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RELATIVE STRENGTH OF TOP-DOWN, BOTTOM-UP, AND CONSUMER SPECIES RICHNESS EFFECTS ON POND ECOSYSTEMS

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Abstract. Theory and experiments demonstrate that the number of species in a local area can determine rates of ecosystem processes, but we know little about how the strength of that control compares with other influences or how it might vary across ecological gradients. Here I report results of a pond mesocosm experiment where consumer (snail) species richness, predation intensity, and nutrient availability were crossed in a full-factorial design. This design allowed a direct comparison of the strength of the different factors on food web properties and ecosystem functioning (i.e., system-level fluxes of energy or matter), and an evaluation of how the factors may interact.

Systems with higher snail species richness had greater secondary production, consumer biomass, ecosystem respiration, and macrophyte stem growth, and lower epiphyton and periphyton biomass. However, snail species richness effects on periphyton and epiphyton were context dependent; predators reduced the effect of increasing snail richness on the biomass of attached algae. Species richness effects were most often the result of a biological mechanism (e.g., differential resource use), rather than being solely artifacts of the experimental design (e.g., sampling effects). The effects of nutrient enrichment and predation were mostly predictable from simple food chain models; increases in nutrient availability led to increased algal biomass, primary production, and snail biomass, while predators decreased snail biomass and indirectly augmented algae.

Snail species richness effects on the biomass of many functional groups were as strong or stronger than those of a substantial nutrient enrichment or of the addition of a voracious predator (*Belostoma flumineum*). Nutrient enrichment had the most pronounced effects on several system-level processes (e.g., primary production, sedimentation). Species richness had weaker effects on ecosystem properties than on particular functional groups, probably because of compensatory responses among different producer functional groups. In summary, this experiment suggests that the number of consumer species in a system can have large and meaningful effects on the distribution of biomass in a food web, and that these effects can depend on ecological context.

Key words: Belostoma flumineum; *bottom-up; consumer; context dependent; ecosystem function; effect size;* Fossaria obrussa; *gastropods;* Helisoma trivolvis; Physa gyrina; *species richness; top-down.*

INTRODUCTION

The effect of species richness on the functioning of ecosystems has been the focus of much ecological research (Loreau et al. 2001). Empirical evidence is equivocal (Schalpfer and Schmid 1999, Tilman 1999), and has sparked an intense debate over the interpretation of diversity-ecosystem function experiments (Huston 1997, Wardle 1999, Petchey 2003). While some ecosystem processes do appear sensitive to the number of species present (Tilman et al. 2001, Downing and Leibold 2002), many important questions have only begun to be addressed empirically. For instance, how do species richness effects on ecosystem function compare in strength to other effects (e.g., keystone species, trophic effects) and what system properties (e.g., food web structure, underlying productivity) mediate richness effects on ecosystems?

The first question goes to the heart of many ecologists' concerns about the importance of species-richness–ecosystem-function experiments. The magnitude of a statistically significant effect of richness on ecosystem function in a tightly controlled and well-replicated experiment is hard to interpret in isolation of other important factors. In contrast, if the magnitude of richness effects could be compared directly to that of factors known to frequently regulate community structure, then meaningful inferences could be drawn about how important richness effects could be in natural systems. Only the magnitudes of compositional effects (e.g., Hooper and Vitousek 1997, Downing and Leibold 2002) and resource availability (terrestrial plants [Fridley 2002], stream fungi [Bärlocher and

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Corkum 2003]) have been compared to those of diversity, and in most cases diversity effects were relatively weak. A wider set of comparisons (more factors and more systems) is needed to evaluate the importance of richness effects relative to other factors ecologists routinely consider.

How other biotic and abiotic factors strengthen or weaken diversity effects on ecosystem function is of theoretical interest for ecologists, but also is important to appropriately interpret diversity–ecosystem-function experiments performed to date. We do not yet know, for instance, whether the particular experimental conditions used in a study provide a liberal or conservative test of diversity effects on ecosystem function (Fridley 2001). By examining diversity–function relationships in a number of ecological contexts, we may begin to learn what factors mediate those relationships. The first diversity–function studies to examine context dependency have explored resource availability (Jonsson et al. 2001, Fridley 2002), the presence of mutualists (Klironomos et al. 2000), and disturbance (Cardinale et al. 2000, 2002), and in each case there was a particular condition that enhanced the strength of diversity effects. All species face threats from predators, pathogens, and/or parasites, and all species must acquire resources to grow and reproduce. Therefore, predation intensity and resource availability may provide general gradients on which to focus study of context-dependent species richness effects on ecosystem function.

Prey respond in many ways to predation (see Lima 1998 for review), but very often reduce their activity, invest in defensive structures or chemicals, modify their life-history or restrict their use of habitat. By employing antipredator defenses, prey often sacrifice some ability to acquire resources (Sih 1980, Gilliam 1982, Werner and Gilliam 1984). High-predation environments will generally be dominated by predator-resistant taxa, and these taxa are expected to be less effective in their resource use (Leibold 1989). Predation is therefore predicted to reduce functional diversity among prey species, and species diversity effects on ecosystems that depend on functional uniqueness (e.g., differential resource use) may be less likely or less intense when predation is strong.

The availability of resources (Jeffries 1990), an organism's energetic state (Kohler and McPeek 1989, Sih 1992), or the intensity of competition (Pettersson and Brønmark 1993) can influence prey's response to the risk of predation. Thus, species effects on ecosystems should be influenced by both predation and resource availability. For instance, prey are often willing to accept more risk when resources are scarce (Anholt and Werner 1995), and one might predict that functional diversity should not be as sensitive to predation under low-resource conditions, because prey may not respond to predation risk as strongly. Resource abundance could also mediate species effects on ecosystems if resource heterogeneity increases with resource abundance. For most parameters variance does increase with the mean, and patchy distributions of resources can provide an axis for niche differentiation (Chase et al. 2001).

Here, I investigate consumer species richness and composition effects on ecosystem functioning and food web properties in a replicated mesocosm experiment with pond snails, their invertebrate predators, aquatic plants, and algae. The experiment was performed in four distinct ecological contexts to examine how underlying system productivity and predators influence the effects of consumer species richness on system properties. This design allows both a consideration of the context-dependency of richness effects on whole systems, and a comparison of effect strength between diversity effects and two factors that frequently structure aquatic communities, top-down (predation) and bottom-up (resource availability) forces.

Methods

The experimental design consisted of a snail species richness and composition manipulation replicated in four ecological contexts, defined by the four possibilities of a 2×2 factorial crossing nutrient enrichment and predator presence/absence. Each combination of snail richness/composition, nutrient status, and predator presence was replicated four times, with the exception of the most species-rich treatments which were replicated six times. The purpose of this unbalanced design was to partially alleviate the difference in sample size for species richness main effects (which average over several levels of composition at low species richness and only one level of composition at the highest richness level).

Setup

The experiment was established in 120 aquatic mesocosms (outdoor ''cattle tanks'') at the W. K. Kellogg Biological Station Experimental Pond Facility, each filled with 275 L of filtered well water (conductivity, ~300 μS; pH, ~9.6; total nitrogen (TN), ~96 μg/L; total phosphorus (TP), ~17 μg/L) on 20 May 2002. Phosphorus and nitrogen were added to all tanks in the form of KH_2PO_4 and NH_4NO_3, respectively; ''low-nutrient'' tanks were raised to two times ambient nutrient concentrations, while ''high-nutrient'' tanks were raised to eight times ambient concentrations. These nutrient levels are nominally high, but are reasonable because all of the production in the tanks would stem from the dissolved nutrients (there were no nutrients stored in organic sediments as in a natural pond). Moreover, small forested ponds in Michigan routinely have water column concentrations of TN $>$ 1750 μg/L and TP $>$ 250 μg/L (P. Geddes, *personal communication*). Sand was added to each tank as substrate. Fiberglass screen lids covered each tank to limit entry/exit of organisms.

Organisms

A diverse algal inoculum collected from 10 local ponds was introduced into each tank soon after they were filled. Vascular macrophytes (*Potamogeton illinoensis*) were added to each tank on 9 Jun at 4.09 g/m^2 dry mass. Zooplankton, fungi, bacteria, and some insects (mainly odonates and notonectids) colonized the tanks through the introduction of algae and macrophytes.

Three snail species, *Physa gyrina*, *Fossaria obrussa*, and *Helisoma trivolvis* (hereafter referred to by generic names), comprised the grazer species assemblage. All are common snails that co-occur in shallow ponds and lakes in Michigan, and were selected for use because of their ubiquity (these species account for >82% of snail biomass in small Michigan ponds on average [n = 16 ponds]; Wojdak 2004). Chase et al. (2001) have described the different foraging modes employed by these snail taxa; *Helisoma* finds resources patches slowly but efficiently removes most of the available resource (''digger''), while *Physa* finds new patches quickly but removes less of the algae in a patch before moving on (''grazer''). *Fossaria* was not studied by Chase et al. (2001), but is likely intermediate in both traits as were two members of its taxonomic family (*Pseudosuccinea columella* and *Lymnaea elodes*; Family Lymnaeidae).

