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## Predicting community outcomes from pairwise interactions: integrating density- and trait-mediated effects

Received: 4 June 2001 / Accepted: 14 February 2002 / Published online: 13 April 2002  
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**Abstract** Understanding how species interactions shape the structure of ecological communities based on pairwise comparisons has been a difficult undertaking for ecologists because effects in reassembled communities can be different than simple density-mediated interactions would suggest. Part of this complexity occurs because many species change their behavior and morphology with different predators and competitors and, thus, change their per-capita interaction rates (i.e. trait-mediated interactions). Our objective was to use a simple experimental community of two predators (larval dragonflies, *Anax longipes*, and larval salamanders, *Ambystoma tigrinum*), two prey (larval green frogs, *Rana clamitans*, and larval bullfrogs, *R. catesbeiana*), and a shared prey resource to determine whether we can predict interactions in a reassembled community by combining our knowledge of density- and trait-mediated interactions. We combined pairwise laboratory experiments on predation rates and predator-induced behaviors with a mesocosm experiment to examine density- and trait-mediated effects. We used a factorial combination of no predators, caged *Anax* (to induce anti-predator traits without changing prey density), and lethal *Anax* crossed with no predators, caged *Ambystoma*, and lethal *Ambystoma*. The species interactions in the reassembled community were qualitatively predictable based on the pairwise experiments. Lethal *Anax* preyed upon *Ambystoma* and green frogs while lethal *Ambystoma* only preyed upon green frogs. *Anax* also reduced the activity of the green frogs; this caused a decrease in salamander predation on green frogs, a decrease in green frog acquisition of resources, and an increase in bullfrog acquisition of resources. *Ambystoma* had no effect on green frog activity, no effect

on resource acquisition by green frogs, and no effect on resource acquisition by bullfrogs. These results suggest that we can better understand how species interact in natural communities if we have a more detailed understanding of trait-mediated mechanisms. However, if predicting the structure of large communities requires identifying how each species alters its traits in the presence of all other species along with altering density, improving our predictive ability may be a prohibitively large undertaking.

**Keywords** Amphibians · Community ecology · Larval anurans · Phenotypic plasticity · Trait-mediated interactions ·

### Introduction

One challenge for ecologists is to understand how species interactions shape the structure of ecological communities. This has been a daunting task for several decades as ecologists attempted to predict the outcome of species interactions in a community based upon experimental manipulations of species pairs (see reviews by Werner 1992; Adler and Morris 1994; Wootton 1994; Abrams 1995). Typically, investigators have found that community-level outcomes are not predictable from adding up pairwise interactions. Often, pairwise interactions are multiplicative (Sih et al. 1998), leading to the conclusion that communities are both unpredictable and complex (Wilbur and Fauth 1990; Werner 1992). A primary reason for this complexity is that early studies focused on documenting how each species in the community affected the density of the other species in the community either through direct interactions or density-mediated indirect interactions. However, many traits are phenotypically plastic (including behavior, morphology, and life history; Lima and Dill 1990; Karban and Baldwin 1997; Kats and Dill 1998; Tollrian and Harvell 1999) and these trait changes can alter the outcome of species interactions (Turner and Mittlebach 1990; Werner and

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Anholt 1996; Beckerman et al 1997; Soluk and Richardson 1997; Relyea 2000). In this case, the strength of species interactions depends upon the ecological context in which the species pair is embedded. These effects have been termed “trait-mediated interactions” (Abrams 1995; also termed “high-order interactions” or “interaction modifications”).

Although much more empirical work is required before any generalities can be made, trait-mediated interactions appear to be common in ecological communities. Recent work has focused on the role that predators and competitors play in altering a target species' behavior or morphology and how these trait changes alter the growth and survival of other species in the community (Wissinger and McGrady 1993; McIntosh and Townsend 1996; Beckerman et al. 1997; Peacor and Werner 2000; Relyea 2000). The consensus from these studies is that trait-mediated effects can have profound effects on interspecific interactions. Thus, some of the complexity observed in earlier studies that prevented predictions of community structure based on pairwise density-mediated effects might be clarified if we simultaneously consider trait-mediated interactions.

Many studies of trait-mediated interactions involve either a single predator or a single prey species (Lima and Dill 1990; Tollrian and Harvell 1999). However, because most communities are composed of multiple predators and multiple prey, we need to expand our empirical studies to larger food webs to obtain a more realistic picture of interaction complexity. However, simply documenting the presence of trait-mediated interactions is no longer the challenge; the existence of trait-mediated interactions is now rarely debated. The challenge is to determine how different environments change an individual's traits, how altered traits change individual performance, and how changes in individual performance translate into changes in interspecific interactions (Worthen and Moore 1991; Wootton 1992; Schmitz 1998; Peacor and Werner 2000).

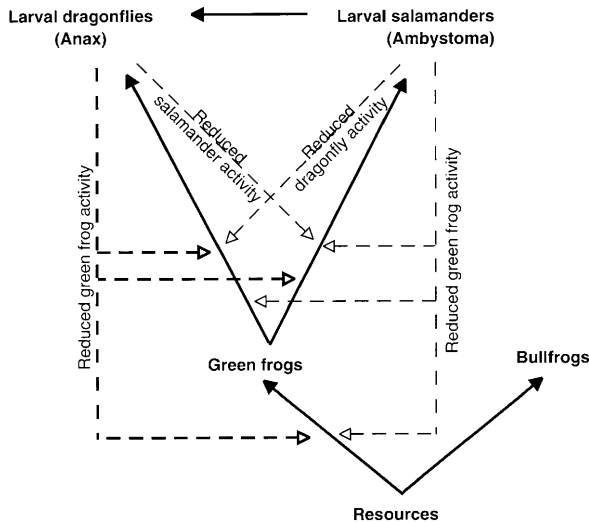
Our objective was to examine the importance of trait-mediated effects in altering interspecific interactions in pond communities containing larval anurans. This work draws upon a great deal of past research that we and others have conducted on trait- and density-mediated interactions (Werner and Anholt 1996; Peacor and Werner 1997; Van Buskirk and Yurewicz 1998; Relyea and Werner 1999; Relyea 2000, 2001a, b; Yurewicz, unpublished data). Much of this work has tested for trait-mediated effects using predatory dragonfly larvae (*Anax junius*, *A. longipes*, *Tramea* sp.) because dragonflies are abundant and easy to experimentally manipulate. While dragonflies have provided a great deal of insight into predator-prey interactions, it is important that we begin to incorporate other predators, alone and in combination, because predators have the potential to interact with the prey and with each other (Polis et al. 1989; Polis and Holt 1992; Wissinger and McGrady 1993; Soluk and Richardson 1997; Eklöv and Werner 2000).

