter habitat complexity, and stabilize food webs that would be otherwise unstable (Moore et al. 2004). Although there appear to be strong effects of detritus on attributes of many systems, investigations of how detritus-derived productivity affects species richness or variation in trophic structure are relatively rare.

Interactions among trophic levels are fundamental for our understanding of the dynamics of natural communities, although the single trophic level focus dominates investigations of productivity–richness relationships (Petchey et al. 2004). Primary productivity can affect higher trophic levels (trophic cascades) in aquatic ecosystems by affecting biotic (e.g., biomass) and abiotic (e.g., temperature, turbidity) ecosystem properties (Carpenter and Kitchell 1993; Hairston and Hairston 1993). Empirical (Worm et al. 2002) and theoretical (Huston 1996) work suggests that the combined effects of productivity and the presence of higher trophic levels can have non-additive effects on richness of lower trophic levels. Productivity also is an important factor in trophic regulation, potentially limiting the number of trophic levels in a food chain (Huston 1996). The addition of higher trophic levels as productivity increases may decrease the number of competitively dominant prey, allowing the addition of inferior competitors, ultimately yielding a positive effect on diversity (Abrams 1995; Moen and Collins 1996). In this way, higher trophic levels that are limited by productivity can affect richness of lower trophic levels. The effects of productivity, either plant or detritus-derived, on richness within different trophic levels in the same community has received little theoretical or empirical attention (although see Kneitel and Miller 2002).

To predict the effects of productivity on richness of multi-trophic level systems, we considered biomass partitioning among trophic levels and its relationship to productivity (Leibold et al. 1997). Biomass within communities is jointly determined by resource control of higher trophic levels and consumer control of lower trophic levels (Lindeman 1942; Fretwell 1977; Oksanen et al. 1981; Leibold et al. 1997). This theoretical work predicts that, for a single trophic level (producers), productivity has a positive effect on biomass. For a two-trophic-level system (producers and herbivores), biomass of the lowest trophic level is controlled by consumers, so that only consumer biomass benefits from increasing productivity (Fretwell 1977; Oksanen et al. 1981). Additional higher trophic levels with further increases in productivity may cause the system to be resource or consumer controlled, depending on whether there are an odd or even number of levels (Fretwell 1977; Oksanen et al. 1981).

Although there is currently no comparable theory to predict effects of productivity on richness within different trophic levels, the predictions for biomass within trophic levels provide a starting point. All else being equal, greater biomass or number of individuals in a community should be associated with greater number of species. This "More Individuals hypothesis" (MIH, Srivastava and Lawton 1998) postulates that greater productivity supports higher population densities, lowering the extinction rates of rare species and increasing richness (Srivastava and Lawton 1998). If the MIH is correct, abundance and richness within a trophic level should respond similarly to productivity. In a two-trophic-level system, we predict that consumer richness will increase with increasing productivity but that prey richness will be unrelated to increasing productivity. Support for these predictions would imply that abundance and species richness of consumers have a negative and limiting effect on the richness of their prey. Recent experimental work in a terrestrial (Dyer and Letourneau 2003) and an aquatic system (Kneitel and Miller 2002) supports this conjecture.

Tree holes are natural microcosms consisting of cavities in trees that collect water and detritus and are colonized by a diversity of aquatic invertebrates, protozoans, fungi, and bacteria (Kitching 2000). Allochthonous inputs including senescent plant parts (e.g., leaves, Kitching 2001), terrestrial invertebrate carcasses (Daugherty et al. 2000, Yee 2006), and stem flow (Carpenter 1983), and all inputs serve as energy sources for tree holes, as primary production is effectively absent (Carpenter 1983). Detrital inputs are a good surrogate for productivity in tree holes, having positive effects on richness and abundance of invertebrates (Jenkins et al. 1992; Srivastava and Lawton 1998; Yee and Juliano 2007), and on microorganism energy utilization rates (Yee and Juliano 2006, 2007; Yee 2006). Tree hole food webs in the temperate United States of America typically consist of one or two trophic levels of invertebrates and two levels of microorganisms. Bacteria and fungi are supported by detritus, protozoans are supported by bacteria or, for predaceous protozoans, by bacteria and other protozoans, and invertebrate consumers are supported by any of the more basal levels, including detritus. Larvae of the mosquito *Toxorhynchites rutilus* are the dominant predators of invertebrates, although this species is highly seasonal and infrequent in mid-western tree holes, especially in the north (Bradshaw and Holzapfel 1985).

We tested the predicted relationships among productivity, number of individuals, and number of species within two trophic levels (invertebrate consumers and protozoan prey) with data from the aquatic communities of 87 tree holes we surveyed across the State of Illinois, USA. Richness of invertebrates in tree holes has been shown to increase with manipulations of productivity surrogates (e.g., added leaf litter, Srivastava and Lawton 1998; Jenkins et al. 1992; leaf litter and animal detritus, Yee and Juliano 2007), and changes in invertebrate richness with increasing productivity have been shown to be mediated by changes in abundance (Yee and Juliano 2007). It is unknown how protozoans respond to natural variation of productivity in the field, or how natural levels of productivity affect richness of any taxonomic group. We used observational data to determine whether there were productivity–richness relationships for all taxa combined, and then for each trophic level separately. We then tested whether effects of productivity on individuals is the route by which increasing productivity affects richness, and we identified the strength and nature of the links between trophic levels as a test of predictions of how individual trophic levels should respond to changes in productivity.