Snail species richness and composition were manipulated by stocking tanks with every possible combination of one, two, and three species, resulting in seven snail treatments. In a field survey of 16 southern Michigan ponds, snail species richness averaged 2.25 (mode = 3), and ranged from 0 to 4 (Wojdak 2004). Thus, a manipulation of snail species richness including three species treatments covers a majority of the natural range in richness, and is ideal for understanding the consequences of species loss from communities of this type. Snails were stocked on 19–20 June at 275 mg dry animal (without shell) mass per tank, with that mass divided equally by the number of species present (i.e., monoculture tanks had 275 mg of snail biomass, two species tanks had 137.5 mg of each species, etc.). The snail biomass used in this experiment was within the natural range of snail biomass found in local ponds (n = 16, mean mass per volume (275 L) equal to one tank = 310 mg, SE = 105 mg, range = 0–1340 mg [Wojdak 2004]). This starting biomass was appropriate for the mesocosms given their inherent productivity, as the average final live biomass of snails per tank (271.4 mg) was nearly identical to the starting biomass despite much growth, death, and reproduction. Because of differences in average body size between species, starting with equal biomass across treatments necessitated differences in the number of individuals of each species used (i.e., monocultures contained 64 *Fossaria*, 64 *Physa*, or 16 *Helisoma*).

One adult waterbug (Hemiptera: *Belostoma flumineum*) was added to each of 60 randomly chosen predator tanks. *Belostoma* are efficient snail predators, able to consume up to six adult snails per day in lab settings (Crowl and Alexander 1990), and 0.5 snails/day in the field (Kesler and Munns 1989). All snails were susceptible to *Belostoma* except for the largest *Helisoma*, which can reach a size refuge (>10 mm shell length) where they are essentially invulnerable (Chase 1999). In laboratory experiments, *Belostoma* displayed a hierarchy of prey preference; *Physa* was the most preferred prey species used here, followed by *Helisoma*, while *Fossaria* was least preferred (Wojdak 2004). Several *Belostoma* died during the experiment and were replaced within 24 h.

Response variables

Some variables were measured more than once during the experiment to ensure adequate estimation, not because temporal dynamics were of primary interest. Multiple measurements for a single response were averaged over time for all subsequent analyses.

Snail biomass

At the end of the experiment each tank's contents were sieved (1-mm mesh), and snails were preserved in 70% ethanol. All snails were counted and the shell length of the first ~100 live and ~100 dead individuals encountered for each species from each tank was measured. Length measurements were converted to dry mass using species-specific length–weight regressions derived locally, and an average snail mass was calculated. Snail production was calculated as the biomass of all live and dead snails minus the initial biomass of snails, while standing snail biomass reflects only snails alive at the end of the experiment.

Primary producers

Periphyton (algae attached to surfaces) biomass was estimated on 8 July, 2 August, and 29 August. A section of plastic tape (3.63 cm^2), which had been adhered to the tank wall at the start of the experiment, was removed on each sampling date. These pieces were placed into 95% ethanol to extract chlorophyll *a*, and the chlorophyll concentrations were determined using narrow-band flourometry (Welschmeyer 1994).

Epiphyton (algae attached to macrophytes), metaphyton (mats of floating macroscopic algae), and macrophytes were censused during the first week of August and again at the end of the experiment (31 August–2 September). I assessed epiphyton biomass visually using a six-point scale (i.e., 0 = no visible epiphyton; 1, 2, 3 = most stems are covered; 4, 5 = macrophyte completely covered/significant damage). On 18 August, I calibrated the qualitative scale to actual chlorophyll *a* concentrations by haphazardly removing one 10 cm long stem of macrophyte from each of 24 random tanks, brushing the epiphyton onto a glass fiber filter,

and then determining the chlorophyll *a* concentration as above. The qualitative epiphyton score was strongly and linearly related ($P < 0.0001$, $R^2 = 0.764$) to chlorophyll *a* of the epiphyton, therefore I converted epiphyton scores to chlorophyll *a* concentrations using that regression equation. I estimated metaphyton algal abundance visually as percent cover of the surface. Macrophyte growth was estimated on 2 August by counting the number of new stems emerging from the sediment. Macrophyte biomass was measured at the end of the experiment by weighing the plants after washing off epiphyton and wringing away excess water. Macrophyte wet weights were converted to dry mass using a regression ($R^2 = 0.891$) derived for *Potamogeton illinoensis*. Phytoplankton biomass was measured on 9 August by filtering 100 mL of water from each tank onto a glass fiber filter, then determining chlorophyll *a* concentration as above. Phytoplankton chlorophyll *a* concentrations were very low (averaged 3.6 μg/L), and did not respond to the treatments (ANOVA not shown), therefore phytoplankton is ignored in the remaining analyses.

Whole-system properties

Whole-system primary productivity and respiration rates were measured by determining the diel changes in dissolved oxygen concentrations (Howarth and Michaels 2000). I measured oxygen concentrations in each tank with a YSI Model 600XL-100-m (YSI, Yellow Springs, Ohio, USA) at sunset and sunrise at the beginning of the experiment (13–14 July), and at sunset, sunrise, and the next sunset during the middle (6–7 August) and end of the experiment (28–29 August). Respiration rates were calculated as the decrease in oxygen concentration during the night, adjusted for oxygen exchange with the atmosphere. Primary productivity rates were calculated as the increase in oxygen concentration during the day, plus the amount of oxygen used for daytime respiration (assuming equal respiration during the day and night), and were adjusted for oxygen exchange with the atmosphere. The oxygen exchanged with the atmosphere was calculated as in Howarth and Michaels (2000) and Howarth et al. (1992): flux = $k(C_w - C_a/H)$, where k is an empirically derived parameter that describes the resistance of water to oxygen diffusion, C_w and C_a are the concentrations of oxygen in the water and air respectively, and H is the Henry's law constant. Parameters (k, H) that are sensitive to temperature were adjusted to the average temperature (22.5°C) of the tanks during the observations (following Wanninkhof et al. 1985); k was estimated from published regressions of k vs. wind speed (Howarth and Michaels 2000), assuming wind was negligible because the water's surface was 15 cm below the tank lip and the tanks were covered by window screen lids. The size of the oxygen concentration gradient ($C_w - C_a$) should change through time (i.e., over the course of a night), and ideally one would measure oxygen concentrations many times to calculate accurate flux rates through time. Frequent measurements of dissolved oxygen in each tank were logistically impossible, so instead I followed the methods of Howarth et al. (1992): I averaged the DO concentrations measured at sunset and the following dawn (for respiration calculations) or sunrise and the following sunset (for productivity calculations), and calculated a flux rate based on those average concentrations. The estimated rates of respiration and primary productivity therefore are somewhat coarse and are best interpreted in a relative sense.

I measured the accumulation of sediments during the experiment on 16–18 August by randomly placing a small circular quadrat (314 cm^2) on the bottom of each tank. A large syringe was used to withdraw the sediment within the quadrat, which was then filtered onto a glass fiber filter for ash-free dry mass analysis. Ash-free dry mass was calculated as the difference in mass between a dried (48 h at 50°C) sample and that sample after combustion (1 h at 550°C), and represents the dry mass of organic material in the sample. It is possible that attached algae could be inadvertently included in the sediment samples, but visually the sediment was dominated by snail feces in all tanks.

Statistical methods

Sampling effects (Huston 1997, Aarssen 1997) are positive changes in some response with increasing diversity because of the greater chance of including a particularly influential species in a diverse system compared to a less diverse system. Various methodologies (Loreau 1998, Wardle 1999, Petchey 2003) have been proposed to separate sampling effects from ''real'' diversity mechanisms like differential resource use and facilitation. Here I use the statistics suggested by Loreau (1998). Two important parameters, D_i and D_{max}, are defined:

$$D_i = \frac{O_i - E_i}{E_i}$$

where O_i is the observed yield of species i in mixture and E_i is the expected yield of species i in mixture, and

$$D_{max} = \frac{O_T - \mathrm{MAX}(Mi)}{\mathrm{MAX}(Mi)}$$

where O_T is the observed yield of all species in a mixture and MAX(Mi) is the maximum yield in monoculture of any species.

Thus, D_i is the proportional deviation of species i's yield in polyculture from the yield predicted from its monoculture performance (positive D_i means a species had net positive interactions with the other species, relative to when by itself), and D_{max} is the proportional deviation of the total polyculture yield from the highest yielding monoculture. Loreau (1998) argues that D_{max}

> 0, or $D_i > 0$ for all species, indicates a positive effect of diversity (e.g., niche complementarity or facilitation) beyond any potential sampling effect, and I use those criteria here.

The above definitions, developed for studies of plant diversity and production, can also be used to reveal diversity effects that cause reductions in some process or in the biomass of a functional group. For example, increasing snail richness is expected to increase snail biomass and consequently decrease attached algal biomass (e.g., periphyton, epiphyton), so the snail species that reduced algae the most was the ''dominant,'' and $D_{\max} > 0$ for algae would mean that the three species treatment had less algae than the ''dominant'' species treatment had in monoculture.

