

LETTER

Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities

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Abstract

Communities assemble through a combination of stochastic processes, which can make environmentally similar communities divergent (high β -diversity), and deterministic processes, which can make environmentally similar communities convergent (low β -diversity). Top predators can influence both stochasticity (e.g. colonization and extinction events) and determinism (e.g. size of the realized species pool), in community assembly, and thus their net effect is unknown. We investigated how predatory fish influenced the scaling of prey diversity in ponds at local and regional spatial scales. While fish reduced both local and regional richness, their effects were markedly more intense at the regional scale. Underlying this result was that the presence of fish made localities within metacommunities more similar in their community composition (lower β -diversity), suggesting that fish enhance the deterministic, relative to the stochastic, components of community assembly. Thus, the presence of predators can alter fundamental mechanisms of community assembly and the scaling of diversity within metacommunities.

Keywords

Beta-diversity, community assembly, determinism, *Lepomis cyanellus*, local richness, predation, regional richness, stochasticity.

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Discovering how local communities assemble from a regional species pool is a fundamental goal of metacommunity ecology, which investigates patterns and processes leading to variation in species diversity and composition across spatial scales (Holyoak *et al.* 2005). Two types of processes operate simultaneously to influence the assembly of species into a local community. Stochastic processes include colonization/extinction dynamics (MacArthur & Wilson 1967), ecological drift and dispersal limitation (Hubbell 2001). These, when coupled with priority effects (reviewed in Samuels & Drake 1997, Chase 2003; Beisner *et al.* 2003), can create highly divergent communities among otherwise similar localities. That is, when stochastic processes predominate, communities with high site-to-site variation in species composition can emerge – creating high β -diversity (*sensu* Whittaker 1972) – even when environmental conditions among sites are similar. Alternatively, deterministic processes, including niche differentiation, trait by environment matching and interspecific interactions (e.g.

Chase & Leibold 2003) operate to create communities that generally have little site-to-site variation in species composition (low β -diversity) when environmental conditions are similar.

The debate regarding the relative importance of stochastic vs. deterministic processes in the assembly of local communities has been a theme in the ecological literature for decades (e.g. Gleason 1927; Clements 1936; Connor & Simberloff 1978; Drake 1991; Chase 2003). Most recently, these issues manifested in the debate regarding the relative role of neutral processes (stochasticity) relative to those based on niche relations (determinism) (see e.g. Hubbell 2001; Chase & Leibold 2003), and it is becoming well accepted that both processes occur simultaneously in the assembly of local communities (e.g. Gravel *et al.* 2006; Leibold & McPeck 2006; Adler *et al.* 2007). Several factors are known to alter the relative importance of stochastic vs. deterministic processes in community assembly, which can influence the level of β -diversity among environmentally

similar sites. These include landscape features such as habitat connectivity and habitat size (Drake 1991; Forbes & Chase 2002; Chase & Ryberg 2004; Fukami 2005; Orrock & Fletcher 2005) and environmental conditions such as habitat productivity (Chase & Leibold 2002; Fukami & Morin 2003; Chalcraft *et al.* 2008) and disturbance (Chase 2007; Jiang & Patel 2008). However, to date, the majority of studies on the niche vs. neutral debate, and more generally, stochastic vs. deterministic factors in community assembly, have been agnostic towards interactions among species at multiple trophic levels.

Top predators might also be expected to alter community assembly (e.g. Morin 1984; Louette & De Meester 2007) and the relative importance of stochastic vs. deterministic processes in prey community assembly because they can shift patterns of prey coexistence, relative abundance and diversity (e.g. Brooks & Dodson 1965; McPeck 1998). While the effects of top predators on local richness have been well studied (reviewed in Proulx & Mazumder 1998; Chase *et al.* 2002), much less attention has been paid to how those local effects scale-up to alter compositional divergence (β -diversity) and regional diversity at the metacommunity scale (but see Shurin & Allen 2001). However, because top predators are often distributed heterogeneously across landscapes, their presence/absence can greatly alter prey colonization and extinction rates, the realized pool of species that can live in a given locality, and potentially the relative importance of stochastic vs. deterministic processes in prey community assembly.

Predators can increase the importance of stochastic processes by reducing the number of individuals that can live in a given locality and thus the community size (Orrock & Fletcher 2005), and by increasing the probability of species going extinct locally (Ryberg & Chase 2007). Because there are fewer individuals per locality when community size is smaller, there is a greater likelihood that stochastic processes can play a strong role in the structure of the community leading to increases in compositional divergence (higher β -diversity) among environmentally similar sites. However, it is also possible that predators are more likely to drive rare species stochastically extinct, and if the same species are rare in every locality, this could lead to compositional convergence (lower β -diversity) among environmentally similar sites.