Methods

Tree hole sampling

We sampled 87 natural tree holes from six sites in three regions of Illinois, USA, at two times (May and July 2004). Southern sites were Horseshoe Lake State Park, Alexander County, $n = 15$ tree holes (37°21′76″ N, 88°55′65″ W) and Cache River State Park, Johnson and Pulaski Counties, $n = 13$ (37°07′74″ N, 89°20′74″ W); central sites were ParkLands Merwin Preserve, McLean County, $n = 17$ (40°39′20″ N, 88°52′55″ W) and Moraine View State Park, McLean County, $n = 13$ (40°24′06″ N, 88°43′60″ W); and northern sites were Morton Arboretum, DuPage County, $n = 15$ (41°48′76″ N, 88°02′04″ W) and Fermi National Accelerator Laboratory, DuPage County, $n = 14$ (41°50′46″ N, 88°16′73″ W). Sites were 16–53 km apart, whereas regions were separated by ≥190 km. All sites were within a narrow band of longitude (i.e., <2°). Sampling always began with southern sites, ended with northern sites, and took approximately 2 weeks. At each time, we destructively sampled all invertebrates and identified them to species or morphospecies (see Appendix for taxa and feeding modes). Prior to collecting invertebrates, we removed 20 ml of fluid from each tree hole to quantify our productivity measures (see below) and for quantification of protozoans. This sample was extracted from within a few centimeters of the surface and away from container walls. We then removed the entire tree hole contents and measured the volume of water (milliliters) and wet mass of all detritus (grams). Detritus and remaining liquid were returned to each tree hole. We quantified protozoan richness of each tree hole by first gently mixing samples, extracting 1.0 ml into a Sedgewick rafter cell, and enumerating at 100× magnification in a phase-contrast microscope (Kneitel and Chase 2004). Preliminary tests had indicated that this technique captured 87% of the protozoan diversity in samples. Protozoan identifications were made based on Pennak (1989) and Foissner and Berger (1996).

For each tree hole, we used the cumulative number of species of protozoans and invertebrates collected over the two sampling periods. Some invertebrate groups are highly seasonal (e.g., mosquitoes), and combining data from both sampling periods tends to decrease temporal variation in richness values within each tree hole. In constructing trophic levels, we acknowledge that all protozoans may not be equally edible to invertebrates, although none of the invertebrates is susceptible to predation by protozoans. Protozoan populations are negatively affected by mosquitoes (the dominant group in tree holes, Kneitel and Chase 2004; Kaufman et al. 2002; Eisenberg et al. 2000; Cochran-Stafira and von Ende 1998; Paradise and Dunson 1998). We further recognize that additional trophic levels (e.g., omnivorous protozoans) are likely present within some tree holes. We separated protozoans into two trophic levels (bacterivores, $n = 41$ species and bacterivores/protozoan predators, $n = 18$ species) and conducted regression analyses (see below) for each group, separately. The results from these grouped analyses did not differ from results obtained by lumping protozoans into a single trophic level. Moreover, for lower trophic levels containing edible and inedible prey, increasing productivity is less likely to benefit consumer biomass, because it is the inedible taxa that primarily benefit from enhanced productivity (Leibold et al. 1997). Thus, lumping species with different edibilities into the lowest trophic level (protozoans) would make it more difficult to detect differences in productivity–richness relationships within the consumer (i.e., invertebrate) trophic level.

Measuring productivity

Total amount of leaf detritus has been used as a surrogate for productivity in experimental tree holes (e.g., Srivastava and Lawton 1998). However, the species, age, and condition of leaves can influence the energy available to microorganism decomposers and higher consumers (Carpenter 1983; Walker et al. 1997), making leaf detritus mass alone potentially unreliable as the indicator of system productivity. In addition, tree holes with and without leaves appear to yield similar production of mosquitoes (the dominant consumers, Walker and Merritt 1998), suggesting further

that detritus biomass by itself is inadequate as a measure of system productivity. To quantify productivity we measured both detritus mass and the metabolic rates (MRs) of microorganisms. The latter measure has significant effects on tree hole invertebrate populations (Yee and Juliano 2006; Yee 2006) and communities of invertebrates in artificial tree holes (Yee and Juliano 2007). MR values and detritus have been shown to be correlated in experimental studies (Yee and Juliano 2007; Yee et al. 2007), and are correlated with production of new bacterial biomass in realistic laboratory microcosms (Yee et al. 2007). Whole community MRs, which represent respiration of the lowest trophic levels (i.e., bacteria, fungi, and protozoans), were measured with a Gilson differential respirometer (GDR) (Middleton, WI, USA). Values for MR were in microliters of O_2 consumed per hour for each tree hole at each time and, thus, are analogous to GPP, as this measure is related to growth of microorganism populations. Values for MR typically are positive, but values near zero (i.e., no net difference between gas consumption and production) or negative values (i.e., gas production in excess of consumption) can result in cases of low biological activity on low quality detritus (Yee and Juliano 2006, 2007; Yee 2006; Yee, unpublished data). Although primary production is low to absent in tree holes, we took the step of incubating 8 ml fluid samples in the dark. For MR, values for individual tree holes were obtained under the mean tree hole temperature for each site at each collection time. For analysis, we used means of detritus amount and MR over the two sampling dates for each tree hole.