ANOVA (GLM procedure) was used to identify treatment effects and interactions for each response variable. Species composition was modeled as a nested factor within species richness because a given composition (e.g., *Helisoma* + *Physa*) was only possible at a single level of richness. Interactions between species composition and nutrient enrichment and predation were not included in the ANOVA models; they were never significant and did not qualitatively affect the significance of other effects if included. Periphyton biomass and sedimentation data were log transformed, and metaphyton cover data were arcsine-square root transformed, to meet the assumptions of normality and homogenous error variances. Subsequently all response variables met ANOVA assumptions (examined with Levene's tests and probability plots of residuals).

In an experiment such as this with many factors, interactions, and response variables, there is a nontrivial possibility that several null hypotheses will be rejected erroneously (i.e., type I errors). One would expect four or five such errors to be committed among the 86 main tests presented here (Appendices A–C); however, 30 of the 86 tests returned a P value less than 0.05, an outcome very unlikely due to chance. Fearing type I errors, one might apply the Bonferroni correction, or Benjamini and Hochberg's (1995) less conservative false discovery rate procedure; a null hypothesis would then only be rejected at $P \leq 0.000581$, or $P \leq 0.009302$, respectively. However, little would be gained as one would be more likely to commit type II errors (Gotelli and Ellison 2004), which in this study would be no less serious. For this reason, and reasons detailed elsewhere (Perneger 1998, Moran 2003, Gotelli and Ellison 2004, Nakagawa 2004), no such adjustments were made. Tukey's HSD multiple comparison tests, which protect against excessive type I error rates, were used to dissect significant species composition effects because the comparisons were repetitious, exploratory, and not founded on a priori hypotheses. All statistics were performed using SYSTAT 8.0 (1998).

Anax dragonflies invaded many tanks (44/120), most likely entering as eggs attached to macrophytes. *Anax* are effective snail predators (J. Wojdak, *personal observation*), and had direct effects on snails and indirect effects on other response variables. Invasion was random with respect to treatment (χ^2 goodness of fit tests for each factor, all $P > 0.19$). *Anax* presence/absence (observed during routine attempts to remove them) was used as a concomitant variable in all ANOVAs to reduce error variance.

Calculating effect sizes in factorial experiments is complicated by the potential for significant interactions to make interpreting main effects problematic (i.e., main effects may be small or zero if a factor has strong positive effects at one level of another factor and strong negative effects at the other level of the other factor). Although methods have been developed to calculate effect sizes for main and interactive effects in simple factorial experiments (2×2 factorial; Gurevitch et al. 2000), it remains unclear how to expand those methods for more complex experimental designs like the one presented here (e.g., three–way factorial with a nested factor).

Thus, in order to assess the relative importance of the three factors for each response variable, I calculated the percent change in the mean induced by manipulating the focal factor, separately at each level of the other factors. I then averaged the absolute values of those percent changes, which results in a statistic that describes the average percent change (ignoring direction) in a response because of changes in the focal factor. Except for taking the absolute value, this index is computationally identical to the ''relative competitive intensity'' index used elsewhere (Paine 1992, Wilson and Tilman 1993, Grace 1995, Goldberg et al. 1999) and is related to the commonly used ''log response ratio'' as LRR = ln(1 − percent change). Goldberg et al. (1999) found these two conceptually similar indices (RCI and LRR) behaved alike, and here I use percent change because it is more easily interpreted.

To use this methodology in a simple 2×2 factorial experiment, one would determine the change in the mean of a response variable induced by manipulating factor A separately at levels 1 and 2 of factor B (e.g., +30% at B1, −20% at B2). Then, one would calculate the average of the absolute values of those means (e.g., 25%). This statistic would be interpreted as the average percent change in the response resulting from changes in factor A across factor B. One would likewise calculate this statistic for factor B, and then could compare their relative importance for the response of interest. Effect sizes of different treatments were not compared statistically because the magnitude of any treatment effect should depend critically on the magnitude of the experimental manipulation. I could not apply a predation manipulation ''equal'' to a species richness manipulation, for example, and therefore there would be little meaning in declaring one factor ''significantly'' more important than another. Interpretation of these effect sizes must be couched in a consideration of the

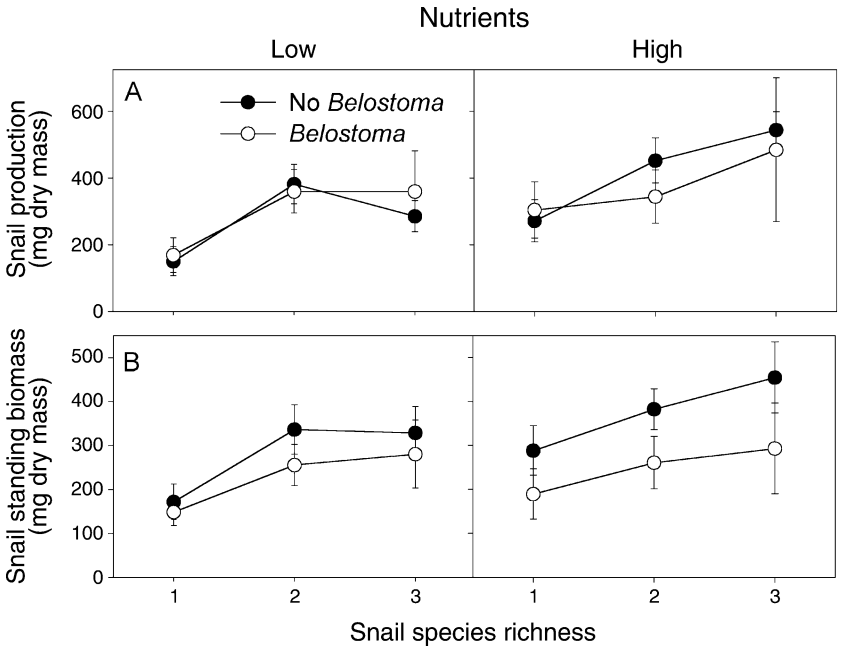

FIG. 1. The response of (A) snail production and (B) snail standing biomass to manipulations of species richness, nutrients, and predation. The left-hand panels are from low-nutrient tanks, and the right-hand panels are from high-nutrient tanks. Solid symbols represent the absence of *Belostoma* predators; open circles represent the presence of *Belostoma*. Values are means ± SE. Statistics are reported in the ANOVA table in Appendix A.

manipulations. Predation and nutrient availability are factors thought to strongly regulate ecological communities of all types across wide ranges of conditions; species richness effects on the same scale as factors we know to be important would suggest species richness may be an important factor determining how communities function.

This methodology does result in the loss of some potentially important information (e.g., direction of responses), but is useful here to summarize the effect of a large number of factors and interactions on a long list of responses, and captures information that is difficult to extract from figures (e.g., relative magnitude of effects). Moreover, the figures presented provide all the information necessary to examine particular interactions and the direction of responses.

RESULTS

Snail biomass

Total snail production was 87% higher on average in tanks with three species than in monocultures (Fig. 1A; Appendix A, species richness, $P = 0.0019$) and the effect of species richness on total snail production was essentially the same in all four ecological contexts (Appendix A, no significant interactions with species richness). ''High'' nutrient tanks had 18% greater total snail production (Fig. 1A; Appendix A, nutrients, $P = 0.0004$) than ''low'' nutrient tanks. Tanks with *Physa* present had less snail production than those without (Fig. 2A; Appendix A, species composition, $P = 0.0053$).

The total production of snails did not depend on *Belostoma* presence (Fig. 1A; Appendix A, *Belostoma*, $P = 0.4839$), but the standing biomass of live snails at the end of the experiment did (Fig. 1B; Appendix A, *Belostoma*, $P = 0.0377$). In contrast, both the total production of snail biomass and standing snail biomass were lower when *Anax* invaded (Appendix A, *Anax*, both $P < 0.0001$). Snail species richness, composition, and nutrient enrichment had qualitatively similar effects on standing snail biomass as they did on production.

The number of snails increased from the original 16–64 individuals added per tank to a mean of 1037 (SE = 75.3) per tank, and total snail biomass at the end of the experiment was nearly identical to that at the beginning. Thus, snail age and size distributions changed from highly skewed towards older, larger adult snails to being dominated by younger, smaller animals, much as it does in natural lakes from spring to summer.