Predators can also alter the community assembly process by changing the size of the realized pool of species that are able to colonize a given locality (Schoener & Spiller 1996; Wellborn *et al.* 1996). First, predators can often decrease the overall pool of species that can persist in a given locality, particularly by deterministically driving certain highly vulnerable species extinct. In this case, a smaller predation-filtered pool of potential colonists decreases the likelihood that stochasticity can play a role in final community

structure leading to decreases in compositional divergence (β -diversity) among environmentally similar sites (Law & Morton 1996; Chase 2003, 2007; Fukami 2004). That is, predators may simultaneously increase the importance of stochastic processes, by reducing the total number of individuals locally (community size), leading to community divergence, while increasing the importance of deterministic processes by decreasing the realized species pool available for colonization, leading to community convergence; the net effect would then depend on the relative importance of community size vs. the size of the species pool on community assembly. Alternatively, predators can act in a keystone manner, increasing the number of species that can possibly persist in a habitat area by suppressing the competitive dominants and allowing more predator-tolerant species to persist (Paine 1966; Leibold 1996). In this case, predators would act to increase the likelihood of community divergence if they both decrease community size (fewer total individuals) and increase the pool of potential species that can persist in a given habitat.

Predators can also alter the traits of species with which they coexist (e.g. Hall *et al.* 1970; Wellborn *et al.* 1996; McPeck 1998; Chase *et al.* 2002), which can in turn alter the assembly process. For example, species in communities with predators will tend to be weaker competitors overall owing to an often observed competition-predation trade-off (e.g. Paine 1966; Leibold 1996). Such weaker competitors should be less likely to create priority effects in communities once they colonize (Chase 2003), and thus would express low β -diversity. Alternatively, if prey species in the presence of predators are strong apparent competitors and this trades off with the ability to compete for resources, the presence of predators could lead to more intense priority effects and higher β -diversity (Holt *et al.* 1994; Chase & Leibold 2003).

Importantly, by potentially influencing β -diversity, either positively or negatively, top predators can alter the partitioning of local (α) and regional (γ) diversity ($\gamma = \alpha * \beta$ or $\gamma = \alpha + \beta$) within metacommunities. For example, if predators decrease β -diversity across a metacommunity, they strongly reduce regional diversity relative to a metacommunity with no predators, even if their effects on local diversity are small or even positive. Alternatively, if predators increase β -diversity across a metacommunity, negative effects of predators locally can be tempered at the regional scale.

Small freshwater ponds represent an ideal study system in which to examine the influence of top predators on the scaling of diversity within metacommunities because: (1) they represent insular systems in which α -, β -, and γ -diversity can be easily partitioned (Chase & Leibold 2002; Chase 2003, 2007; Chase & Ryberg 2004); (2) Fish represent important, but dispersal-limited, top predators that can have

strong influences on prey diversity and community composition in these systems (e.g. Wellborn *et al.* 1996; McPeck 1998; Ryberg & Chase 2007). Although fish in small ponds are generally known to cause severe limitations on local species richness and cause shifts in community composition (e.g. McPeck 1998; Knapp *et al.* 2001; Ryberg & Chase 2007), their influence on β -diversity and γ -diversity are unknown.

In this study, we took a two-pronged approach to examine the influence of predatory fish on the scaling of diversity in prey metacommunities. First, we took advantage of a series of constructed ponds in natural areas, some of which were invaded by one or more species of Centrarchid sunfishes. Second, we established an experiment in artificial ponds (mesocosms) to explicitly manipulate the introduction of predatory green sunfish (*Lepomis cyanellus*). For both studies, we examined the effects of fish on patterns of diversity among a diverse group of invertebrates and amphibians.

METHODS

Pond surveys

We surveyed macroinvertebrates, zooplankton and amphibians from ponds at each of four protected natural areas located near St Louis, MO (USA) (Table S1). Each of these natural areas has a number of small constructed ponds that were a minimum of 35 years old, and located within a matrix of mixed prairie and oak-hickory woodlands. We considered a pond to be fishless if no fish were found after seining 10–20% of a pond's surface area with a 4.5-m, 10-mm mesh seine. The majority of the fish ponds used for this study only had one species of Centrarchid sunfishes [most ponds had *L. cyanellus* (green sunfish), several had *Lepomis macrochirus* (bluegill) and two had *Micropterus salmoides* (largemouth bass)], which are among the most common and voracious predators in these ponds. Although these common sunfishes differ to some degree in their preferred diets, all of these species are generalist predators that readily consume both zooplankton from the water column, as well as many species of pelagic and benthic macroinvertebrates (Werner 1977). A few of the fish ponds we surveyed also had one or more small fish species present [e.g. Cyprinidae (minnows) or *Gambusia affinis* (mosquitofish)] in addition to the Centrarchids.