Data analysis

Resources and net primary productivity (NPP) are correlated in observational studies (Schmid 2002), rendering productivity dependent on both inherent site resources and the utilization of those resources (i.e., metabolism). We assumed that detritus amount and MR were mutually related to overall detrital productivity, but we expected neither of them to be a perfect indicator of the rate at which detritus-derived energy flows through a system. With this in mind, we used principal component analysis (PROC FACTOR, SAS Institute, 2004) (Hatcher and Stepanski 1994) to synthesize MR and detritus amount into a single descriptor of productivity (P). We then ran multiple regressions of measures of richness against P, mean tree hole volume (habitat area surrogate), and latitude, at each site. Stepwise regression models were used, with an inclusion criterion of $\alpha = 0.05$ for each new parameter (PROC REG, method = stepwise, SAS Institute, 2004). We determined the form of the relationship between richness and productivity (i.e., monotonic, unimodal) by testing for a significant contribution of a quadratic term to the linear model. Regression models were generated for all taxa (invertebrates and protozoans combined) and for each trophic level (invertebrates, protozoans), separately.

Path analysis (PROC CALIS, SAS 2004) (Wright 1921, 1934) was used to test for the importance of direct effects of productivity on richness and indirect effects of productivity on richness via abundance of each trophic level. Path analysis has been used to test for indirect effects in ecology (e.g., Wootton 1994; Daugherty and Juliano 2001; Mitchell 2001). Path coefficients are standardized regression coefficients that quantify the direct effect on a dependent variable caused by variation in a particular independent variable, while removing the effects of other independent variables (Hatcher 1994; Mitchell 2001). The importance (both direct and indirect) of a particular path is tested by assessment of the fit of reduced models in which one or more paths are eliminated from a full model (Hatcher 1994; Mitchell 2001).

We constructed two sets of path diagrams; one set to test the More Individual hypothesis (MIH), and the second to test for the nature and strength of top-down trophic links. For the MIH, we constructed a full path diagram with direct (causal) relationships from productivity (P) to total abundance and richness for each trophic level separately, and indirect effects of productivity on richness via abundance (Fig. 1a, b). In addition, we devised two reduced path models. The first model removed the direct path from productivity to richness (Fig. 1c, d). If this reduced model were to yield significant lack of fit, then the direct effect of productivity on richness would be important. The second model removed the indirect effect of productivity on richness via abundance (Fig. 1e, f). If this reduced model were to yield significant lack of fit, then the indirect effect of productivity on richness via abundance would be important, and the MIH would be supported. These models were compared with the full model using a goodness-of-fit χ^2 test (PROC CALIS, SAS 2004) (Hatcher 1994). Because there could be variation in the strength of the relationships among richness, abundance, and productivity with latitude, we also ran these same path analyses for each region, separately.

In order to test whether top-down effects of invertebrate richness or abundance were important for protozoans, we began by constructing a full model (Fig. 2a) that assumed top-down control of protozoan abundance and diversity by invertebrates (consistent with the study by Oksanen et al. 1981). Based on the previous results testing the MIH, we removed any paths that did not change significantly the fit of the model, and then we tested sequentially reduced models, removing paths linking invertebrates to protozoan richness and abundance. Specifically, we removed singly the paths linking invertebrate abundance and richness to protozoan variables, and then we removed pairs of paths linking

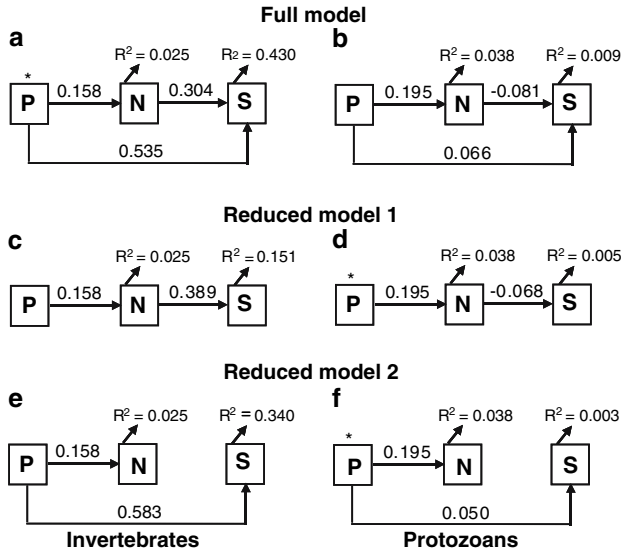

Fig. 1 Path diagrams testing the More Individuals hypothesis for invertebrates and protozoans. **a**, **b** Full model: direct effects of productivity (P) and abundance (N) on richness (S); indirect effects of productivity on richness through abundance. **c**, **d** Reduced model 1: no direct effects of productivity on richness. **e**, **f** Reduced model 2: no indirect effects of productivity on richness via abundance. Standardized path coefficients next to each line indicate the direction and magnitude of effects of one variable on another. Values for R^2 are provided next to each variable. An *asterisk* appears next to the most parsimonious model based on χ^2 tests