Primary producers

Increases in snail biomass and production should reduce the abundance of snails' primary forage, attached algae. Indeed, the most diverse tanks (which had more snail biomass and production) had 38.3% less periphyton on average than species-poor tanks (Fig. 3A; Appendix B, species richness, $P = 0.0110$), but the effects of snail richness on periphyton depended on the presence of *Belostoma* (Fig. 3A; Appendix B, species richness × predation, $P = 0.0497$). Hence, ecological context mediated the effects of consumer species richness

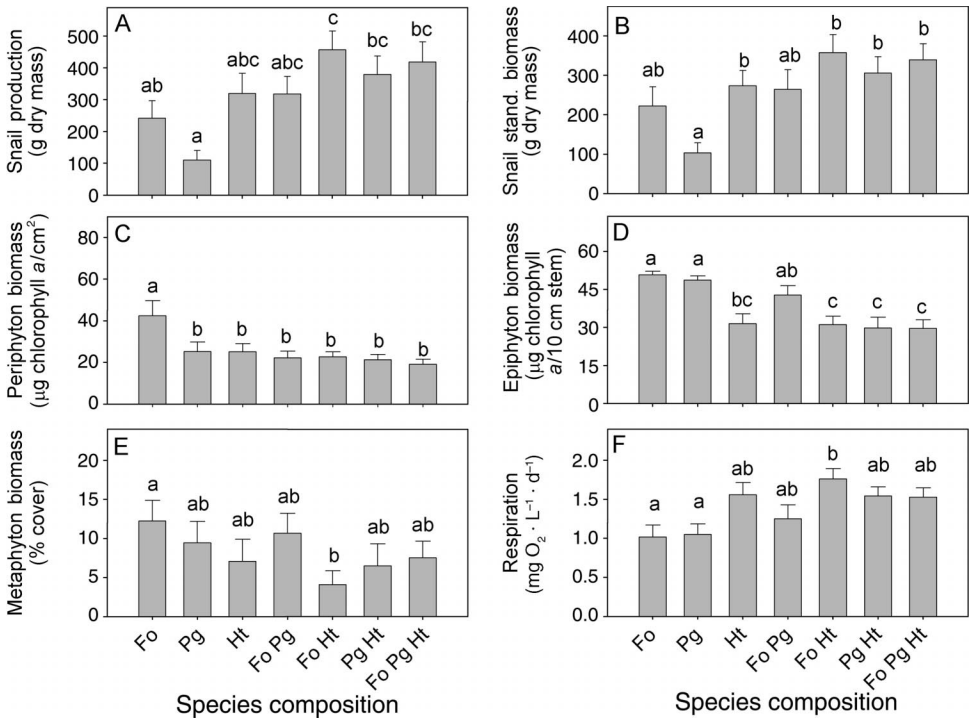

FIG. 2. Species composition effects on (A) snail production, (B) snail standing biomass, (C) periphyton, (D) epiphyton, (E) metaphyton, and (F) ecosystem respiration. Values are means + SE. Abbreviations are: Fo, *Fossaria obrussa*; Pg, *Physa gyrina*; Ht, *Helisoma trivolvis*; Fo Pg, *Fossaria obrussa* + *Physa gyrina*; etc. Statistically significant differences (Tukey's hsd multiple comparisons, $P < 0.05$) are noted with different lowercase letters.

on periphyton. This seemed especially true in low nutrient tanks, but the species richness × predation × nutrient interaction was not statistically significant. Nutrient enrichment enhanced periphyton biomass overall (Fig. 3A; Appendix B, $P = 0.0481$), as expected. The strength of the interactions between snails and the periphyton community depended on which snail species were present (Appendix B, species composition, $P = 0.0204$), with *Fossaria* monocultures interacting particularly weakly and thus having abundant periphyton (Fig. 2C).

Like periphyton, epiphyton biomass was lower in more species-rich mesocosms (Fig. 3B; Appendix B, species richness, $P = 0.0002$); three species tanks had 32.2% less epiphyton than monocultures on average. Epiphyton always decreased with increasing snail species richness, but the shape of that relationship depended on the presence or absence of *Belostoma* (Fig. 3B; Appendix B, species richness × predation, $P = 0.0158$). When *Belostoma* were present, three-species treatments had significantly less epiphyton than one- and two-species treatments, but in the absence of *Belostoma*, treatments with two and three species had less epiphyton than monocultures. Epiphyton biomass was less abundant in treatments with *Helisoma* relative to those without (Fig. 2D; Appendix B, species composition, $P < 0.0001$). Both *Belostoma* and *Anax* predators had indirect positive effects on epiphyton biomass (Fig. 3B; Appendix B, *Belostoma*, $P = 0.014$; *Anax*, $P < 0.0001$). *Belostoma* also had indirect positive effects on the abundance of metaphyton (Fig. 3C; Appendix B, predation, $P = 0.0229$). Treatments with *Helisoma* had less metaphyton than did treatments without (Fig. 2E; Appendix B, species composition, $P = 0.0460$).

Growth of new macrophyte stems was 36% greater in three snail species systems relative to systems with only one species (Fig. 3D; Appendix B, species richness, $P = 0.0287$). *Belostoma* predators had indirect negative effects on macrophyte stem growth (Fig. 3D; Appendix B, predation, $P = 0.0115$). Macrophytes reached a higher final biomass in low nutrient tanks than in high nutrient tanks (Fig. 3E; Appendix B, nutrient enrichment, $P < 0.0001$).

Whole-system properties

Primary producer functional groups responded in a variety of ways to the treatments, but we can also ask what effects the treatments had on whole-system production and respiration. Nutrient enrichment was the only factor to have significant effects on primary production (Fig. 4B; Appendix C, nutrient enrichment, $P < 0.0001$). Nutrient concentrations decreased greatly during the course of the experiment in all tanks (average soluble reactive phosphorus <3 μg/L on 30 July). Tanks with more snail species had greater rates of respiration than species-poor tanks (Fig. 4A; Appendix C,

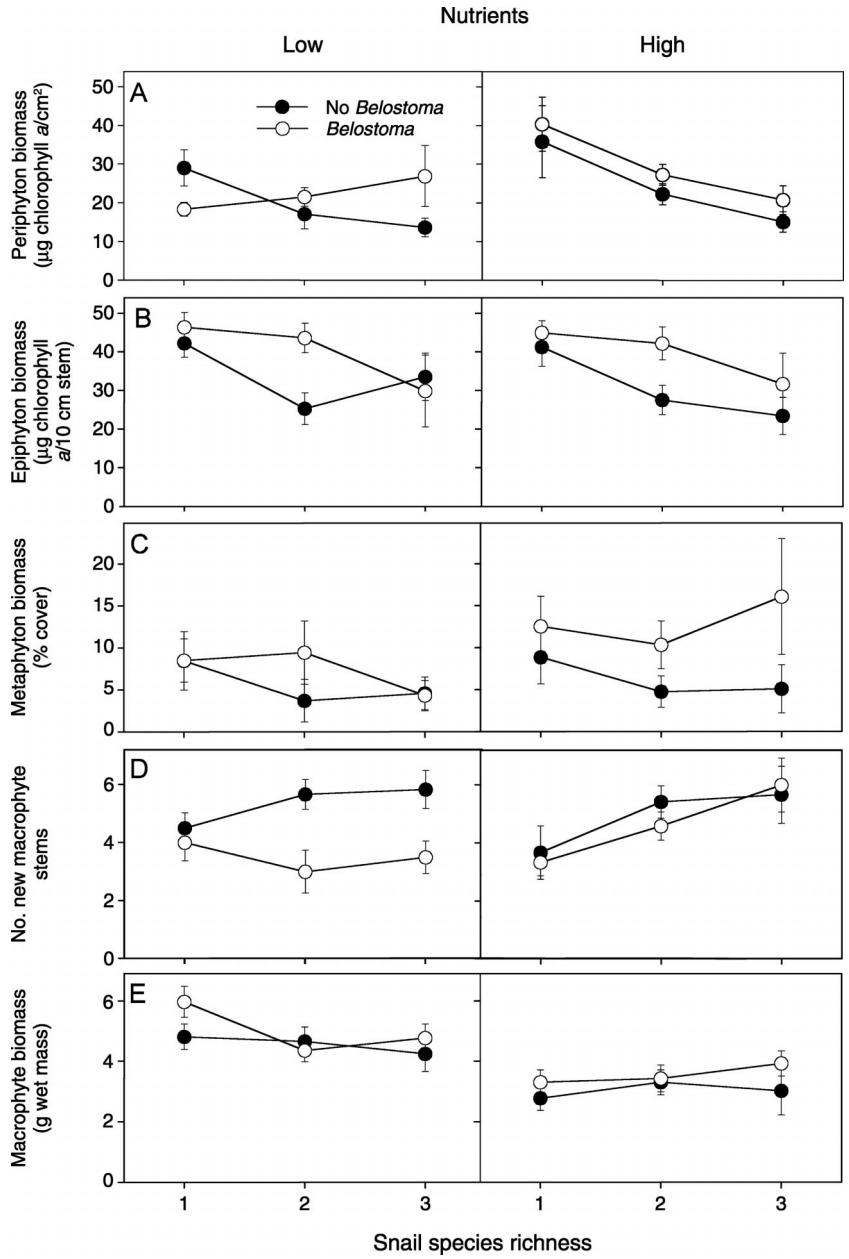

FIG. 3. The response of (A) periphyton, (B) epiphyton, (C) metaphyton, (D) emergence of new macrophyte stems, and (E) macrophyte biomass to manipulations of species richness, nutrients, and predation. The left-hand panels are from low-nutrient tanks, and the right-hand panels are from high-nutrient tanks. Solid circles represent the absence of *Belostoma* predators; open circles represent the presence of *Belostoma*. Values are means ± SE. Statistics are reported in the ANOVA table in Appendix B.

species richness, $P = 0.0370$). The composition of snails influenced respiration rates (Fig. 2F; Appendix C, species composition, $P = 0.0029$) as did the presence of *Anax* predators (Appendix C, *Anax*, $P = 0.0238$). Accumulation of organic sediments (the result of snail consumption and defecation) was more than two times greater in high nutrient treatments (Fig. 4C; Appendix C, nutrient enrichment, $P < 0.0001$) than in low nutrient treatments. The presence of *Anax* reduced the rate of sedimentation (Appendix C, *Anax*, $P = 0.0178$).