We specifically chose ponds to minimize variation in pond area, chemistry (e.g. pH, conductivity, total nitrogen and total phosphorus), tree canopy density, and the density of emergent and submerged vegetation (Table S1). We found no systematic differences in these variables between the fish and fishless ponds. While there was an overall marginal effect of site (MANOVA Wilks' Lambda = 0.04,

$F_{27,24} = 1.88$, $P < 0.06$), indicating that sites differed to some degree in pond characteristics, there was no effect of pond type (fish vs. fishless; Wilks' Lambda = 0.75, $F_{9,8} = 0.30$, $P > 0.95$), nor was there an interaction between site and pond type (Wilks' Lambda = 0.49, $F_{27,24} = 0.49$, $P > 0.99$). Univariate results are given in Table S2.

At each of the four natural areas, aquatic invertebrates and amphibians were sampled from three ponds with fish predators and three ponds without (for a total of 24 ponds sampled). Each pond was sampled twice in 2006, once during May 15 to June 5 and once during August 15 to September 3, to capture the natural phenology of pond species (e.g. both early and late breeding amphibians and Odonates, zooplankton with seasonal succession). Species found in either of the sampling periods were included in analyses for presence–absence data. For analyses based on abundance data, we totalled the estimated biomass of each species from across the two sample dates.

Macroinvertebrates and larval amphibians were censused using standard 'stove-pipe' sampling (e.g. Turner & Trexler 1997); we specifically used a 36 cm diameter x 1 m tall plastic cylinder, and sampled three such cylinders exhaustively (i.e. no live animals in five consecutive sweeps) with a 15 cm rectangular net with 0.33 mm mesh netting. Invertebrates were preserved in 70% ETOH for later identification and enumeration under a dissecting microscope, while amphibians were identified, counted and released after the pond census was complete. To capture rare species for the presence–absence data, we made 20 sweeps with a 30 cm-wide D net with 1 mm mesh throughout the volume of the pond; any individual from a taxon not collected, or from difficult to differentiate taxa, was preserved for later identification. Five stratified zooplankton samples were collected from across each pond by pulling a 10 cm diameter 80 μ m zooplankton net through the water column for ~5 m. Zooplankton samples were concentrated to 50 mL and preserved in Acid Lugols solution for later identification and enumeration.

In the laboratory, with a few notable exceptions, we identified individuals to species (or in rare cases, to broader taxonomic grouping when species was too difficult to discern) using a variety of keys and/or comparisons to a library of collected specimens identified to species by taxonomic experts. Particularly cryptic species of some difficult to distinguish taxa were lumped into a single category (particularly some genera of Coleoptera, Odonata and Diptera; Table S3). Such minimal lumping should not alter our qualitative results comparing the community structure and predictability of fish vs. fishless ponds, unless there was a systematic bias in our ability to detect taxa in the different pond types. Nevertheless, these taxa represented less than 5% of the species present, and eliminating them

from the analyses provided no qualitative changes to the results.

Mesocosm experiment

Although we minimized environmental variation other than fish presence in our surveys above, fish presence and/or prey composition may have been correlated among ponds due to any number of unmeasured variables. Thus, to test for a causative effect of fish predators, we established a controlled experiment in simulated pond communities (i.e. mesocosms). In May 2005, we established ~1000 L experimental mesocosms in arrays of three spread across the 800 ha facility of Washington University's Tyson Research Center. Sites for arrays were selected to be similar in environmental and spatial conditions (i.e. 10–20% canopy cover, old-field edges, minimum of 200 m from other experimental units or existing ponds). Each mesocosm was initiated with ~4–6 cm of topsoil and well water with nutrient concentrations known to be intermediate relative to surrounding pond habitats ($25 \pm 4 \mu\text{g L}^{-1}$ P : $625 \pm 43 \mu\text{g L}^{-1}$ N). Arrays were randomly assigned to two treatments – fish present or absent – and were replicated four times for a total of eight arrays of three mesocosms (24 total mesocosms).

Experimental communities were initiated using a protocol known to often create variation in communities among otherwise similar habitats (Wilbur & Travis 1984; Chase 2007). Specifically, over the course of the first summer, we inoculated small numbers of individuals of species that were poor colonizers. These included: eight species of submerged macrophytes and their associated filamentous algae (data not presented here); 100 mL aliquots of water containing zooplankton, phytoplankton and other associated microorganisms from a homogenate of water collected from 20 local ponds and concentrated through an 80 μm mesh zooplankton net; and small numbers (three to five individuals per mesocosm depending on the species and numbers available) of several invertebrates that are relatively dispersal limited, including snails (five species), amphipods (two species) and several relatively flightless insects (five species). Additionally, a majority of species that occur in ponds in the area are highly effective colonizers, and readily establish in newly created mesocosms, although colonization and extinction across mesocosms can be stochastic. More than one-half of the taxa that were sampled were not introduced, but colonized and maintained populations in at least one mesocosm on their own (see Table S3).