either invertebrate abundance or invertebrate richness to both protozoan richness and abundance. Finally, we tested a reduced model, removing all paths linking the two trophic levels. Thus, the final model (Fig. 2b) included only those paths that are important in linking trophic levels, given our results concerning important paths obtained through testing the MIH within trophic levels.

Results

Principal component analysis

The first principal component (PC1) explained 63% of the variance in MR and detritus values among tree holes. Both variables displayed positive loadings (+79) on PC1, suggesting they were positively correlated ($r = 0.24$), with tree holes with high positive scores on this axis having high MR and high amounts of detritus.

Richness and productivity

When all taxa were considered, richness increased linearly with PC1, volume, and latitude (Table 1; Fig. 3a), although productivity (P = PC1) explained the most variance (Table 1). When the invertebrate trophic level was considered alone, P, volume, and latitude were all associated with richness, with P accounting for the majority of variation explained among variables tested (Table 1; Fig. 3b). No parameters were significantly associated with protozoan richness (Fig. 3b). In no case was the quadratic term significant, indicating that, where appropriate, a linear model best described the relationship between variables.

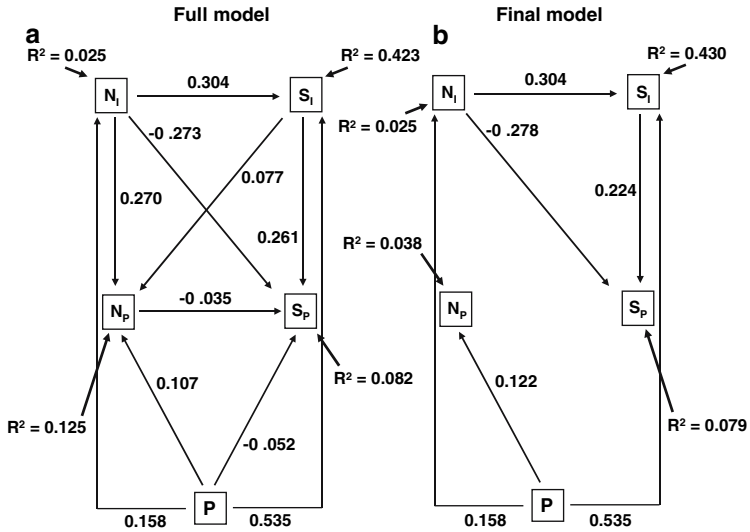

Fig. 2 Path diagrams testing importance of links between trophic levels in **a** the full model and **b** the final model. **a** Full model: direct effects of productivity surrogate (P) and abundance (N) on richness (S) in each trophic level; indirect effects of productivity on richness through abundance; effects of invertebrate abundance (N_I) and richness (S_I) on protozoan abundance (N_P) and richness (S_P). **b** Final model: removal of paths consistent with results from testing the More Individuals hypothesis and paths that did not change the fit of the model from N_I and S_I to N_P and S_P. Standardized path coefficients next to each line indicate the direction and magnitude of effects of one variable on another. Values for R^2 are provided next to each variable

Table 1 Results of stepwise multiple regression for the relationship assessing the degree to which productivity (P, as defined by PC1), volume (milliliters), and latitude (degrees) affect richness of tree hole organisms. The order of each parameter reflects entry into the model. All taxa represents the combined richness of invertebrates and protozoans

Dependent variable	Parameter	R^2	*P* value	Model
All taxa	P	0.175	<0.001	$Y = 0.937\ x\ \text{PC1} + 0.001 \times \text{volume} - 0.870 \times \text{latitude} + 16.617$
	Volume	0.038	0.047	
	Latitude	0.035	0.053	
Invertebrates	P	0.340	<0.001	$Y = 1.001 \times \text{PC1} + 0.001 \times \text{volume} - 0.295 \times \text{latitude} + 29.290$
	Volume	0.059	0.005	
	Latitude	0.032	0.034	
Protozoans	None	–	–	–