## Study system

Larval anurans have been an excellent study system for ecological investigations for nearly a century (Adolph 1931; Martof 1956; Wilbur 1972; Morin 1983; Werner and McPeck 1994). In North America, tadpoles coexist with diverse predator assemblages (Collins and Wilbur 1979; Dale et al. 1985; Skelly et al. 1999; Relyea 2001b) that can reduce prey density and have a positive indirect effect on the prey's resources (a density-mediated indirect effect; Wilbur 1988; Van Buskirk and Yurewicz 1998; Relyea 2002b). Predators also emit chemical cues (Petranka et al. 1987; Kats et al. 1988) that induce adaptive changes in tadpole behavior, morphology, and life history (Hews 1988; Lawler 1989; McCollum and Van Buskirk 1996; Relyea and Werner 1999). These predator-induced trait changes can alter interaction rates between prey and predators and between prey and resources (Werner and Arnolt 1996; Peacor and Werner 1997; Relyea 2000).

We focused on two species of larval anurans (newly hatched green frog tadpoles and second-year bullfrog tadpoles) and two species of predators (larval dragonflies, *Anax* spp., and larval tiger salamanders, *Ambystoma tigrinum*) that naturally coexist. We chose these particular species and size classes of tadpoles because they compete for periphyton (Werner and Anholt 1996; Peacor and Werner 1997; Relyea and Werner 1999), but only the green frogs are susceptible to predation. Second-year bullfrogs are large and invulnerable to predators (Relyea and Yurewicz, personal observations). Thus, any changes in bullfrog growth would be due to density- or trait-mediated effects of green frogs on the shared resource; in short, the bullfrogs served as a biometer of indirect effects transmitted through a shared resource (Fig. 1). *Ambystoma* and *Anax* both kill green frog tadpoles, although predation by *Ambystoma* is higher (based on laboratory experiments; Relyea 2001b). In contrast, only *Anax* causes significant reductions in green frog activity (Werner 1991; Relyea 2001a). Based on laboratory experiments, both predators should have little effect on green frog morphology (Relyea 2001a). *Anax* and *Ambystoma* also have the potential to kill each other and affect each other's behavior. *Anax* can kill *Ambystoma* of similar size but, because of gape limitations, it was unlikely that *Ambystoma* could consume *Anax* of similar size (K. L. Yurewicz, personal observations). Whether the predators could affect each other's behavior was unknown. In summary, we manipulated two components of a five-component system that contained numerous potential density-mediated and trait-mediated effects (Fig. 1).

Based on the above food web and our knowledge of trait changes in laboratory experiments, we manipulated the presence and absence of caged and lethal predators and predicted the effects on the growth and survival of green frogs and bullfrogs. We had a number of hypotheses: (1) neither predator should affect green frog morphology; (2) *Ambystoma* should kill more green frogs than *Anax*; (3) because only *Anax* reduces green frog activity, adding caged *Anax* should decrease the predation rate of



**Fig. 1** An aquatic food web of predators, prey, and resources used in the mesocosm experiment. Potential density-mediated effects are indicated by *solid lines* (arrows pointing to the consumer). Potential trait-mediated effects are indicated by *dashed lines*, demonstrating how one species can potentially alter the traits of another species and thereby alter the per-capita interactions of the latter. *Thicker lines* indicate those effects that proved to be important at the end of the experiment

lethal *Ambystoma* on green frogs, but adding caged *Ambystoma* have no effect on the predation rate of lethal *Anax* on green frogs; (4) because only *Anax* reduces green frog activity, caged *Anax* should reduce green frog growth, but caged *Ambystoma* should have no effect; (5) any reductions in green frog resource acquisition (either through density- or trait-mediated effects) should have a positive effect on bullfrog growth (through their shared resource); and (6) *Anax* should kill *Ambystoma*, but *Ambystoma* should not kill *Anax*.

## Materials and methods

### Animal collection and rearing

All animals used in the experiments were collected on the E.S. George Reserve in southeastern Michigan. Green frogs were collected as a mixture of ten egg masses from several nearby ponds whereas large second- and third-year bullfrog tadpoles (which are typically two orders of magnitude more massive) were seined from a single nearby pond. We reared all tadpoles outdoors in 300-l wading pools containing aged well water under 60% shade cloth and fed them rabbit chow ad libitum until their use in the experiments. Predatory dragonfly larvae also were collected from the experimental ponds; they were held individually in 500-ml plastic cups and fed green frog tadpoles until used in the experiments. *Ambystoma* larvae were collected as eggs from two natural ponds in Livingston County in southeastern Michigan. The larvae were raised first in outdoor wading pools and then in individual 500-ml plastic cups in the lab; they were fed zooplankton and green frog tadpoles until used in the experiments.

### Laboratory experiments

The laboratory experiments were designed to quantify predator-induced behavioral responses. Behavioral responses of green frog

tadpoles to *Anax* and *Ambystoma* were documented in an earlier study (Relyea 2001a) and these data were used to develop our predictions in the mesocosm experiment. In that experiment, groups of ten newly hatched green frogs (mean mass=20 mg) were reared in plastic tubs containing 7 l of aged well water. Tubs were placed on shelves in two spatial blocks and each tub was equipped with a predator cage constructed of two wooden slats that suspended a 1-mm-mesh bag. Each cage contained either no predator, a single caged *Anax*, or a single caged larval *Ambystoma*. All treatments were replicated 4 times in a randomized block design. Predators and prey were fed 3 times per week; prey were fed at a per-capita rate of 6% of mean mass and predators were fed 3–10 green frog tadpoles (total mass of approximately 100 mg). The experiment lasted for 35 days; every 7 days the tadpoles were weighed and the tub water was changed. Activity was measured using 37 scan samples (Altmann 1974) to count the number of active (moving) tadpoles throughout the day. Activity level was quantified for each tub as the mean proportion of active tadpoles across the 37 observations.

We also conducted new (previously unpublished) laboratory experiments to quantify the behavioral responses of bullfrog tadpoles to each of the predators, and the behavioral responses of the two predator species to each other. In this case, experimental units were 40-l aquaria filled with aged well water, arranged in a completely randomized design along shelves in the laboratory. Fluorescent lighting above the aquaria operated on a 14:10 light:dark cycle. Each aquarium contained a predator cage consisting of a plastic cup with a small piece of polystyrene for flotation and a screen covering on one end.