In early spring (April) of the second year of the experiment (2006), after allowing time for priority effects and random extinction/colonization dynamics to take place, we introduced green sunfish (*L. cyanellus*), to each of the mesocosms in one-half of the experimental arrays. *Lepomis*

cyanellus is among the most common fishes in small Missouri ponds and often is the only fish species present. Further, it is a voracious generalist predator that readily consumes zooplankton, amphibians, and benthic and pelagic macroinvertebrates (Werner 1977). For each mesocosm identified to receive fish, we introduced three medium-sized (30–40 mm) individuals, approximating the average natural density of this species (mean = 0.36 m^{-2}) in nearby ponds (J.M. Chase unpublished data). To our knowledge, few if any individuals died over the course of the experiment, although they did reproduce in some mesocosms.

Because mesocosm sampling was relatively destructive, we only sampled them once per year in July 2006 and 2007. We sampled at this time to capture the majority of species present in one sampling bout (early and late breeding species). To sample macroinvertebrates and amphibians, we used two placements of a $0.2 \text{ m}^2 \times 1 \text{ m}$ stovepipe sampler sampled as above. To capture animals that preferentially use mesocosm walls (e.g. snails) and to more accurately estimate abundances, we used a 25 cm wide 0.33 mm mesh rectangular net pressed firmly against the side of the tank at the bottom and rapidly pulled up towards the surface; this was repeated twice. Individuals were collected, preserved and identified as above. To discover any rare species for the presence-absence data, we swept a 1 mm mesh D-net five times through the water column. Finally, zooplankton were sampled with five haphazardly placed pulls (~15 L total of water collected) of a modified integrated tube sampler (5-cm diameter PVC pipe x 1 m tall) (Paggi *et al.* 2001), concentrated to ~50 mL with an 80 μm mesh zooplankton net, preserved and identified as above.

Although we sampled mesocosms for 2 years, there were no time effects between years; for ease of presentation, we only present results from the final sampling year (2007).

Analysis of local and regional richness

We calculated α -diversity for fish and fishless ponds and mesocosms as the average number of species within each three pond comparison in natural areas or mesocosm arrays, and γ -diversity as the total number of species encountered in each three mesocosm array or three pond region. This gave us a single replicated (average) value of α -diversity and (total) value of γ -diversity for each area and array. Because our interest is in comparing the γ -diversity among fish vs. fishless ponds, our estimate of γ -diversity is not that of the entire region in the natural surveys, but only of the fish or fishless ponds considered separately. Our estimate of γ -diversity from the mesocosm experiment totals the three mesocosms in the array, and thus is not an estimate of the total γ -diversity of fish or fishless mesocosms, but is simply a larger-scale estimate of richness among which we can compare the different treatments. We compared average

local and regional richness values, as well as biomass values, between fish and fishless ponds using paired *t*-tests for the natural areas (fish and fishless ponds were nested within natural areas) and standard *t*-tests for the mesocosm arrays.

A null model approach for comparing incidence-based similarities

Similarity metrics, including incidence-based (e.g. Jaccard's, Sorenson's) and abundance-based (e.g. Bray–Curtis, Morista–Horn) are often used to estimate the inverse of β -diversity (or one-minus the similarity metric). However, most similarity metrics are confounded by variation in local species richness (α -diversity) (e.g. Connor & Simberloff 1978; Raup & Crick 1979; Jost 2007), and predation by fish is known to affect α -diversity. Thus, we could not simply compare the values of similarity among ponds with and without fish. Instead, to evaluate how fish predation altered patterns of community divergence and ultimately the relative importance of stochastic and deterministic processes, we used a null model approach modified from Chase (2007) (based on Connor & Simberloff 1978; Raup & Crick 1979).

Because we were primarily interested in comparing the composition of fish and fishless ponds in each natural area and among treatments, we calculated Jaccard's similarities within each pond category (fish, fishless) from each natural area or mesocosm array. There were three ponds/mesocosms of each treatment in each area/array, and thus we obtained three non-independent pairwise similarity values for each area/array, which we call J_{obs} . We then calculated the null expectation for what pairwise Jaccard's values would look like if community assembly were completely random (stochastic), which we call J_{exp} . J_{exp} can be calculated using the known α -diversity values for each pond, the number of species in the regional species pool, and the proportional occupancy of each species. We used EcoSim v. 7 (Gotelli & Entsminger 2005) to randomly shuffle communities (using the 'Independent Swap' algorithm), holding species richness per locality and the localities occupied per species constant relative to that which was observed. This shuffling was repeated 1000 times to generate a set of null expected communities from which J_{exp} for each pairwise comparison of interest was computed. Finally, we calculated the difference between J_{obs} and J_{exp} for every pairwise comparison as an index of the magnitude by which observed communities deviated from the null expectation; we call the deviation J_{dev} (Jaccard's deviation). We interpret the magnitude of J_{dev} as an index of the strength of determinism acting against otherwise stochastic forces (Chase 2007).