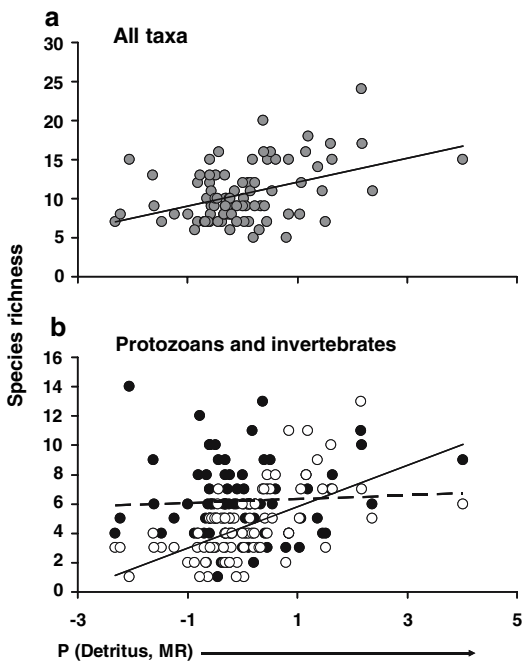

Fig. 3 Linear regressions between species richness and productivity for **a** patterns for all taxa combined (*filled gray circles*), **b** protozoans only (*filled circles*), and invertebrates only (*open circles*). Productivity (P) is defined by principal component 1 (detritus amount and metabolic rates of microorganisms, MR). Regression lines are significant (see Table 1) except the *dashed line* in **b** for protozoans

Path analyses

The full path model for invertebrates explained 3% of the variation in abundance but 43% of the variation in richness (Fig. 1a). There were strong positive effects of P on richness, but weaker positive effects for abundance on richness and for P on abundance (Fig. 1a). The first (Fig. 1c) and second (Fig. 1e) reduced models produced significant lack of fit (reduced model 1, $\chi^2 = 32.21$, $df = 1$, $P < 0.001$; reduced model 2, $\chi^2 = 12.59$, $df = 1$, $P < 0.001$), indicating that neither was as satisfactory an explanation of the relationships among variables as the full model was. For protozoans, the full model (Fig. 1b) explained 4% of the variation in abundance and much less variation for richness. The first reduced model (Fig. 1d) did not fit significantly worse than the full model ($\chi^2 = 0.37$, $df = 1$, $P = 0.546$), and there was no change in the path coefficient between abundance and richness, and only a minor decrease in the explained variation for richness. The second reduced model (Fig. 1f) also did not fit significantly worse than the full model ($\chi^2 = 0.55$, $df = 1$, $P = 0.460$), although there was a decrease in the path coefficient linking productivity to richness. Thus, either reduced model was as good an explanation for the relationships among protozoan richness, abundance, and productivity as the saturated full model was, though all fit poorly. Although all three models fit equally well, the path coefficient from abundance to protozoan richness was negative or absent in all models (Fig. 1b, d). Path analyses for each region were consistent with the overall models (not shown). Specifically, the full model displayed the best fit for invertebrates in the south and north, and reduced model 1 gave the best fit for the central region. For protozoans, reduced model 1 or 2 was better than the full model in the south or north, whereas model 1 was the best explanation among variables in the central region.

For the trophic link models (Fig. 2a), the full model explained a low amount of variation for protozoan richness ($R^2 = 0.082$) and invertebrate abundance ($R^2 = 0.025$), moderate variation for protozoan abundance ($R^2 = 0.125$), and the highest variation for invertebrate richness ($R^2 = 0.423$). Consistent with the results for testing the MIH for each trophic level separately, we removed the paths from productivity surrogates to protozoan richness (see Fig. 1d) and from protozoan abundance to richness (see Fig. 1f), but retained these paths for invertebrates (Fig. 1a). Regardless of how we removed the paths from invertebrate abundance and richness to either variable for protozoans, we obtained the same results (Fig. 2b). Specifically, removing direct paths from invertebrate richness to protozoan abundance ($\chi^2 = 8.470$, $df = 4$, $P = 0.080$) or invertebrate abundance to protozoan abundance ($\chi^2 = 6.115$, $df = 3$,

$P = 0.106$) did not significantly alter the fit, although both tests were nearly significant. In contrast, removing direct paths from invertebrate abundance to protozoan richness ($\chi^2 = 12.037$, $df = 4$, $P = 0.017$) and invertebrate richness to protozoan richness ($\chi^2 = 12.375$, $df = 5$, $P = 0.030$) resulted in significant decrease in fit. The final model suggested that invertebrate abundance negatively affected protozoan richness, whereas invertebrate richness had a positive effect on protozoan richness (Fig. 2b).

Discussion

Our survey of tree holes yielded four major conclusions: (1) productivity–richness relationships for the two trophic levels differed from one another and from relationships for all taxa combined; (2) the effect of latitude on richness, though present, was small compared to that of productivity; (3) predictions of the More Individuals hypothesis (MIH) are consistent with the observed productivity–richness relationship of invertebrates, but not that of protozoa, and (4) trophic links, specifically top-down effects of invertebrate abundance, have important effects on richness of the protozoan trophic level. Although some of these conclusions have previously been reached (e.g., Kneitel and Miller 2002), ours is the first study to examine how richness within trophic levels, trophic links, and abundance interact to produce patterns of productivity and richness in nature.