For the bullfrog experiment, we placed five tadpoles (mean individual mass=11.22 g) in each aquarium on 23 June 1998 and randomly assigned one of three treatments: an empty cage, one caged *Anax*, or one caged *Ambystoma*. Each treatment was replicated 5 times. Each caged predator was fed 15 green frog tadpoles (a total mass of approximately 150 mg), and the animals were left overnight to acclimate to the experimental conditions. It is likely that bullfrog tadpoles respond the same way to predators consuming green frog tadpoles as they would to predators fed bullfrog tadpoles; previous work has shown that ranid tadpoles cannot discriminate between predators fed conspecific tadpoles versus congeneric tadpoles (Relyea and Werner 2000). On 24 June 1998, we observed behavior in each aquarium using 40 scan samples to count the number of active tadpoles throughout the day. Activity level was quantified for each aquarium as the mean proportion of active tadpoles across the 40 observations.

The experiments testing the response of *Anax* to *Ambystoma*, and vice versa, followed the same protocol, with three exceptions. First, only one individual was placed in each aquarium because both *Anax* and *Ambystoma* larvae can be cannibalistic. Second, in the *Anax* experiment, each aquarium contained three wooden dowels so that *Anax* could perch as they often do in natural habitats. Third, we observed each of the aquaria in the *Anax* and *Ambystoma* experiments using 40 scan samples on 24 June and an additional 20 scan samples on 25 June 1998, after feeding the target individuals a mixture of zooplankton collected from a nearby pond. We performed more observations on the predators than the prey because we expected that behavioral data based on one focal individual would be more variable than our data from the tadpole experiments where we observed groups of 5–10 individuals. The proportion of activity was calculated by dividing the number of times each individual was active by the 60 observations taken. *Ambystoma* individuals used in this experiment weighed an average of 990 mg; *Anax* individuals were not measured but were all in the penultimate instar (typically 4–5 cm) and similar in size to the *Ambystoma* larvae. In these observations of predator behavior, it is important to note that we were testing how each predator responded to the other predator eating green frogs, not how each predator responded to the other predator eating predators. This is the more appropriate design because the mesocosm experiment focused on how interspecific interactions change when predators eat green frogs.

For each of the laboratory experiments, we analyzed mean activity using an analysis of variance (ANOVA), and used Fisher's test to conduct mean comparisons. For the green frog experiment,

we arcsine-square-root transformed the data to meet the assumptions of normality and homoscedasticity of errors. The behavioral data for the bullfrog experiment and the predator experiment did not depart seriously from the assumptions of normality and homoscedasticity as assessed using Lilliefors' and Bartlett's tests, respectively. Thus, we did not transform the data. For experiments containing randomized block designs, the block effects were never significant and were dropped from the analyses.

### Mesocosm experiment

To quantify the density- and trait-mediated effects of the two predator species on tadpole morphology, growth, and survivorship, we reared green frog and bullfrog tadpoles together under a 3×3 completely randomized factorial design: three *Anax* treatments (no *Anax*, two nonlethal (caged) *Anax*, or two lethal *Anax*) crossed with three *Ambystoma* treatments (no *Ambystoma*, two nonlethal *Ambystoma*, or two lethal *Ambystoma*). The entire design was replicated five times for a total of 45 experimental units. Additionally, we set up five extra replicate tanks assigned to the lethal *Anax*/lethal *Ambystoma* treatment for destructive sampling during the experiment. These tanks helped us assess the rate of predation so that we could stop the experiment before all of the green frog tadpoles were killed. After sampling three of the five tanks, we decided to terminate the experiment, leaving two replicates that we included in the statistical analysis (for a total of 47 experimental units).

Experimental units were 1,000-l cattle watering tanks which we filled with well water on 20 June 1998. At that time, we also added to each tank 300 g of *Quercus* leaves, 25 g of rabbit chow, and a 250 ml aliquot of phytoplankton from an experimental pond. The leaves added structure to the environment and provided a surface for periphyton growth whereas the rabbit chow and aliquot of pond water were added to stimulate the growth of bacteria and algae. On the following day, we added a 125 ml aliquot of zooplankton (collected from a natural pond) to each tank. These additions were intended to make the cattle tanks contain many of the components of natural ponds. We covered the tanks with lids made from 60% shade cloth to prevent unwanted insects and amphibians from colonizing the experiment.

We equipped each tank with four predator cages. Each cage was a piece of slotted sewer drain pipe (10×11 cm) with 2 mm fiberglass screening over each end, so that predators were not lethal to tadpoles in the tank but chemical cues could be produced by the predators and diffuse out into the tank. We placed a small piece of polystyrene in each cage for flotation. Each cage was either empty or contained a single predator individual, depending on the treatment. Tanks contained four empty cages (four of the treatments), two empty and two occupied cages (four of the treatments), or four occupied cages (one of the treatments).

On 27 June 1998, we added 200 green frogs (113/m<sup>2</sup>, mean individual mass=20 mg) and 5 bullfrogs (3/m<sup>2</sup>, mean individual mass=10.71 g) to each tank. Based on five years of survey data, first-year green frog tadpoles can achieve pond-wide densities of up to 87/m<sup>2</sup> and microhabitat densities of up to 670/m<sup>2</sup>; second-year bullfrog tadpoles can achieve pond-wide densities of up to 1.7/m<sup>2</sup> (Werner et al., unpublished data). Thus our initial densities were relatively high, but we anticipated that predation would quickly reduce green frog densities to more natural levels. Predators were added to the tanks on 27 June. The lethal predators were caged for the first 2 days of the experiment (27–29 June) to give the tadpoles an opportunity to detect the predators' presence before any direct predation was allowed. Caged predators were fed green frogs 3 times per week throughout the experiment. At each feeding, a predator was given 2–3 tadpoles (mean total mass=370 mg). Empty cages were picked up and gently dropped back into the tanks to control for tank disturbance. We randomly assigned predators to the lethal predator treatments but did not note their initial size. Throughout the experiment, all caged predators that died or began metamorphosis were replaced. Only one bullfrog tadpole died during the course of the experiment and the death was not predator-related. The dead bullfrog was replaced

with a similar-sized bullfrog tadpole to maintain a constant competitor density.