Importantly, value of the null expectation (J_{exp}) and thus J_{dev} is critically dependent on the number of species in the regional species pool; this dependence is shared by similar

randomization procedures (e.g. Raup & Crick 1979). For the pond surveys, we designated the regional species pool in two ways. First, we defined the regional pool as the total number of species found in all of the ponds surveyed at all sites, including both fish and fishless ponds. Because ponds that are closer together are also more likely to experience spatial autocorrelation in their community composition, this will positively bias the values of J_{dev} , but will not influence the relative difference observed between fish and fishless ponds. However, to correct for this bias, we also calculated the regional pool as only those species found in the six surveyed ponds in a given natural area, including both fish and fishless ponds. This regional pool represents the species present in a given area, and by including species that could live in both the fish and fishless ponds, allows the species sorting processes to be observed. For the mesocosm arrays, we only designated the regional species pool as the total number of species observed among all mesocosms in the experiment, including both fish and fishless treatments, so that we could detect the species sorting process. It would not be appropriate to include only those species in the regional pool that occurred in only one mesocosm array. While this could be spatially biased as above, and would again influence the absolute value of the J_{dev} metric, it would not influence the relative difference between treatments. Additionally, we found no indication of spatial autocorrelation between communities that were more closely aligned when all communities were compared separately in a Mantel test comparing community composition and spatial distance ($P > 0.05$), suggesting that our definition of the regional species pool as all species encountered in all of the mesocosms is a reasonable one for the null model analysis.

Other similarity metrics

Because there is still much confusion and debate surrounding the most appropriate similarity metrics to use, and because in some cases, different answers can be obtained from different metrics, we also performed analyses with several other frequently used pairwise similarity metrics. These included simple incidence-based similarity metrics despite their being confounded by variation in α -diversity (Jaccard's, Sorenson's), Raup & Crick's (1979) simulation-based metric estimating probabilities of communities deviating from the null expectation and several similarity metrics that incorporate difference in the relative abundances of species (Chao's Abundance-based Jaccard's, Chao's Abundance-based Sorenson's, Bray–Curtis, Morista–Horn). All of these metrics were calculated using EstimateS version 8.0.0 (Colwell 2005), except for Raup–Crick which was calculated using PAleontological STatistics (PAST) version 1.88 (Hammer *et al.* 2001).

Although pairwise similarity metrics are not independent from one another, and are thus not appropriately analysed with parametric statistics, they can be analysed parametrically if those non-independent values are averaged and the analysis is performed at a higher level on those averages (e.g. Chase & Leibold 2002; Chalcraft *et al.* 2008). By averaging among the pairwise similarity values within sites for the surveys and mesocosm arrays for the experiment, we get an average similarity for the region/array for fish and fishless ponds, which can then be analysed with paired *t*-tests for the natural areas and standard *t*-tests for the mesocosm arrays (with Bonferroni corrections for multiple comparisons) as above. Because similarity data are bounded by 0 and 1, we arcsine square-root transformed all similarity data prior to analyses.

RESULTS

Of the 125 species observed in the pond surveys, 45 species were encountered exclusively in fishless ponds, while seven species occurred exclusively in fish ponds (Table S3); the remainder were found in both pond types, but many varied in their propensity to occur in one pond type or the other. The presence of fish significantly reduced both local (paired *t*-test; d.f. = 3, $t = 4.37$, $P = 0.022$; Fig. 1) and regional richness (paired *t*-test; d.f. = 3, $t = 8.25$, $P = 0.004$; Fig. 1) within each area surveyed. A comparison of the log-response ratio effect sizes of fish ($\ln[\text{fishless richness}] - \ln[\text{fish richness}]$) at local (0.31) and regional (0.72) scales from each pond region showed that the effect of fish was considerably smaller at the local relative to the regional spatial scale (Paired *t*-test; d.f. = 3, $t = -23.59$, $P = 0.0001$). This difference in the magnitude of fish effects at local and

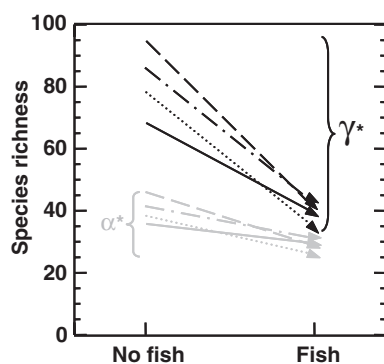


Figure 1 Effect of fish predators on local (grey, α) and regional (black, γ) prey species richness from the surveyed ponds. Arrows show directional effect of fish predators for paired samples (solid – Tyson Research Center, dotted – Reifsneider State Forest, dash-dot – Shaw Nature Reserve, dashed – Augustus Busch Conservation Area). Asterisks indicate a significant difference ($P < 0.05$) among groups using paired *t*-tests (see text).

regional spatial scales is explained by differences in the similarity among fish and fishless ponds. Each similarity metric analysed, including incidence-based and abundance-based similarity metrics, showed the average community similarity was considerably higher in fish ponds than in fishless ponds (Table 1). Finally, the biomass of prey species was more than threefold higher in the absence relative to the presence of fish ($1189 \pm 369 \text{ mg m}^{-2}$ vs. $375 \pm 282 \text{ mg m}^{-2}$; paired *t*-test; d.f. = 3, $t = 3.67$, $P = 0.035$).