Trophic levels responded differently to productivity, consistent with the food web patterns based on biomass proposed by Oksanen et al. (1981) and Fretwell (1977). Consumer richness increased with productivity, whereas protozoan richness was unrelated to productivity, suggesting consumer control of richness within individual tree holes. Our results are consistent with those of Kneitel and Miller (2002), who found that in pitcher plant communities, richness of a higher trophic level (protozoans) was positively affected by initial resources (dead ants), but richness of a lower trophic level (bacteria) was unrelated to similar increases in resources. Biomass of protozoa in the water column is negatively affected by the presence of filter-feeding mosquito larvae (Kneitel and Chase 2004; Kaufman et al. 2002; Eisenberg et al. 2000; Cochran-Stafira and von Ende 1998; Paradise and Dunson 1998). Moreover, protozoan community composition (Kneitel and Chase 2004) varies with the intensity of predation by mosquito larvae. Although filter-feeding taxa such as mosquitoes are likely to have direct effects on free-swimming protozoans (e.g., *Paramecium*, *Bodo*), other invertebrates that ingest or shred detritus (e.g., syrphids, psychodids) also may directly or indirectly affect attached protozoans (e.g., *Vorticella*) and attached rotifers.

An increase in consumer richness with increasing productivity is consistent with the results of other tree hole studies (Jenkins et al. 1992; Srivastava and Lawton 1998; Yee and Juliano 2007), although ours is the first study to measure ambient productivity in unmanipulated containers. Our path analysis results are consistent with the MIH because the indirect path from productivity to richness through abundance could not be omitted. Positive relationships between richness and productivity in the consumer trophic level may arise because productivity lowers the extinction risk of rare taxa (MIH), although this hypothesis has found mixed support from studies of aquatic container systems (Kneitel and Miller 2002; Srivastava and Lawton 1998; Yee and Juliano 2007). Based on the magnitudes of the path coefficients (Fig. 1a), it appears that the MIH, quantified as the products of the two path coefficients that form the connection between productivity and richness, makes a lesser contribution to productivity–richness relationships than does the direct effect of productivity on richness, quantified by the direct path coefficient. Total abundance of tree hole invertebrates was unrelated to all measures of productivity, although invertebrate abundance did increase with the volume of the container ($R^2 = 0.15$, $P = 0.002$). Thus, richness of tree hole invertebrates does not simply increase in proportion to increases in numbers of individuals but may be related to other factors that are unique to this system (e.g., behavioral decisions of ovipositing adults, disturbances, species interactions, Srivastava and Lawton 1998) as well as to variation in productivity. In addition, the short life cycles of tree hole invertebrates may make extinction risk less important than these other factors. The small proportion of variation in this trophic level explained by our model suggests that these other factors could be important in explaining variation in community and population patterns in natural tree holes. In contrast to results for invertebrates, we found no support for the MIH for protozoans, because effects of protozoan abundance on richness were absent or negative. For protozoans, top-down control appears to be more important than links among productivity, abundance, and richness within the protozoan trophic level. The potential for increased abundance of rare protozoan taxa with increasing productivity may be diminished by invertebrate consumers.

Analysis of trophic linkage indicated that invertebrates exert top-down control of protozoans. Invertebrate abundance had negative effects on protozoan richness, likely due to direct reduction of predator-susceptible protozoans, as shown in previous work (e.g., Kneitel and Chase 2004). Even though there was no direct effect on protozoan abundance, invertebrates may induce changes in abundance or foraging behavior of certain predaceous protozoans that selectively feed on certain protozoan groups. Unlike invertebrate abundance, invertebrate richness was positively related to protozoan richness. This could result from the addition of predaceous invertebrates that exhibit top-down

control on invertebrates who, in turn, feed on protozoans (i.e., trophic cascade, Carpenter and Kitchell 1993). This was unlikely in our study, as the only top predator of invertebrates, the mosquito *Toxorhynchites rutilus*, was encountered in only the southern region, and we could detect no quantitative effects of its presence on the observed communities of invertebrates (i.e., non-significant regressions of invertebrate abundance or richness on *T. rutilus* at sites where it occurred). Alternatively, the addition of certain types of invertebrate grazers may have benefited certain protozoan groups by enhancing detritus breakdown (Lopez et al. 1977; Smith et al. 1982; Kneitel and Chase 2004). Taken together, it appears that multiple direct and indirect interactions between invertebrates and protozoans may contribute to observed cross-trophic level effects structuring richness–productivity relationships within tree holes.

In tree holes, energy is derived from inputs of detritus rather than from intrinsic primary productivity, a situation that is typical of many communities (Moore et al. 2004). Because detritus inputs into tree holes take a variety of forms, a single metric for productivity is unlikely to quantify energy flow as thoroughly as does primary productivity in systems driven by photosynthesis. Yee and Juliano (2007) have shown that, even when other potential surrogates of productivity are measured in container systems (e.g., production of new bacterial biomass, conductivity), metabolic rates of microorganisms and detritus amount are significantly related to richness and abundance of tree hole invertebrates. As our study was designed to describe relationships of productivity and richness, we cannot determine the mechanisms by which productivity affects different species, although aquatic microorganisms appear to be limited by availability of carbon, nitrogen, and phosphorous (Wetzel 1995; Pace and Cole 1996; Sterner and Elser 2002), and some of these nutrients are correlated with primary productivity in other aquatic systems (Leibold 1999; Chase and Ryberg 2004). For tree holes, carbon is thought to be the primary limiting nutrient (Kaufman et al. 2002), as most carbon in these systems is in a refractory form (e.g., tannins, cellulose, and lignins). Future studies investigating the effects of productivity in detritus-based aquatic systems should make use of multiple measures of productivity, which may act in concert to affect richness and have different effects on separate trophic levels.