The destructively sampled tanks indicated that the predators had killed nearly all of the green frogs after 3 weeks, so we terminated the experiment. During this time, we attempted to quantify tadpole activity in the tanks. However, our attempts were unsuccessful because water clarity differed among treatments (previous experiments have shown good agreement between activity observed in the laboratory and activity observed in pond mesocosms; Peacor and Werner 1997; Relyea 2002b). On 17–18 July 1998, we drained the tanks, sorted through the leaf litter, and quantified the survival and growth (mean final mass – mean initial mass) of the tadpoles and the survival and final size of the predators (standard length of *Anax*, mass of *Ambystoma*). A random sample of up to ten green frogs from each tank was preserved in 10% formalin for subsequent morphological analysis. To measure green frog morphology, we used the BioScan Optimas digitizing program which allowed us to trace seven linear measures of tadpole shape from an image captured on a video monitor. We measured five traits from a lateral view of each tadpole (tail length, tail depth, tail muscle depth, body length, body width) and two traits from a dorsal view [tail muscle width, body width; see Relyea (2000) for a photograph of tadpole dimensions]. Each tadpole was weighed after being measured.

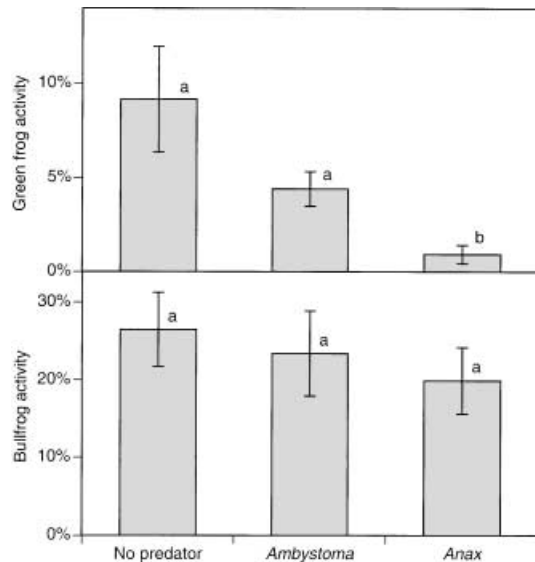
### Statistical analyses of the mesocosm experiment

Our statistical analyses of the mesocosm experiment required the omission of three tanks. In two tanks that contained lethal *Ambystoma*, only one *Ambystoma* survived; this mortality was not due to predation by lethal *Anax* (treatments: caged *Anax* plus lethal *Ambystoma*, no *Anax* plus lethal *Ambystoma*). In one tank that contained lethal *Anax*, only one *Anax* survived; this mortality was not due to predation by lethal *Ambystoma* (treatment: caged *Ambystoma* plus lethal *Anax*). For all of the analyses, we used Lilliefors' and Bartlett's tests to examine whether there were any serious departures from normality and homoscedasticity, respectively. All pairwise mean comparisons were conducted using Fisher's test.

We began by analyzing the effects of the two predators on each other. The effects of the *Ambystoma* treatments on lethal *Anax* survival and *Anax* body length were analyzed with a multivariate analysis of variance (MANOVA). The effect of the *Anax* treatments on lethal *Ambystoma* survival was analyzed with the non-parametric Kruskal-Wallis test because the survival data were heteroscedastic and were not correctable by transformation. We used an ANOVA to test the effect of *Anax* treatment on *Ambystoma* mass.

We then conducted MANOVAs to analyze the effects of the *Anax* and *Ambystoma* treatments on green frog growth, survival, and morphology. The first MANOVA analyzed the effects on growth and survivorship. After survivorship data were arcsine-square-root transformed, there were no serious departures from normality or homoscedasticity. The second MANOVA analyzed the effects of the *Anax* and *Ambystoma* treatments on the relative morphology of green frogs. To quantify relative morphology, we first had to generate size-independent morphological measurements. We did this by first regressing log-transformed morphological measurements against log-transformed mass (transformed to correct for nonlinearities) for all individuals and saving the residuals (which represented size-independent morphology; Van Buskirk and Relyea 1998; Relyea 2000). The residuals from this regression were averaged by tank, and these mean residuals were entered into a MANOVA with *Anax* and *Ambystoma* treatments as the fixed factors. The nonsignificant *Anax*-by-*Ambystoma* interaction term was removed to increase the power of the analysis.

Larval bullfrogs in the experiment achieved a maximum mass at Gosner stage 41 (Gosner 1960) and then declined as individuals stopped feeding and began to undergo metamorphosis. For our purposes, we wanted to know how much biomass the bullfrog tadpoles had accumulated prior to initiating metamorphosis (i.e. peak bullfrog mass). Therefore, we first regressed Gosner stage



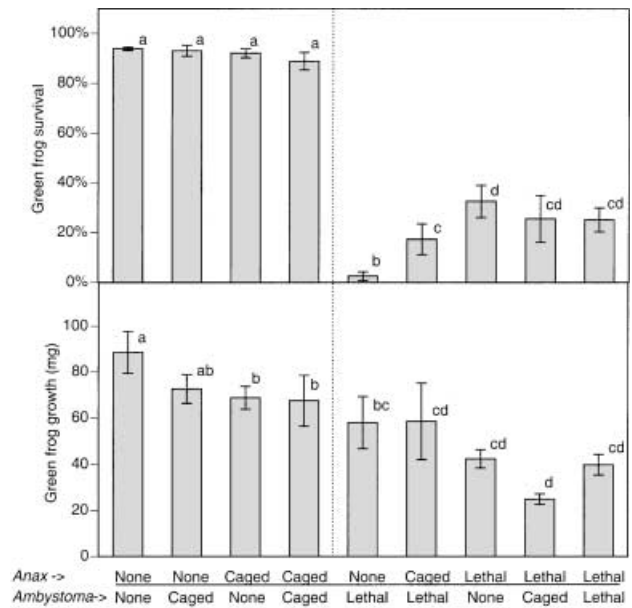
**Fig. 2** The activity of first-year green frogs (*upper panel*) and second-year bullfrogs (*lower panel*) when reared under laboratory conditions with either no predators, caged *Ambystoma*, or caged *Anax* (means $\pm$ 1 SE). Means with common superscripts are not significantly different ( $P>0.05$ )

against mass (for all individuals of stage  $\geq 41$ ) to quantify mass loss during metamorphosis. Using the resulting regression coefficient and knowing the Gosner stage of each bullfrog, one can estimate the peak mass for each bullfrog that had metamorphosed (Werner and Anholt 1996). We used these estimated masses, combined with untransformed masses of individuals  $< 41$  Gosner stage, in a MANOVA to test for the effects of *Anax* and *Ambystoma* treatments on bullfrog growth (mean final mass – mean initial mass). Finally, to examine whether changes in bullfrog growth were due to competition between bullfrogs and green frogs, we regressed bullfrog growth against total green frog biomass (number of green frog survivors  $\times$  mean green frog growth) across all tanks. A negative relationship between green frog growth and bullfrog growth would be evidence of competition, particularly in light of past mesocosm experiments that have demonstrated competition between these two species at similar densities (Werner and Anholt 1996; Peacor and Werner 1997)