Mechanisms

I tested for species richness effects that could not be explained by sampling effects using the *D* statistics suggested by Wardle (1999) and Loreau (1998) (see *Methods* for definitions), and found convincing support for the presence of a biologically based diversity mech-

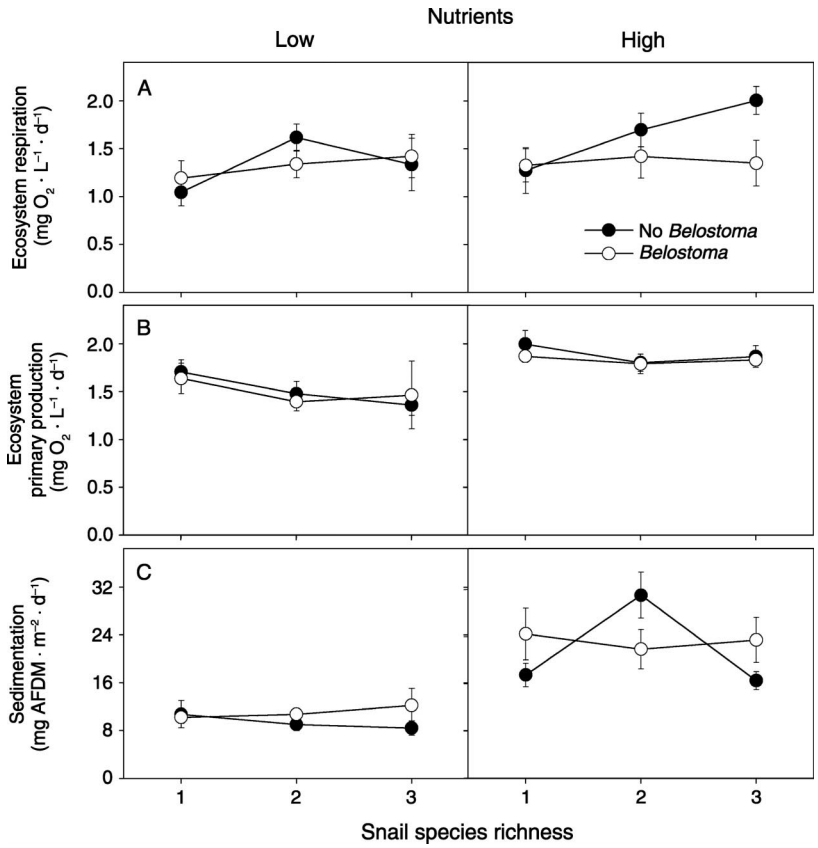

FIG. 4. The response of (A) ecosystem respiration, (B) ecosystem primary production, and (C) sedimentation to manipulations of species richness, nutrients, and predation. The left-hand panels are from low-nutrient tanks, and the right-hand panels are from high-nutrient tanks. Solid circles represent the absence of *Belostoma* predators; open circles represent the presence of *Belostoma*. Values are means ± SE. Statistics are reported in the ANOVA table in Appendix C.

anism. D_i was nearly always positive, for all species in all contexts, for both snail production and live standing biomass (Table 1), which suggests that for these snails interspecific interactions are either positive (e.g., facilitation) or less negative (e.g., niche differentiation) than intraspecific interactions. D_i could not be calculated for the remaining response variables because the aggregate community response could not be partitioned into species-specific responses (Petchey 2003). The only D statistic that could be calculated for these response variables was D_{max}, which again represents the proportional increase in performance in polyculture relative to the ''best'' monoculture (which was usually *Helisoma*). In this experiment, D_{max} was almost always positive (Table 1) for epiphyton and periphyton biomass, and macrophyte stem growth, indicating significant overyielding. However, there was one context for each of these responses where D_{max} was negative. Also, D_{max} was negative for respiration rates in every context and across all contexts, suggesting species richness effects on respiration were driven by the presence of a dominant species, *Helisoma*.

Variation in D_{max} across the contexts could have two sources: variation in the strength of diversity effects, and variation in the relative contribution of sampling effects to the overall diversity effect. For instance, the D_{max} for periphyton in low nutrients/no predator treatments was 0.32, while it was −0.89 in low nutrients/predator treatments (Table 1C), because the overall diversity effect was negative in the first case and positive in the second (e.g., variation in the overall effect of diversity; Fig. 3A). In contrast, the D_{max} for periphyton in high-nutrient–no-predator treatments was 0.263, while it was 0.097 for high-nutrient–predator-present treatments (Table 1C). In both of these cases, the effect of diversity on periphyton was negative and fairly strong (Fig. 3A), but in the presence of predators sampling effects were stronger (i.e., the dominant monoculture was closer to the three-species mean in the presence of predators than in the absence, data not shown).

Comparison of species richness effects in natural and artificial communities

Although sampling effects alone cannot explain the effects of diversity in this experiment, it is possible that some combinations of species present in the experiment never occur in nature, and therefore the conclusions reached here would be less directly applicable

TABLE 1. D_i and D_{max} statistics calculated for (A) snail production, (B) snail standing biomass, and (C) other response variables sensitive to snail species richness.

Nutrient	Predator	D_{Fo}	D_{Pg}	D_{Ht}	D_{max}	Dominant
A) Snail production						
Low	no predator	0.180	0.343	0.449	0.060	Ht
Low	predator present	0.436	−0.071	1.033	0.339	Pg
High	no predator	0.376	0.764	0.477	0.204	Ht
High	predator present	−0.062	0.318	0.660	0.018	Ht
Overall	overall	0.212	0.320	0.627	0.167	Ht
B) Snail standing biomass						
Low	no predator	0.715	1.190	0.953	0.236	Ht
Low	predator present	1.103	−0.130	2.117	0.653	Pg
High	no predator	0.131	2.635	0.482	0.098	Ht
High	predator present	0.276	1.954	0.591	−0.005	Ht
Overall	overall	0.440	1.079	0.803	0.241	Ht

Nutrient	Predator	Epiphyton‡	Periphyton‡	Macrophyte stems	Respiration
C) D_{max} for other response variables†					
Low	no predator	0.050 Ht	0.320 Pg	0.061 Pg	−0.036 Ht
Low	predator present	0.190 Ht	−0.890 Fo	−0.440 Fo	−0.098 Pg
High	no predator	−0.158 Ht	0.263 Pg	0.079 Ht	−0.055 Ht
High	predator present	0.067 Ht	0.097 Ht	0.500 Pg	−0.165 Ht
Overall	overall	0.062 Ht	0.240 Ht	0.292 Ht/Fo	−0.020 Ht

Notes: The ''dominant'' species (i.e., those with the highest value in monoculture) are noted for each response in each context. Species names are abbreviated with the initials of the genera and species names: Fo, *Fossaria obrussa*; Pg, *Physa gyrina*; Ht, *Helisoma trivolvis*.

† Only D_{max} could be calculated for these variables because responses could not be decomposed into species-specific effects.

‡ Response variables where the effect of snails is expected to be negative, so a positive D_{max} means that the polyculture reduced that response more than the most dominant species in monoculture did.

to natural systems. A survey of 16 ponds in southwest Michigan (Appendix D; see Wojdak [2004] for details) revealed that most compositions used in this experiment are in fact represented in nature (although *Gyraulus parvus*, a biomass subordinate, was often present as well). However, a comparison of the degree of nestedness (using NestCalc; Atmar and Patterson [1995]) in the experimental and natural communities revealed important differences in the frequency of occurrence of various snail community compositions. Nestedness measures the degree to which less diverse communities are nested subsets of more diverse communities and to what degree the order of species' ''extinction'' is constant, and is expressed on a temperature scale (0° equals complete nestedness, 100° equals complete antinesting). Examples of every possible order of ''extinction'' are present in the experimental communities—the result is significant ''anti-nesting'' (T = 54.78°, $P(t > T) = 0.029$, where t = random temperature calculated using 500 Monte Carlo simulations). In contrast, the natural communities surveyed were marginally more nested than one would expect by chance (T = 24.44°, $P(t < T) = 0.106$), and had a regular order of ''extinction.'' For instance, *Physa gyrina* was most often the first species lost as pond snail diversity declined, and *Physa* was never observed in a pond with only one or two species.

I explored the implications of these differences in the distribution of community types in the natural and experimental settings by examining the effects of species richness on various response variables after weighting the data by the frequency with which the particular snail composition was seen in the survey of ponds. For instance, if *Fossaria* and *Helisoma* were equally represented in natural ponds with only one snail species, the new mean for ''species richness = 1'' would be calculated as 0.5 × mean(*Fossaria* monocultures) + 0.5 × mean(*Helisoma* monocultures). In order to perform this analysis, I had to ignore the frequent presence in the natural ponds of *Gyraulus parvus* (almost always <5% of snail community biomass), and the infrequent presence (two ponds) of *Pseudosuccinea columella*, which were not used in the experiment.