Results from the mesocosm arrays mirrored those from the pond surveys. Of the 51 species found among the entirety of mesocosms, 33 were found exclusively in fishless mesocosms while only three were found exclusively in mesocosms with fish (Table S3); the remainder were found in both treatments. Fish significantly reduced both local (*t*-test; d.f. = 6, $t = 7.44$, $P = 0.001$; Fig. 2) and regional richness (*t*-test; d.f. = 6, $t = 8.64$, $P < 0.0001$; Fig. 2) in mesocosm arrays. To discern whether there were differences in the proportional effect of fish on prey richness at the local and regional scales, we randomly paired data from fish arrays with fishless arrays. For each pair, we used the log response ratio to calculate an average local and a regional richness effect size ($\ln[\text{fishless richness}] - \ln[\text{fish richness}]$). A paired *t*-test was used to compare the magnitude of the local and regional effect sizes. Mean effect sizes were considerably smaller at the local (0.62) than at the regional (1.1) scale (paired *t*-test; d.f. = 3, $t = -15.276$, $P = 0.001$). This significant result was achieved with all possible pairings of fish and fishless regions. For each similarity metric analysed, the average community similarity was much higher in fish ponds than in fishless ponds (Table 2). Finally, the biomass of prey species was more than sixfold higher in the absence relative to the presence of fish ($2334 \pm 772 \text{ mg/tank}$ vs. $375 \pm 148 \text{ mg/tank}$; *t*-test; d.f. = 6, $t = 4.98$, $P = 0.002$).

DISCUSSION

Our study is the first to explore the effects of predators on site-to-site similarity (β -diversity) and to address the possible scale-dependent effects of predation on α - and γ -diversity. In both the surveys of ponds in natural areas and in the mesocosm experiment, we found that predators decreased richness at both spatial scales, but that the magnitude of their negative effects was more pronounced on γ -diversity than on α -diversity (Figs 1 and 2). That is, effects of predators were scale-dependent, whereby the reduction in prey species richness was greater at the larger spatial scales (Figs 1 and 2), owing to a re-structuring of site-to-site similarity (β -diversity) by fish predators (Tables 1 and 2).

Although our study can not explicitly elucidate the mechanisms behind the observed effects of fish, we suspect

Table 1 Results of community similarity from the pond surveys. Means [\pm standard deviation (SD)] for each similarity metric in fish vs. fishless habitats. Paired *t*-tests compared the average similarity value calculated from the three pairwise comparisons for fish and fishless ponds among each of the four natural areas

Similarity metric	Mean (\pm SD) without fish	Mean (\pm SD) with fish	d.f.	<i>t</i>	<i>P</i>
Jaccard's deviation	0.059 \pm 0.047	0.458 \pm 0.039	3	-46.904	0.0001
Jaccard's deviation (constrained pool)	0.030 \pm 0.027	0.340 \pm 0.037	3	-16.32	0.001
Raup-Crick	0.139 \pm 0.056	0.994 \pm 0.011	3	-26.657	0.0001
Jaccard's	0.255 \pm 0.027	0.580 \pm 0.065	3	-7.509	0.005
Sorenson's	0.416 \pm 0.026	0.723 \pm 0.049	3	-9.999	0.002
Chao-Jaccard's	0.269 \pm 0.044	0.618 \pm 0.089	3	-7.961	0.004
Chao-Sorenson's	0.396 \pm 0.048	0.716 \pm 0.026	3	-10.905	0.002
Morisita-Horn	0.384 \pm 0.051	0.731 \pm 0.039	3	-14.344	0.001
Bray-Curtis	0.222 \pm 0.046	0.531 \pm 0.179	3	-4.530	0.020

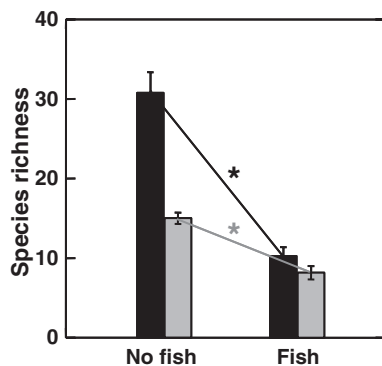


Figure 2 Effect of fish predators on mean (\pm SE) local (grey) and regional (black) prey richness from experimental mesocosm arrays. Asterisks indicate a significant difference ($P < 0.01$) among groups using *t*-tests (see text).

that the reduction in α -diversity in the presence of fish primarily resulted because fish: (1) strongly reduced the overall biomass of all prey species, thus reducing community size and increasing the probability that some species will not be present by chance alone, and (2) having particularly large negative impacts on several of the more vulnerable prey species, including most amphibians, as well as many of the larger species of invertebrates (e.g. dragonfly larvae). Both of these processes would lead to overall lower prey species richness. Additionally, prey species richness could be lower locally due to reduced colonization rates if predators choose habitats to colonize based on their predator regime (Resetarits *et al.* 2005).