## Results

### Laboratory experiments

The laboratory experiments documented how the two prey species behaviorally responded to the two predators and how the two predators behaviorally responded to each other. First-year green frogs responded to the predators by reducing their activity ( $F_{2,9}=8.89$ ,  $P=0.007$ ; Fig. 2). Relative to the control, the reduction was not sig-



**Fig. 3** The effect of *Anax* and *Ambystoma* predators (either absent, caged, or lethal) on larval green frog growth and survivorship (means $\pm$ 1 SE). Means with common superscripts are not different ( $P>0.09$ )

nificant ( $P=0.118$ ) in the presence of *Ambystoma* but it was significant in the presence of *Anax* ( $P=0.002$ ). Activity in the presence of caged *Anax* was lower than in the presence of caged *Ambystoma* treatment ( $P=0.036$ ). In contrast, second-year bullfrogs did not alter their activity with either predator ( $F_{2,12}=0.461$ ,  $P=0.641$ ). In the experiments that tested how the predators responded to each other, we found that *Anax* did not alter their activity in the presence of *Ambystoma* eating green frogs ( $F_{1,8}=2.30$ ,  $P=0.168$ ) and *Ambystoma* did not alter their activity in the presence of *Anax* eating green frogs ( $F_{1,8}=0.01$ ,  $P=0.914$ ).

### Mesocosm experiment

#### Predators

In the mesocosm experiment, the predators affected each other's survivorship, but not each other's final size (unless mentioned otherwise, all mean comparisons are given relative to the control treatment). *Anax* experienced no differences in survivorship or size among the three *Ambystoma* treatments (Wilks'  $F_{4,26}=1.07$ ,  $P=0.393$ ). In contrast, *Ambystoma* survivorship was high with no *Anax* and caged *Anax*, but reduced to zero with lethal

**Table 1** MANOVA results from the analysis examining the effect of *Anax* (absent, caged, and lethal) and the effect of *Ambystoma* (absent, caged, and lethal) on larval green frog growth and survival in the pond mesocosm experiment

Source	Multivariate	Univariate Survivorship	Univariate Growth rate
<i>Anax</i>	$F_{4,64}=20.0$ , $P<0.001$	$F_{2,33}=41.8$ , $P<0.001$	$F_{2,33}=20.2$ , $P<0.001$
<i>Ambystoma</i>	$F_{4,64}=32.0$ , $P<0.001$	$F_{2,33}=118.3$ , $P<0.001$	$F_{2,33}=5.2$ , $P=0.011$
<i>Anax</i> $\times$ <i>Ambystoma</i>	$F_{8,64}=11.6$ , $P<0.001$	$F_{4,35}=37.8$ , $P<0.001$	$F_{4,35}=2.2$ , $P=0.089$

**Table 2** Multivariate MANOVA results from the analysis examining the effect of *Anax* (absent, caged, and lethal) and *Ambystoma* (absent, caged, and lethal) on larval green frog morphology in the pond mesocosm experiment

Source	df	Wilks' F	P
<i>Anax</i>	14,62	1.98	0.035
<i>Ambystoma</i>	14,62	0.96	0.499

**Table 3** Univariate MANOVA results from the analysis examining the effect of *Anax* (absent, caged, and lethal) and *Ambystoma* (absent, caged, and lethal) on larval green frog morphology in the pond mesocosm experiment

Source	df	F statistic (upper value) and P-value (lower value)							
		Body depth	Body length	Body width	Tail depth	Tail length	Muscle depth	Muscle width	
<i>Anax</i>	2,37	(0.07)	(5.02)	(0.03)	(0.58)	(9.49)	(1.23)	(1.65)	
		0.935	0.012	0.968	0.566	<0.001	0.303	0.206	
<i>Ambystoma</i>	2,37	(1.69)	(0.424)	(2.86)	(0.60)	(0.67)	(0.35)	(1.25)	
		0.199	0.657	0.070	0.555	0.519	0.706	0.299	

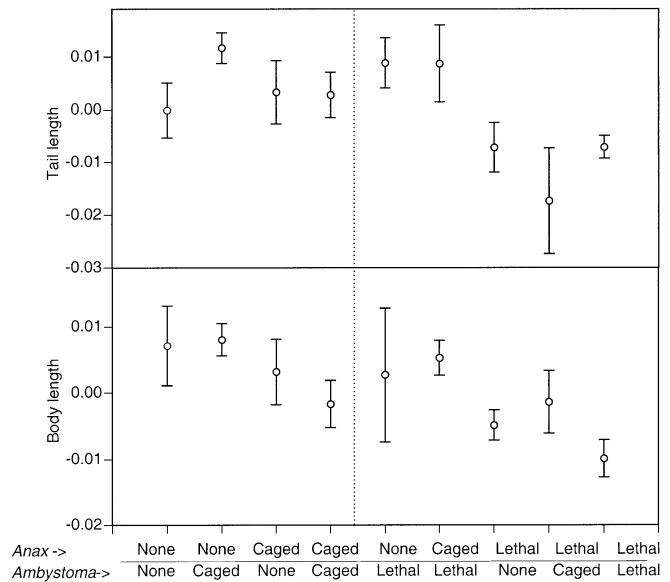
*Anax* (Kruskal Wallis test statistic=14.1,  $P=0.001$ ). *Ambystoma* mass was unaffected by the presence of caged *Anax* ( $F_{1,8}=2.42$ ,  $P=0.159$ ).