In general, weighting the experimental data by the frequency of occurrence of various compositions in natural ponds did not change responses to species richness qualitatively (Fig. 5). Statistically, the effects of species richness in the weighted data are rarely significant, even where they had been with the unweighted data. However, because weighting the data to represent only the compositions seen in nature rarefies the dataset from 120 observations to 88, the power to detect effects and the precision of estimates decreases substantially.

Effect sizes

Because methods for calculating main and interactive effect sizes in factorial experiments have not been established (except in the simplest case; Gurevitch et al. [2000]), here I developed a simple statistic that describes the average magnitude of change in a response variable that results from manipulating a focal factor. For instance, manipulating species richness from one

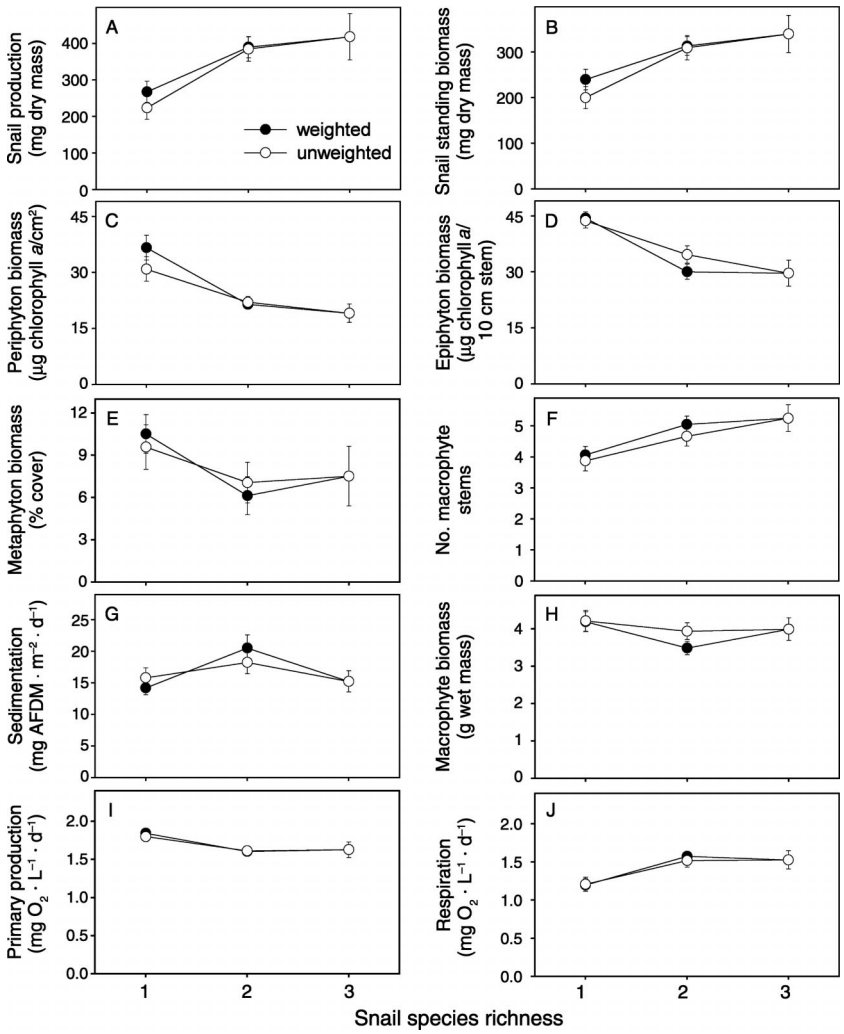

FIG. 5. Effects of species richness in the original data and data weighted by the frequency of specific snail compositions in a survey of 16 natural ponds for (A) snail production, (B) snail standing biomass, (C) periphyton, (D) epiphyton, (E) metaphyton, (F) new macrophyte stems, (G) sedimentation, (H) macrophyte biomass, (I) ecosystem primary productivity, and (J) ecosystem respiration. Open circles represent original, unweighted data; solid circles represent weighted data. Values are means ± SE.

species to three species resulted in a 37% to 53% increase in snail production depending on nutrient and predation treatments, for an average 46.9% change across the other factors. In contrast, adding predators to the mesocosms had +6% to −38% effects on snail production in the various nutrient and species richness treatments, an average 21.7% change in mean snail production.

Fig. 6 reports the average percent change resulting from predation, nutrient, and species richness manipulations for each response variable. Snail species richness had the largest effects on snail production and standing biomass, epiphyton, periphyton, metaphyton, and respiration (Fig. 6A–E, J). Nutrient enrichment had stronger effects on macrophyte biomass and on whole-system properties like primary production and sedimentation (Fig. 6G–I) than did either predation or consumer species richness. *Belostoma* predators had the strongest effects only on the emergence of macrophyte stems (Fig. 6F). Because of the infrequence of significant interactions between treatment factors in this study, qualitatively similar results were observed when effect sizes were calculated as simple main effects.

DISCUSSION

The goals of this experiment were to determine how species richness effects would depend on ecological context, to identify possible mechanisms operating to generate diversity effects, and to compare the strength of species richness effects with other factors (e.g., predation and resource availability) that often shape community structure and ecosystem processes.

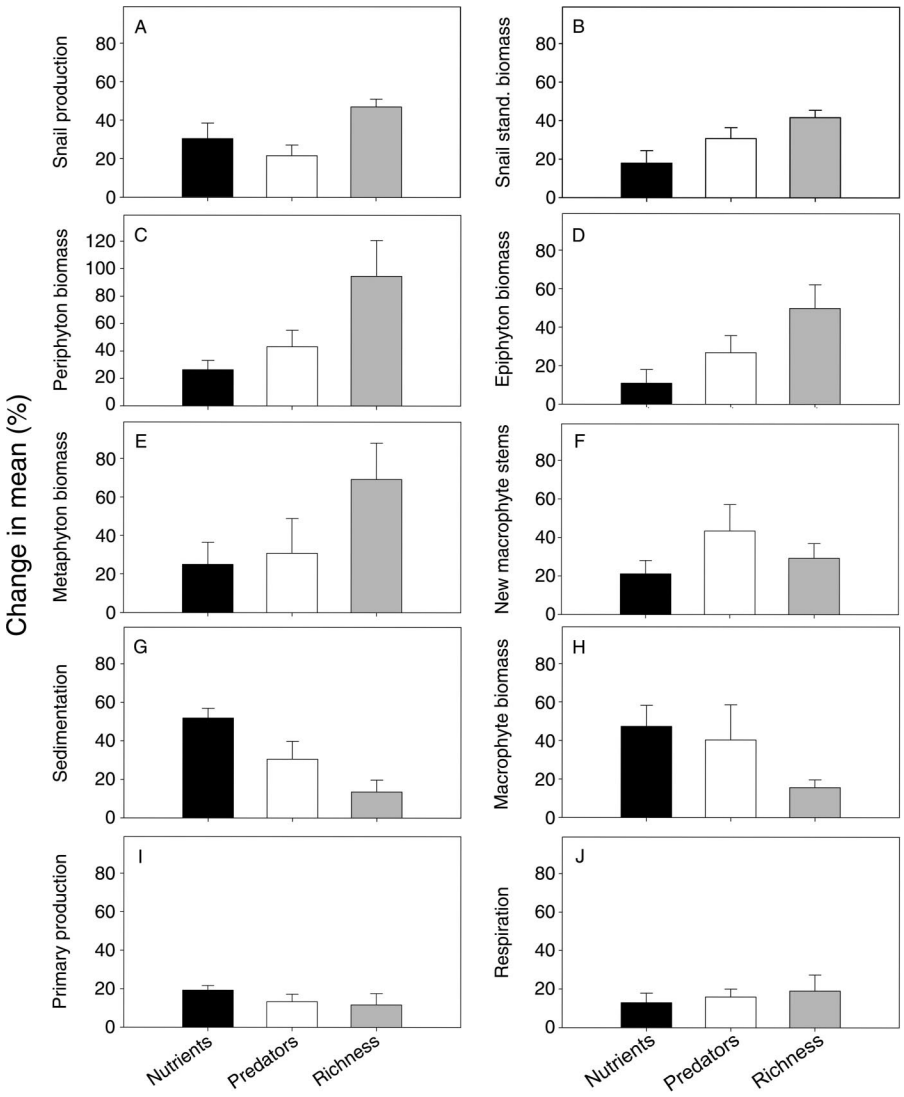

FIG. 6. Average percentage change in (A) snail production, (B) snail standing biomass, (C) periphyton, (D) epiphyton, (E) metaphyton, (F) new macrophyte stems, (G) sedimentation, (H) macrophyte biomass, (I) ecosystem primary productivity, and (J) ecosystem respiration, induced by snail species richness, nutrient, and predation manipulations. All effect sizes are calculated with untransformed data. Error bars (SE) describe the variability in the strength of a focal factor's effects on the response variable, across the levels of the other factors. The number of observations for these means is the number of unique levels of the other factors; $n = 4$ for species richness effects, $n = 6$ for nutrient and predator effects. Note the different scale of the *y*-axis for (C) periphyton biomass. Black bars represent nutrient effects, open bars represent predator effects, and gray bars represent the effects of snail species richness.