The single-trophic-level perspective dominates investigations of richness and ecosystem function relationships (Petchey et al. 2004), even though there is considerable evidence that interactions among trophic levels can have important implications for diversity (Oksanen et al. 1981; Hairston and Hairston 1993; Huston 1996). Richness was positively associated with productivity for all taxa combined and for invertebrates, whereas, for protozoans, richness was unrelated to any measure of productivity. Richness–productivity relationships for invertebrates seem to drive the patterns for all taxa, despite the fact that invertebrates constitute a much smaller portion of overall species richness than do protozoans (see Fig. 3). Thus, it appears that the lumping of different trophic groups may obscure the variety of responses of richness to productivity that occurs within groups, and this hidden heterogeneity may affect the interpretation of community patterns.

Theory on how productivity should affect richness within and among trophic levels is in its infancy compared to theory for how productivity affects total trophic level biomass or abundance of individuals. Our demonstration that there are relationships between abundance and richness of consumers and those of prey provides a start toward developing a body of theory on this topic. As trophic dynamics are a key component of our understanding of community processes (Hairston and Hairston 1993), development of theory to predict how different trophic levels respond to productivity may be important for our understanding of determinants of biodiversity.

Acknowledgments We thank L. Kling, S. Hohm, C. Villanueva, J. Rackauskas, H. Les, and B. Kesavaraju, for assistance in the field and in the laboratory, and the Illinois Department of Natural Resources, the ParkLands Foundation, the Morton Arboretum, and the Fermi National Accelerator Laboratory for allowing us access to their properties to sample tree holes. This research was conducted by S. H. Yee independent of US E.P.A. employment, and the conclusions are solely those of the authors and not necessarily of the Agency. This project benefited from our conversations with J. Chase, M. Willig, and M. Kaufman, and the comments of two anonymous reviewers, and was supported by grants to D. A. Yee from the ISU Department of Biological Sciences and the Phi Sigma Biological Society, and to S. A. Juliano and D.A. Yee from the National Institute of Allergy and Infectious Disease (R15 AI−051374).

References

Abrams PA (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019–2027

Bradshaw WE, Holzapfel CM (1985) The distribution and abundance of tree holes mosquitoes in eastern North America: perspectives from Florida. In: Lounibos LP, Rey JR, Frank JH (eds) Ecology of mosquitoes: proceedings of a workshop. Florida Medical Entomology Laboratory, Vero Beach, pp 3–23

Carpenter SR (1983) Resource limitation of larval treehole mosquitoes subsisting on beech detritus. Ecology 64:219–223

Carpenter SR, Kitchell JF (1993) The trophic cascade in lakes. Cambridge University Press, Cambridge

Chase JM, Ryberg WA (2004) Connectivity, scale-dependence, and the productivity–diversity relationship. Ecol Lett 7:676–683

Cochran-Stafira DL, von Ende CN (1998) Integrating bacteria into food webs: studies with *Sarracenia purpurea* inquilines. Ecology 79:880–898

Daugherty MP, Juliano SA (2001) Factors affecting the abundance of scirtid beetles in container habitats. J North Am Benthol Soc 20:109–17

Daugherty MP, Alto BM, Juliano SA (2000) Invertebrate carcasses as a resource for competing *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). J Med Entomol 37:364–372

Dodson SI, Arnott SE, Cottingham KL (2000) The relationship in lake communities between primary productivityand species richness. Ecology 81:2662–2679

Dyer LA, Letourneau D (2003) Top-down and bottom-up diversity cascades in detrital vs living food webs. Ecol Lett 6:60–68

Eisenberg JNS, Washburn JO, Schreiber SJ (2000) Generalist feeding behaviors of *Aedes sierrensis* larvae and their effects on protozoan populations. Ecology 81:921–935

Foissner W, Berger H (1996) A user-friendly guide to the ciliates (Protozoa, Ciliophora) commonly used by hydrobiologists as bioindicators in rivers, lakes, and waste waters, with notes on their ecology. Fresh Biol 35:375–482

Fretwell SD (1977) The regulation of plant communities by food chains exploiting them. Perspect Biol Med 20:169–185

Hairston NGJ, Hairston NGS (1993) Cause-effect relationships in energy flow, trophic structure and interspecific interactions. Am Nat 142:379–411

Hatcher L (1994) A step-by-step approach to using the SAS system for factor analysis and structural equation modeling. SAS Institute Inc.,

Hatcher L, Stepanski HE (1994) A step by step approach to using SAS system for univariate and multivariate analyses. SAS Institute Inc., Cary