### Green frogs

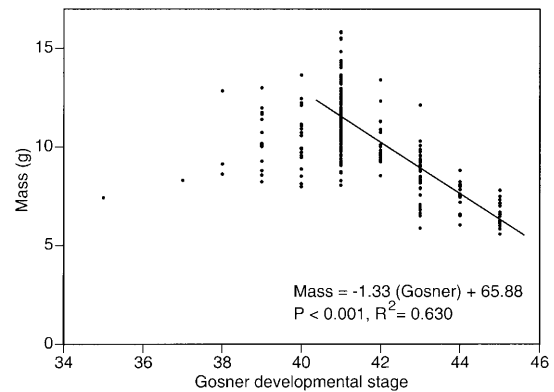
The mesocosm treatments had a significant multivariate effect on green frog growth and survival (Table 1, Fig. 3). Relative to the control, green frog survival was not affected by caged *Ambystoma* ( $P=0.949$ ), caged *Anax* ( $P=0.801$ ), or caged *Ambystoma* plus caged *Anax* ( $P=0.444$ ). However, green frog survivorship was greatly reduced by lethal *Ambystoma*, lethal *Anax*, and lethal *Ambystoma* plus lethal *Anax* ( $P<0.001$ ). Fewer green frogs survived with lethal *Ambystoma* than with lethal *Anax* or lethal *Ambystoma* plus lethal *Anax* ( $P=0.001$ ); the latter two treatments did not differ ( $P=0.243$ ). When lethal *Ambystoma* were present, adding caged *Anax* increased green frog survivorship ( $P=0.020$ ). However, when lethal *Anax* were present, adding caged *Ambystoma* did not affect green frog survivorship ( $P=0.314$ ).

The predator treatments also affected green frog growth (Table 1, Fig. 3). Relative to the control, green frog growth was not reduced with caged *Ambystoma* ( $P=0.173$ ) but tended to be reduced with caged *Anax* ( $P=0.094$ ) and caged *Ambystoma* plus caged *Anax* ( $P=0.075$ ). Lethal *Ambystoma*, lethal *Anax* ( $P<0.02$ ), and lethal *Ambystoma* plus *Anax* all reduced green frog growth ( $P<0.02$ ). When lethal *Ambystoma* were present, adding caged *Anax* did not further reduce green frog growth ( $P=0.965$ ); when lethal *Anax* were present, adding caged *Ambystoma* did not further reduce green frog growth ( $P=0.162$ ).

In the analysis of green frog morphology, we found that *Anax* affected the morphology of green frogs but *Ambystoma* did not (Tables 2, 3, Fig. 4). Both tail length



**Fig. 4** The relative tail length and body length (means $\pm$ 1 SE) of larval green frogs reared with *Anax* (NA no *Anax*, CA caged *Anax*, LA lethal *Anax*) and *Ambystoma* (NT no *Ambystoma*, CT caged *Ambystoma*, LT lethal *Ambystoma*). Differences in overall size were removed prior to analysis by regressing the dimensions against mass and saving the residuals

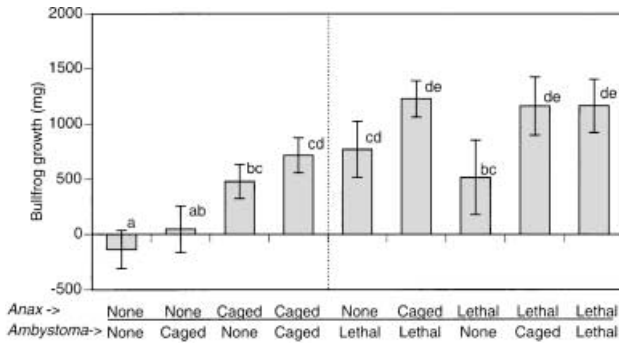


**Fig. 5** The relationship between developmental stage and mass of larval bullfrogs. After Gosner (1960) stage 41, mass significantly declined as the tadpoles underwent metamorphosis ( $R^2=0.630$ ,  $F_{1,196}=333.1$ ,  $P<0.001$ ). The line represents a linear regression across stages 41–45

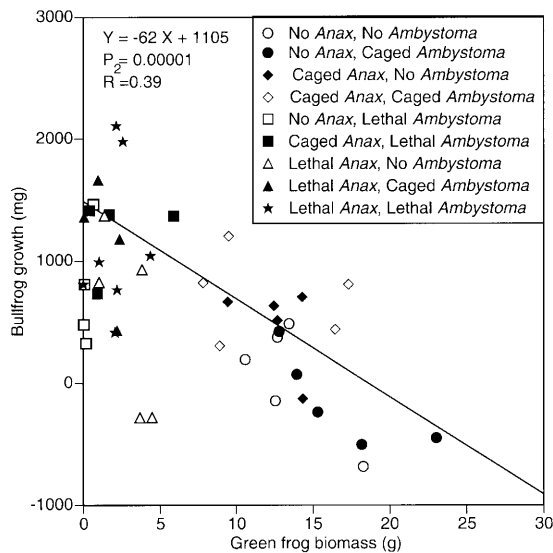
and body length changed in the presence of *Anax*. Green frogs that survived lethal *Anax* had shorter tails ( $P<0.003$ ) and shorter bodies ( $P=0.068$  and  $P=0.003$ , respectively) than green frogs reared with caged *Anax* or no *Anax*.

### Bullfrogs

Bullfrog growth (developmentally adjusted) differed among treatments. Bullfrog mass achieved a maximum at Gosner stage 41 (Gosner 1960) and then declined as the animals began to metamorphose (Fig. 5). The linear



**Fig. 6** Mass of larval bullfrogs raised under different predator treatments. Peak mass was back-calculated for those bullfrogs that had achieved a Gosner (1960) developmental stage >41 based on the linear relationship displayed in Fig. 5. Data are means  $\pm$  1 SE. Means with common superscripts are not significantly different ( $P > 0.07$ )



**Fig. 7** The relationship between the total biomass of green frogs (surviving green frogs  $\times$  mean green frog mass) and bullfrog growth in the mesocosm experiment. Each data point represents one experimental unit. The regression line is a single regression fit through all of the data points

regression of developmental stage against mass (for all individuals of stage=41) produced a significant negative relationship that described mass loss during metamorphosis ( $R^2=0.630$ ,  $F_{1,196}=333.1$ ,  $P < 0.001$ ) and we used this relationship to back-calculate the peak mass of individual bullfrogs that were developed beyond stage 41.