Context dependency

Species richness had meaningful effects on secondary production and standing biomass of snails, periphyton and epiphyton biomass, respiration, and growth of new macrophyte stems. Logically any effect of snail species richness would have to originate as an effect on snail production, standing biomass, or behavior, and only then cascade to affect other food web or system properties. In this experiment, secondary production was higher in diverse mesocosms in all contexts. While there were more snails in species-rich mesocosms, the ability of these snails to affect other organisms was contingent on the other biotic and abiotic conditions of the system. For instance, periphyton biomass decreased with increasing snail richness in all contexts except when *Belostoma* was present in low nutrient tanks (Fig. 3A).

Herbivore guilds often exhibit foraging trade-offs where some species move quickly from patch to patch grazing lightly (e.g., grazers) while other species are more sedentary, exhausting resources before moving on (e.g., diggers) (Schmitt 1996, Chase et al. 2001). Snails often respond to predation by reducing their activity and by seeking refuge (Bernot and Turner 2001,

Turner 1996) and indeed in previous experiments I have observed that *Physa gyrina* moves less, feeds less, and spends more time near the water's surface in the presence of *Belostoma* (Wojdak 2004). Thus under the threat of predation species' foraging strategies may converge on a slow-moving, intense grazing, ''digger'' mode (e.g., *Helisoma*'s default strategy) to maximize energy intake while minimizing encounters with predators, and this would result in a reduction of functional diversity across the guild of snails. The effects of increasing snail species richness on epiphyton biomass were not apparent until high levels of richness (e.g., three species), in the presence of *Belostoma* (Fig. 3B). In contrast, in the absence of predators snail species richness had effects on epiphyton biomass at lower richness levels (e.g., two species; Fig. 3B). These results are consistent with a reduction of functional diversity among the snails because of antipredator behavioral responses. However, snail biomass would be expected to be less sensitive to species richness if predators induced a reduction in functional diversity among the snails. This was not the case here (i.e., species richness effects on snail biomass were equally large in the presence and absence of predators; Fig. 1).

Epiphyton physically covers its macrophyte substrate, and if abundant can shade the plant causing reductions in growth (Brønmark 1985). Macrophyte stem growth was higher in diverse tanks, where snail biomass was higher and epiphyton was lower (Figs. 1 and 3). This was most likely the result of direct consumption of epiphyton by snails (Underwood et al. 1992, Brønmark 1985), but through consumption and defecation snails move organic material from other substrates to the bottom of the tank, which could have increased the availability of nutrients to the plants. The predator *Belostoma* mediated the strength of the snail-epiphyton-macrophyte interactions; when predators were present epiphyton was more abundant, and macrophytes performed more poorly (Fig. 3B, D). The context dependency of the effects of snail richness on epiphyton was not statistically evident in measurements of macrophytes, however.

Mechanisms

Any study of the effects of species richness should identify, to the degree possible, the mechanism responsible for those effects. The sampling effect (Huston 1997, Wardle 1999) can produce richness effects merely by the inclusion of dominant (i.e., disproportionately influential) species in a greater fraction of species-rich units than in species-poor units. Facilitation can allow species to utilize resources or avoid predators that they could not in isolation, and thus polycultures can have higher process rates (e.g., grazing, sedimentation) than monocultures. Differential resource use, where species using unique resources or the same resource in unique ways (e.g., phenological differences), can similarly lead to positive effects of diversity on process rates.

D statistics (Table 1) indicate a biologically based mechanism is largely responsible for effects of diversity in this experiment. Differential resource use is possible, but I did not quantify specialization on different resource types here. Wojdak (2004) demonstrates the existence of differences in foraging mode between species of these aquatic snails. Also, Chase et al. (2001) describe how pond snails can partition patchy periphyton resources and suggest that a trade-off in foraging traits (e.g., digger vs. grazer strategies) can act as a mechanism of coexistence, reducing competition intensity between species. Thus, niche complementarity could explain the effects of diversity seen with these pond snails either through differential use of the same resource or through use of different resources. In a previous experiment, I observed significant differences in the use of habitat among a larger set of snail species (Wojdak 2004). Moreover, the relative magnitudes of diversity effects were predictable using an index of niche overlap between species, strongly suggesting the operation of a niche complementarity mechanism. It may also be true that species with one grazing strategy may facilitate growth of the resources of a second species with another strategy (e.g., low-lying or tightly adhered algae may increase in abundance after an inefficient grazer removes the ''overstory'' [Underwood et al. 1992]).

D_{max}, which describes the degree of overyielding in mixtures, varied across the four ecological contexts studied here because of variation in both the strength of diversity effects and of sampling effects. Thus, it appears that even with a constant pool of species the degree to which sampling effects influence the results of a diversity experiment will depend on the conditions in that experiment (as suggested in Fridley 2001) and the response variables measured. This result is not surprising; sampling effects depend on the dominance of individual taxa, and the relative dominance of species depends on the biotic and abiotic conditions in a community.

There has been debate about whether sampling effects represent a mechanism that could operate in natural systems or are simply experimental artifacts (Huston 1997, Tilman et al. 1997). In general, if species presence across a set of communities is related to the functional attributes of the species (e.g., the functional dominant species is present in all systems and species with little functional effect are found only in diverse systems), experiments that create random communities could misgauge the true functional effect of species richness in nature. It may be true that the relationship between presence in a community and the functional attributes of species is strong in communities primarily structured by competition (where community membership is determined by traits related to resource acquisition), and weaker in communities structured by

disturbance or immigration processes (where community membership is determined by dispersal traits and resistance to harsh conditions). The applicability of species richness-ecosystem function studies to natural systems will be more apparent as this relationship is measured for a variety of taxa, and as the response of ecosystems to species richness is evaluated for sets of random and non-random communities as is done here and elsewhere (Petchey et al. 1999, Jonsson et al. 2002, Smith and Knapp 2003).

Effect sizes

By manipulating species richness, predation, and nutrient availability in the same experiment, comparison of the magnitude of these different effects is possible. However, the absolute magnitude of the different effects depends on the strength of the treatments imposed, which here were reasonably but arbitrarily chosen. Both nutrient and predator manipulations were strong; there was a fourfold difference in starting nutrient concentrations, and predators could potentially consume up to six snails per day (9.4–37.5% of initial snail abundance per day, depending on snail species composition). Despite the predator and nutrient manipulations being quite strong, species richness effects were often as large or larger than those of predators and nutrients. It appears, then, that the effects of consumer species richness can rival the strength of factors that have long been considered the strongest regulators of aquatic community structure: top-down and bottom-up forces.

In contrast, other studies have reported that diversity effects are weaker than those of nutrient enrichment (Bärlocher and Corkum 2003, Fridley 2002). However, in Bärlocher and Corkum's study of stream fungi where nutrient effects on leaf mass loss were three times as large as the effects of diversity, nitrogen and phosphorous were increased 100-fold, while the species richness manipulation was only a fivefold increase (one to five species). If effect sizes are scaled to the magnitude of the manipulations (percent change in response over the percent change in the experimental factor) scaled diversity effects would be nearly seven times as strong as scaled nutrient effects. Similarly, Fridley (2002) used a very strong nutrient manipulation (added 90 g N, 30 g P, 60 g K per m^2 to an old-field plant community), but because ambient nutrient conditions were not described it is impossible rescale the effect sizes by the strength of the manipulations as above. However, Fridley's nutrient addition was much higher than the recommended yearly application rates for cornfields in North Carolina (five times, 15 times, and seven times the rates for nitrogen, phosphorus, and potassium, respectively; Hardy et al. 2003), where that study was performed. This suggests the dominating effects of nutrients in Fridley's experiment were probably due to a large nutrient manipulation, compared with a more modest species richness manipulation. Studies that hope to compare the strengths of various factors need to incorporate, if possible, the strength of the manipulations into calculations of effect size (as when calculating sensitivity analyses). This may be impossible, however, if an experimental manipulation is of a qualitative nature (such as predator presence/absence in this study) and cannot be compared directly to the manipulation of another factor. In this case, careful consideration of the system (i.e., what variation is seen in the manipulated factors across natural systems) and the manipulations should guide interpretation. Alternatively, future experiments could be designed to examine ecosystem functioning across gradients of important ecological factors (e.g., multiple treatments of different magnitudes).

Predator control of prey trophic level biomass is predicted to be weak when some prey species are at least partially invulnerable (Leibold 1989). When abundant, snails were able to reduce algal abundance, but macrophytes were inedible or not preferred. Macrophytes had increased stem emergence rates (but not increased biomass) in treatments where snails reduced algal biomass strongly (e.g., at higher snail richness). Compensatory interactions between algae and macrophytes may explain why despite strong ''local'' food web effects of consumer species richness (i.e., on consumer biomass and the biomass of the functional groups those consumers interact with most directly), ecosystem functioning (e.g., primary production, sedimentation) did not respond as strongly to consumer richness. Whether one would expect this generally is unknown because so few studies have manipulated species richness in complex enough systems (multiple functional groups within a trophic level) to allow for such a compensatory response. Appreciation for the interconnectedness between subcompartments of food webs and ecosystems is growing (Persson 1999, Schindler and Scheurell 2002), but has been largely ignored in diversity-ecosystem function studies. Such interconnectedness may lend stability to ecosystem processes.