At regional spatial scales, the effects of fish were more pronounced than they were locally, and this resulted owing to the fact that the similarity among fish ponds was higher than in fishless ponds (Table 1). Predators reduced the richness of species occurring locally, and reduced the overall abundance of individuals (i.e. community size); both of these effects should increase the strength of stochastic processes

and lead to more divergent communities (Orrock & Fletcher 2005; W.A. Ryberg, K.G. Smith & J.M. Chase, unpublished data). At the same time, predators reduced the size of the realized pool of species that could live in those habitats; this should increase the deterministic component of community assembly and lead to more convergent communities (Chase 2007). Thus, while predators likely altered the strength of stochastic and deterministic processes simultaneously, our results suggest that the increase in deterministic effects overshadowed any increase in stochastic effects.

The deterministic effects of predators on the size of the realized species pool could have occurred through one of two likely processes, or a combination of both. First, while there may be many species in the regional species pool, when top predators are present they can represent a very strong filter on the realized number of species that can actually persist (e.g. Wellborn *et al.* 1996). Thus, from a purely probabilistic standpoint, if only a subset of the total species pool can persist in a given set of localities, those localities will be more similar than the null expectation of random assembly from the entire species pool. Second, divergent community structure may be less likely in localities with top predators due to alterations in the traits of species and structure of their interspecific interactions. For example, when the strengths of interspecific interactions are stronger than intraspecific interactions, priority effects leading to multiple stable equilibria are likely (Chase & Leibold 2003). It is thus possible that species that persist in localities with predators have traits that might make them generally weaker interspecific competitors owing to the competition-predation trade-off (Leibold 1996; McPeck 1998), and are thus less likely to create priority effects leading to divergent community structure among environmentally similar localities. Indeed, experimental results from Louette & De Meester (2007) support the supposition that the presence of a predatory insect reduces the probability that zooplankton communities can exist in multiple stable states.

Table 2 Results of community similarity from the mesocosm experiment. Means [\pm standard deviation (SD)] for each similarity metric in fish vs. fishless habitats. *t*-Tests were performed on the average similarity value calculated from the three pairwise comparisons in each mesocosm array; arrays were replicated four times in each of two treatments (fish vs. fishless)

Similarity metric	Mean (\pm SD) without fish	Mean (\pm SD) with fish	d.f.	<i>t</i>	<i>P</i>
Jaccard's deviation	0.029 \pm 0.035	0.508 \pm 0.077	6	-10.55	0.0001
Raup-Crick	0.237 \pm 0.09	0.999 \pm 0.01	6	-26.028	0.0001
Jaccard's	0.202 \pm 0.018	0.607 \pm 0.077	6	-9.27	0.0001
Sorenson's	0.33 \pm 0.26	0.750 \pm 0.061	6	-10.78	0.0001
Chao-Jaccard's	0.187 \pm 0.049	0.622 \pm 0.191	6	-3.918	0.055
Chao-Sorenson's	0.281 \pm 0.063	0.728 \pm 0.180	6	-4.070	0.046
Morisita-Horn	0.274 \pm 0.091	0.655 \pm 0.182	6	-3.581	0.081
Bray-Curtis	0.197 \pm 0.057	0.433 \pm 0.089	6	-4.333	0.034

Until now, the role of predators in influencing the relative roles of deterministic and stochastic assembly processes has been virtually ignored. This may be because the most popular stochastic assembly models (i.e. neutral models) are zero-sum, assuming that individuals only compete for limited space (e.g. Hubbell 2001), and because the majority of empirical studies focus on a single trophic level or taxonomic group. Here, we suggest that predators can alter the predominant mechanisms underlying the assembly of local communities. We specifically found that in the absence of fish, pond communities were highly divergent among localities that were quite similar environmentally, and that this pattern was predicted by a stochastic assembly process (i.e. neutral). In contrast, we found convergence among otherwise similar localities when predatory fish were present, suggesting a deterministic community assembly process (i.e. niche).