Using these back-calculated bullfrog masses, we found a significant effect of *Ambystoma* ( $F_{2,35}=8.2$ ,  $P=0.001$ ) and *Anax* ( $F_{2,35}=8.0$ ,  $P=0.001$ ) on bullfrog growth, but no *Anax*-by-*Ambystoma* interaction ( $F_{4,35}=0.7$ ,  $P=0.627$ ; Fig. 6). Bullfrog growth was unaffected by caged *Ambystoma* ( $P=0.571$ ), but tended to increase with caged *Anax* ( $P = 0.064$ ). Adding lethal predators, either alone or in combination, also increased bullfrog growth. Adding caged *Anax* to tanks with lethal *Ambystoma* did not significantly increase bullfrog growth

( $P=0.215$ ), but adding caged *Ambystoma* to tanks with lethal *Anax* tended to increase bullfrog growth ( $P=0.068$ ). When we examined whether the above changes in bullfrog growth were due to competition between bullfrogs and green frogs, we found that bullfrog growth linearly increased as green frog biomass declined ( $P=0.00001$ ,  $F_{1,42}=26.5$ ,  $R^2=0.39$ ; Fig. 7), with bullfrogs achieving maximal growth in treatments containing lethal predators.

## Discussion

In our relatively simple five-component community, we observed a wide variety of direct and indirect links among species when we manipulated the presence and absence of caged and lethal predators. These links included direct predation, exploitative competition, interference competition in the form of intraguild predation, trait-mediated effects on interspecific competition, and trait-mediated effects on predation. Despite this complexity, we could qualitatively predict the direct and indirect effects of predators in the mesocosm experiment, either singly or in combination, based on our previous laboratory tests of how the predators affected the densities and traits of each other and their prey. We begin by discussing the density effects observed in our system, and then we discuss the trait-mediated effects.

The density effects involved predation by *Anax* on *Ambystoma*, predation by *Anax* and *Ambystoma* on green frogs, and herbivory by green frogs and bullfrogs on the periphyton resources (Fig. 8). Predation between the two predators was asymmetric. The predation by *Anax* on *Ambystoma* was not surprising given the wide range of prey that *Anax* can kill; *Anax* can be a voracious predator on 300 mg larval *Ambystoma* and 500 mg larval anurans (K. L. Yurewicz, personal observations; Eklöv and Werner 2000). Intraguild predation probably occurred very early in the experiment because green frogs reared with lethal *Anax* plus lethal *Ambystoma* did not differ in their survival or growth from green frogs reared with lethal *Anax* alone. In contrast, there was no predation by *Ambystoma* on *Anax*; this was likely due to a gape limitation of *Ambystoma* (K. L. Yurewicz, personal observations).

Relative predation rates of lethal *Ambystoma* and lethal *Anax* on green frogs and bullfrogs in the mesocosm experiment were consistent with earlier experiments. Second-year bullfrogs were simply too massive to be successively attacked by either predator; thus, there was no predation on bullfrogs. In contrast, recently hatched green frog tadpoles were highly vulnerable to predation. Past experiments in the laboratory have shown that predation by lethal *Ambystoma* is higher than predation by lethal *Anax* (Relyea 2001b) and we observed the same result in the mesocosm experiment. These results are likely due to trait differences between the two predators, including differences in hunting behavior (ambush-hunting *Anax* versus search-hunting *Ambystoma*) and prey

handling time (faster for *Ambystoma* than *Anax*; Relyea 2001b). Because of these differences in predation risk, one might expect that green frogs would decrease their activity more in the presence of *Ambystoma* than *Anax*. However, recent work on anti-predator responses of anurans has demonstrated that anurans can use a suite of defensive responses and the magnitude of any single response frequently does not correlate with predation risk (Relyea 2001b). Differences in predation rate by different predators appear to be the norm in a variety of taxa (Kohler and McPeck 1989; Wissinger and McGrady 1993; Harris 1995; Kurzava and Morin 1998).

Direct consumer links also existed between each tadpole species and their periphyton prey. Reductions in green frog biomass were strongly associated with increases in bullfrog growth, suggesting that the two species were sharing a limited resource (i.e. periphyton). These two species commonly compete under experimental conditions (Werner 1991; Werner and Anholt 1996; Peacor and Werner 1997; Relyea and Werner 1999). While the growth of bullfrogs and green frogs were apparently connected through their shared resource (a density-mediated effect), the growth of both species was additionally impacted by trait-mediated effects (see below).

There were a number of trait-mediated effects in our experimental food web. While the predation rates by lethal *Anax* or *Ambystoma* alone were qualitatively consistent with past predation experiments in the laboratory (Relyea 2001b), the predation rates could be altered in the caged presence of a second predator. That is, the per-capita interaction rate between the predators and prey depended on the ecological matrix in which the predation took place. For example, when *Ambystoma* was foraging on green frog tadpoles, few green frog tadpoles survived; when *Ambystoma* was foraging on green frog tadpoles and *Anax* were in the area producing chemical cues (i.e. caged *Anax*), green frog survival increased seven-fold. This relatively large increase in green frog survival occurred because green frog tadpoles detected the *Anax* cues and reduced their activity level (see Laboratory experiment) to lower their risk of predation (Gerritsen and Strickler 1977; Skelly 1992; Werner and Anholt 1993; Relyea 2001a). In contrast, when *Anax* was foraging on green frog tadpoles, green frog survival was not affected by *Ambystoma* chemical cues (i.e. caged *Ambystoma*). This lack of a survival difference occurred because *Ambystoma* did not reduce the activity of green frog tadpoles (see Laboratory experiment). Of course, these conclusions are based on the premise that the behavioral changes observed in the laboratory were also occurring in the mesocosms, a pattern that is supported by a number of other anuran studies (Peacor and Werner 1997; Relyea and Werner 1999; Relyea 2002b). From the laboratory experiment, we can conclude that the altered predation rates on green frogs were not due to predators affecting each other's activity (although, other traits not measured could have changed). However, past studies have shown that combined predators can have non-additive effects on prey survival either by altering prey behavior

or by altering each other's behavior (Soluk and Collins 1988; Soluk 1993; Wissinger and McGrady 1993; Peacor and Werner 1997; Soluk and Richardson 1997; Levri 1998). In summary, trait-mediated effects from addition of predators can alter per-capita predation rates, and these alterations can be predicted from a knowledge of trait plasticity and trait function.