Conclusions

The number of studies explicitly considering how the richness of consumer species can affect ecosystem properties is small, but growing (see Cardinale et al. 2000, 2002, Jonsson and Malmqvist 2000, Duffy et al. 2001, Downing and Leibold 2002) and is comprised solely of studies in aquatic systems. Interestingly, most studies of the effects of primary producer species richness on ecosystems have been conducted in terrestrial systems. Individual consumer and predator species can have remarkably strong effects on aquatic ecosystems (e.g., Mittelbach et al. 1995), and it appears that in some cases the number of species of aquatic consumers can also have dramatic effects on food webs and ecosystems (this study, Cardinale et al. 2000, 2002, Jonsson and Malmqvist 2000, Downing and Leibold 2002). This study begins to put the strength and generality of

species richness effects on ecosystem function into perspective, relative to well-studied factors like predation and resource availability. Future diversity–ecosystem-function studies should attempt to include as much of the natural food web as possible, to allow for complex and compensatory responses of different functional groups and to increase the applicability of the results to natural systems. Moreover, applicability could be aided by more explicitly considering the differences in the distribution of species compositions across sets of experimental and natural communities.

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Literature Cited

Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? Oikos **80**:183–184.

Anholt, B. R., and E. E. Werner. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. Ecology **76**:2230–2234.

Atmar, W., and B. D. Patterson. 1995. The nestedness temperature calculator: a visual basic program, including 294 presence–absence matrices. AICS Research, Inc. University Park, New Mexico and the Field Museum, Chicago, Illinois, USA.

Bärlocher, F., and M. Corkum. 2003. Nutrient enrichment overwhelms diversity effects in leaf decomposition by stream fungi. Oikos **101**:247–252.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B **57**: 289–300.

Bernot, R., and A. Turner. 2001. Predator identity and trait-mediated indirect effects in a littoral food web. Oecologia **129**:139–146.

Brønmark, C. 1985. Interactions between macrophytes, epiphytes and herbivores—an experimental approach. Oikos **45**:26–30.

Cardinale, B. J., K. Nelson, and M. A. Palmer. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. Oikos **91**:175–83.

Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. Nature **415**:426–429.

Chase, J. M. 1999. To grow or reproduce? The role of life-history plasticity in food web dynamics. American Naturalist **154**:571–586.

Chase, J. M., W. G. Wilson, and S. A. Richards. 2001. Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community. Ecology Letters **4**:304–312.

Crowl, T., and J. Alexander. 1990. Parental care and foraging ability in male waterbugs (*Belostoma flumineum*). Canadian Journal of Zoology **67**:513–515.

Downing, A. L., and M. A. Leibold. 2002. Ecosystem consequences of species richness and composition in pond food webs. Nature **416**:837–841.

Duffy, J. E., K. S. MacDonald, J. M. Rhode, and J. D. Parker. 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. Ecology **82**:2417–2434.

Fridley, J. D. 2001. The influence of species diversity on ecosystem productivity: how, where, and why? Oikos **93**: 514–526.

Fridley, J. D. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. Oecologia **132**:271–277.

Gilliam, J. F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Dissertation. Michigan State University, East Lansing, Michigan, USA.

Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. Ecology **80**:1118–1131.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.

Grace, J. B. 1995. On the measurement of plant competition intensity. Ecology **76**:305–308.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: a meta-analysis of field experiments. American Naturalist **155**: 435–453.

Hardy, D. H., D. L. Osmond, and A. Wossink. 2003. Soil facts: an overview of nutrient management with economic considerations. Publication Number AG 565-01. North Carolina Cooperative Extension Service, Raleigh, North Carolina, USA.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of species composition and diversity on ecosystem processes. Science **277**:1302–1305.

Howarth, R. W., R. Marino, R. Garritt, and D. Sherman. 1992. Ecosystem respiration and organic matter processing in a large, tidally influenced river: the Hudson River. Biogeochemistry **16**:83–102.

Howarth, R. W., and A. F. Michaels. 2000. The measurement of primary production in aquatic ecosystems. Pages 72–85 *in* O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, editors. Methods in ecosystem science. Springer-Verlag, New York, New York, USA.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia **110**:449–503.

Jeffries, M. 1990. Interspecific differences in movement and hunting success in damselfly larvae (Zygoptera: Insecta): responses to prey availability and predation threat. Freshwater Biology **23**:191–196.

Jonsson, L. M., M.-C. Nilsson, D. A. Wardle, and O. Zackrisson. 2001. Context dependent effects of ectomycorrhizal species richness on tree seedling productivity. Oikos **93**: 353–364.

Jonsson, M., O. Dangles, B. Malmqvist, and F. Guerold. 2002. Simulating species loss following perturbation: assessing the effects on process rates. Proceedings of the Royal Society of London Series B **269**:1047–1052.

Jonsson, M., and B. Malmqvist. 2000. Ecosystem process rate increases with animal species richness: evidence from leaf-eating, aquatic insects. Oikos **89**:519–523.

Kesler, D., and W. Munns, Jr. 1989. Predation by *Belostoma flumineum* (Hemiptera) an important cause of mortality in freshwater snails. Journal of the North American Benthological Society **8**:342–350.

Klironomos, J. N., J. McCune, M. Hart, and J. Neville. 2000. The influence of arbuscular mycorrhizae on the relationship

between plant diversity and productivity. Ecology Letters **3**:137–141.
Kohler, S. L., and M. A. McPeek. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology **70**:1811–1825.
Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist **134**:922–949.
Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Animal Behavior **28**:215–290.
Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. Oikos **82**:600–602.
Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. Grime, A. Hector, D. Hooper, M. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science **294**:804–808.
Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Rettig, and C. W. Osenberg. 1995. Perturbation and resilience—a long-term, whole-lake study of predator extinction and reintroduction. Ecology **76**:2347–2360.
Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos **100**:403–405.
Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. Behavioral Ecology **15**:1044–1045.
Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature **355**:73–75.
Perneger, T. V. 1998. What's wrong with Bonferroni adjustments. British Medical Journal **316**:1236–1238.
Persson, L. 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. Oikos **85**:385–397.
Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. Oikos **101**:323–330.
Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature **402**:69–72.
Pettersson, L. B., and C. Brønmark. 1993. Trading off safety against food—state-dependent habitat choice and foraging in Crucian carp. Oecologia **95**:353–357.
Schalpfer, F., and B. Schmid. 1999. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. Ecological Applications **9**:893–912.
Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos **98**:177–189.
Schmitt, R. J. 1996. Exploitation competition in mobile grazers: trade-offs in a limited resource. Ecology **72**:408–425.
Sih, A. 1980. Optimal behavior—can foragers balance two conflicting demands. Science **210**:1041–1043.
Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist **139**:1052–1069.
Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters **6**:509–517.
SYSTAT. 1998. SYSTAT version 8.0. SPPS, Inc. Chicago, Illinois, USA.
Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology **80**: 1455–1474.
Tilman, D., C. L. Lehman, and K. T. Thompson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Science (USA) **94**:1857–1861.
Tilman, D., P. Reich, J. Knops, D. Wedin, T. Mieklke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science **294**:843–845.
Turner, A. M. 1996. Freshwater snails alter habitat use in response to predators. Animal Behavior **51**:747–756.
Underwood, G. J. C., J. D. Thomas, and J. H. Baker. 1992. An experimental investigation of interactions in snail–macrophyte–epiphyte systems. Oecologia **91**:587–595.
Wanninkhof, R., J. R. Ledwell, and W. S. Broecker. 1985. Gas exchange–wind speed relation measured with sulfur hexafluoride on a lake. Science **227**:1224–1226.
Wardle, D. 1999. Is ''sampling effect'' a problem for experiments investigating biodiversity–ecosystem function relationships? Oikos **87**:403–407.
Welschmeyer, N. A. 1994. Flourometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. Limnology and Oceanography **39**:1985–1992.
Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics **15**:393–425.
Wilson, S. D., and D. Tilman. 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology **74**:599–611.
Wojdak, J. M. 2004. Species interactions and the functioning of pond ecosystems. Dissertation. Michigan State University, East Lansing, Michigan, USA.

APPENDIX A

A table showing ANOVA results for snail production and standing biomass is available in ESA's Electronic Data Archive: *Ecological Archives* M075-019-A1.

APPENDIX B

A table showing ANOVA results for algal biomass (periphyton, epiphyton, and metaphyton) and macrophyte (stem growth and biomass) is available in ESA's Electronic Data Archive: *Ecological Archives* M075-019-A2.

APPENDIX C

A table showing ANOVA results for ecosystem respiration, primary production, and sedimentation is available in ESA's Electronic Data Archive: *Ecological Archives* M075-019-A3.

APPENDIX D

A table showing the occurrence of five snail species in a survey of 16 ponds in southwest Michigan is available in ESA's Electronic Data Archive: *Ecological Archives* M075-019-A4.