Huston MA (1996) Biological diversity. The coexistence of species on changing landscapes. Cambridge University Press, Cambridge

Jenkins B, Kitching RL, Pimm SL (1992) Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. Oikos 65:249–255

Kaufman MG, Goodfriend W, Kohler-Garrigan A, Walker ED, Klug MJ (2002) Soluble nutrient effects on microbial communities and mosquito production in *Ochlerotatus triseriatus* habitats. Aqu Microb Ecol 29:73–88

Kitching RL (2000) Food webs and container habitats. The natural history and ecology of phytotelmata. Cambridge University Press, Cambridge

Kitching RL (2001) Food webs in phytotelmata: "bottom-up" and "top-down" explanations for community structure. Ann Rev Entomol 46:729–760

Kneitel JM, Chase JM (2004) Disturbance, predator, and resource interactions alter container community composition. Ecology 85:2088–2093

Kneitel JM, Miller TE (2002) Resource and top-predator regulation in the pitcher plant *Sarracenia purpurea* inquiline community. Ecology 83:680–688

Leibold MA (1999) Biodiversity and nutrient enrichment in pond plankton communities. Evol Ecol Res 1:73–95

Leibold MA, Chase JM, Shurin JB, Downing AL (1997) Species turnover and the regulation of trophic structure. Ann Rev Ecol Syst 28:467–494

Lindeman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399–418

Lopez GR, Levinton JS, Slobodkin LB (1977) The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. Oecologia 30:111–127

Mitchell RJ (2001) Path analysis: pollination. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, 2nd edn. Oxford University Press, Oxford, pp 217–234

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82:2381–2396

Moen J, Collins SL (1996) Trophic interactions and plant species richness along a productivity gradient. Oikos 76:603–607

Moore JC, Berlow EL, Coleman DC, Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. Ecol Lett 7:584–600

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems along gradients of primary productivity. Am Nat 118:240–261

O'Neill RV, Reichle DA (1980) Dimensions of ecosystem theory. In: Waring RH (ed) Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis, pp 11–26

Pace ML, Cole JJ (1996) Regulation of bacteria by resources and predation tested in whole-lake experiments. Limnol Ocean 41:1448–1460

Paradise CJ, Dunson WA (1998) Effects of sodium concentration on *Aedes triseriatus* (Diptera: Culicidae) and microorganisms in treeholes. J Med Entomol 35:839–844

Pennak RW (1989) Fresh-water invertebrates of the United States: protozoa to mollusca. Wiley, New York

Petchey OL, Downing AL, Mittelbach GG, Persson L, Steiner CF, Warren PH, Woodward G (2004) Species loss and the structure and functioning of multitrophic aquatic systems. Oikos 104:467–478

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

SAS Institute (2004) SAS/STAT 9.1 User's guide. SAS Institute Inc., Cary

Schmid B (2002) The species richness–productivity controversy. Trends Ecol Evol 17:113–114

Smith GA, Nickels JS, Davis WM, Martz RF, Findley RH, White DC (1982) Perturbations in the biomass metabolic activity and community structure of the estuarine detrital microbiota: resource partitioning in amphipod grazing. J Exp Mar Biol Ecol 64:125–143

Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. Am Nat 152:510–529

Sterner RW, Elser JJ (2002) Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton

Waide RB, Willig MR, Steiner CF, Mittelbach GG, Gough L, Dodson SI, Juday P, Parmenter R (1999) The relationship between productivity and species diversity. Ann Rev Eco Syst 30:257–300

Walker ED, Merritt RW (1998) The significance of leaf detritus to mosquito (Diptera: Culicidae) productivity from treeholes. Environ Entomol 17:199–206

Walker ED, Kaufman MG, Ayres MP, Riede MH, Merritt RW (1997) Effects of variation in quality of leaf detritus on growth of the eastern tree-hole mosquito, *Aedes triseriatus* (Diptera: Culicidae). Can J Zool 75:706–718

Wetzel RG (1995) Death, detritus and energy flow in aquatic ecosystems. Fresh Biol 33:83–89

Wootton JT (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151–165

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–851

Wright S (1921) Correlation and causation. J Agric Res 20:557–585

Wright S (1934) The method of path coefficients. Ann Math Stat 5:161–215

Yee DA (2006) Effects of species interactions and productivity on aquatic macroinvertebrate diversity and community composition in tree holes: patterns and mechanisms. PhD dissertation, Illinois State University, Illinois

Yee DA, Juliano SA (2006) Consequences of detritus type in an aquatic microsystems: assessing water quality, micro-organisms, and the performance of the dominant consumer. Fresh Biol 51: 448–459

Yee DA, Juliano SA (2007) Abundance matters. A field experiment testing the more individuals hypothesis for richness–productivity relationships. Oecologia 153: 153–162

Yee DA, Kaufman MG, Juliano SA (2007) The significance of ratios of detritus types and microorganism productivity to competitive interactions between aquatic insect detritivores. J Anim Ecol 76. doi:10.1111/j.1365-2656.2007.01297.x