Trait-mediated effects also altered tadpole growth in directions that were qualitatively predictable. In the laboratory, green frog activity was significantly reduced with caged *Anax* ( $P=0.01$ ) but not with caged *Ambystoma* ( $P=0.12$ ). Reducing activity typically reduces resource consumption in tadpoles as well as many other taxa (Lima and Dill 1990; Werner and Anholt 1996; Kats and Dill 1998; Relyea and Werner 1999). In the mesocosms, green frog tadpoles exhibited marginally significant growth reduction in the presence of caged *Anax* ( $P=0.09$ ), but nonsignificant growth reduction in the presence of *Ambystoma* ( $P=0.17$ ). Thus, *Anax* caused a trait-mediated effect by altering the per-capita interaction rate between green frog tadpoles and their resources but *Ambystoma* did not. This type of predator-induced reduction in prey growth is well supported in this and other experimental systems (Werner et al. 1983; Skelly 1994; Beckerman et al. 1997; Turner 1997; Relyea and Werner 1999; Relyea 2000). The effect of caged *Anax* plus caged *Ambystoma* on growth was always similar to caged *Anax* alone, suggesting that green frog activity with both caged predators may have been similar to green frog activity with caged *Anax* alone (we did not collect behavioral data with combined predators). This hypothesis is well supported in a recent experiment that examined a large number of predator combinations; in 90% of comparisons, pairs of predators induced the same trait state as the single predator that induced the more extreme trait state (Relyea, unpublished data).

The changes in green frog survival and growth caused by the simultaneous presence of multiple predators should have caused a feedback affecting the growth of the lethal predators. That is, if the addition of a second, caged predator altered predation rates of the first predator, this reduced consumption rate should have reduced the growth of the first predator. When *Anax* was lethal, the addition of caged *Ambystoma* did not alter *Anax*'s consumption of tadpoles; as expected there was no difference in the final size of lethal *Anax* between the two treatments. In contrast, when *Ambystoma* was lethal, the addition of caged *Anax* significantly reduced *Ambystoma*'s consumption of larval green frogs by 15% and reduced *Ambystoma*'s growth by 20%. Because the reduced growth was not significant ( $P=0.158$ ), we must conclude that the expected reduction in *Ambystoma* mass did not occur. Based on the laboratory study, it is unlikely that these results were influenced by predators altering each other's behavior; *Anax* activity was unaffected by the presence of caged *Ambystoma* and *Ambystoma* activity was unaffected by the presence of caged *Anax*.

The changes in bullfrog growth were another trait-mediated effect. The predators reduced the activity of



green frog tadpoles, less active green frog tadpoles fed less and grew less (presumably leaving more resources uneaten), and bullfrogs consumed the increased resources (as evidenced by their higher growth). Thus, just as one would predict from the laboratory experiments, caged *Anax* indirectly caused an increase in bullfrog growth but caged *Ambystoma* did not. It was the change in green frog traits, and not a change in green frog density (which did not differ among caged *Anax* and caged *Ambystoma* treatments), that accounted for the change in bullfrog growth. This result has been shown in previous anuran experiments (Werner and Anholt 1996; Peacor and Werner 1997, 2000). As mentioned above, when the predators were lethal, there was little change in green frog biomass and, as a result, little change in bullfrog growth.

Predators can affect not only the behavior of their prey but also the morphology of their prey. Predator-induced changes in morphology can be substantial (Havel 1987; Tollrian and Harvell 1999) and can cause trait-mediated effects (Raimondi et al. 2000; Relyea 2000). Our study took an extensive approach that examined both activity and morphology and we found that predator cues (caged *Anax* and *Ambystoma*) altered green frog activity, but not green frog morphology. Thus, we can rule out the possibility that morphology was responsible for the trait-mediated effects observed in the mesocosm experiment. The lack of significant morphological changes by green frog tadpoles, in response to either predator, is in agreement with previous work on green frog tadpoles (Relyea 2001a). The only treatment that caused a difference in morphology was the lethal *Anax* treatment in which surviving green frogs exhibited shorter tails and longer bodies. These changes are most likely the result of several predatory processes including missed strikes that removed the tips of tails, the preferential killing of tadpoles that possessed relatively larger bodies (i.e. natural selection; Van Buskirk et al. 1997; Van Buskirk and Relyea 1998), and reduced competition due to predation (Relyea 2002a, b). Overall, the morphological data inform us that the trait-mediated effects were likely mediated through changes in green frog behavior and not through changes in green frog morphology.

## Conclusions

In the beginning of this study, we began with numerous potential interactions and we experimentally determined which ones were important. In the end, we saw that lethal dragonflies were predators on both salamanders and green frogs while the salamanders were only predators on green frogs (Fig. 1). The dragonflies reduced the activity of the green frogs and this caused a decrease in green frog predation by salamanders, a decrease in resource acquisition by green frogs, and an increase in resource acquisition by bullfrogs. The salamanders had no significant effect on green frog activity, no effect on resource acquisition by green frogs, and no effect on

resource acquisition by bullfrogs. All of these density- and trait-mediated interactions were qualitatively predictable from a knowledge of (1) per-capita interactions between species pairs, (2) the plasticity of traits in the presence of different species pairs, and (3) how changing traits alter per-capita interactions.

Predicting community structure from pairwise changes in species' density has proven to be a difficult endeavor (Vandermeer 1969; Wilbur and Fauth 1990; Billick and Case 1994). It is increasingly clear that our understanding of species interactions has been limited, in part, because we have not given proper attention to the plasticity of species traits and the impact of trait-mediated effects. It has been long known that trait plasticity is common (see reviews by Lima and Dill 1990; Travis 1994; Schlichting and Pigliucci 1998), but only recently has it become clear that trait plasticity is important beyond the individual; it can be vitally important to other species in the community (Wootton 1992, 1993; Beckerman et al. 1997; Peacor and Werner 1997; Raimondi et al. 2000; Turner et al. 2000; Relyea 2000). It is encouraging to find that when we identify relevant plastic traits and understand their function, we improve our ability to predict community changes. Obviously, most natural communities have many more taxa than the system we studied and this may mean that quantifying pairwise density- and trait-mediated interactions to predict community changes remains a prohibitively large task. It seems that continuing our buildup to larger and more complex communities is the path that lies ahead.

**Acknowledgements** We thank Dexter Bakery, Neil Kubica, and Keith Wittkopp for their hard work in assisting us in the experiments. Thanks also go to Ronald Nussbaum and Richard Alexander for providing access to the E.S. George Reserve. Jason Hoverman, Shannon McCauley, Andy Turner, Earl Werner, and Mara Zimmerman provided many helpful comments on the manuscript. This work was supported by University of Michigan research grants, Sigma Xi research grants, a University of Michigan Regents' Fellowship to K.L.Y., and NSF grant DEB-9701111 to R.A.R. Animal care was within institutional guidelines.

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