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REFERENCES

- Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007). A niche for neutrality. *Ecol. Lett.*, 10, 95–104.
- Beisner, B.E., Haydon, D. & Cuddington, K.L. (2003). Alternative stable states in ecology. *Frontiers Ecol. Environ.*, 1, 376–382.
- Brooks, J.L. & Dodson, S.I. (1965). Predation, body size, and composition of plankton. *Science*, 150, 28–35.
- Chalcraft, D.R., Cox, S.B., Clark, C., Cleland, E.E., Suding, K.N., Weiher, E. *et al.* (2008). Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology*, 89, 2165–2171.
- Chase, J.M. (2003). Community assembly: when should history matter? *Oecologia*, 136, 489–498.
- Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proc. Natl. Acad. Sci. USA*, 104, 17430–17434.
- Chase, J.M. & Leibold, M.A. (2002). Spatial scale dictates the productivity-biodiversity relationship. *Nature*, 416, 427–430.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago, IL.
- Chase, J.M. & Ryberg, W.A. (2004). Connectivity, scale-dependence, and the productivity-diversity relationship. *Ecol. Lett.*, 7, 676–683.
- Chase, J.M., Abrams, P.A., Grover, J.P., Diehl, S., Chesson, P., Holt, R.D. *et al.* (2002). The interaction between predation and competition: a review and synthesis. *Ecol. Lett.*, 5, 302–315.
- Clements, F.E. (1936). Nature and structure of the climax. *J. Ecol.*, 24, 252–282.
- Colwell, R.K. (2005). *EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples*, Version 8, University of Connecticut, Storrs, CT. Available at: <http://purl.oclc.org/estimates>.
- Connor, E.F. & Simberloff, D. (1978). Species number and compositional similarity of the Galapagos flora and avifauna. *Ecol. Monogr.*, 48, 219–248.
- Drake, J.A. (1991). Community assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.*, 137, 1–26.
- Forbes, A.E. & Chase, J.M. (2002). The role of habitat connectivity and landscape geometry in experimental zooplankton meta-communities. *Oikos*, 96, 433–440.
- Fukami, T. (2004). Community assembly along a species pool gradient: implications for multiple-scale patterns of species diversity. *Popul. Ecol.*, 46, 137–147.
- Fukami, T. (2005). Integrating internal and external dispersal in metacommunity assembly: preliminary theoretical analyses. *Ecol. Res.*, 20, 623–631.
- Fukami, T. & Morin, P.J. (2003). Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, 424, 423–426.
- Gleason, H.A. (1927). Further views on the succession concept. *Ecology*, 8, 299–326.
- Gotelli, N.J. & Entsminger, G.L. (2005). *EcoSim: Null Models Software for Ecology*, Version 7. Available at: <http://garyentsminger.com/ecosim/index.htm>. Acquired Intelligence Inc. & Kesey-Bear, Jerico, VT.

- Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.*, 9, 399–409.
- Hall, D.J., Cooper, W.E. & Werner, E.E. (1970). An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.*, 15, 839–928.
- Hammer, O., Harper, D.A. & Ryan, P.D. (2001). PAST: Paleontological Statistics software package for education and data analysis. *Paleontologia Electronica* 4(1), 9 pp.
- Holt, R.D., Grover, J. & Tilman, D. (1994). Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.*, 144, 741–777.
- Holyoak, M., Leibold, M.A. & Holt, R.D. (eds). (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. University of Chicago Press, Chicago, IL.
- Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Jiang, L. & Patel, S.N. (2008). Community assembly in the presence of disturbance: a microcosm experiment. *Ecology*, 89, 1931–1940.
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427–2439.
- Knapp, R.A., Mathews, K.R. & Sarnelle, O. (2001). Resistance and resilience of alpine lake fauna to fish introductions. *Ecol. Monogr.*, 71, 401–421.
- Law, R. & Morton, R.D. (1996). Permanence and the assembly of ecological communities. *Ecology*, 77, 762–775.
- Leibold, M.A. (1996). A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *Am. Nat.*, 147, 784–812.
- Leibold, M.A. & McPeck, M.A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399–1410.
- Louette, G. & De Meester, L. (2007). Predation and priority effects in experimental zooplankton communities. *Oikos*, 116, 419–426.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McPeck, M.A. (1998). The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol. Monogr.*, 68, 1–23.
- Morin, P.J. (1984). The impact of fish exclusion on the abundance and species composition of larval Odonates: results of short-term experiments in a North Carolina farm pond. *Ecology*, 65, 53–60.
- Orrock, J.L. & Fletcher, R.J., Jr (2005). Changes in community size affect the outcome of competition. *Am. Nat.*, 166, 107–111.
- Paggi, J.C., Mendoza, R. & Debonis, C.J. (2001). A simple and inexpensive trape-tube sampler for zooplankton collection in shallow waters. *Hydrobiologia*, 464, 45–49.
- Paine, R.T. (1966). Food web complexity and species diversity. *Am. Nat.*, 100, 65–75.
- Proulx, M. & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology*, 79, 2581–2592.
- Raup, D.M. & Crick, R.E. (1979). Measurement of faunal similarity in paleontology. *J. Paleontol.*, 53, 1213–1227.
- Reserits, W.J., Binckley, C.A. & Chalcraft, D.R. (2005). Habitat selection, species interactions, and processes of community assembly in complex landscapes: a metacommunity perspective. In: *Metacommunities: Spatial Dynamics and Ecological Communities* (eds Holyoak, M., Leibold, M.A. & Holt, R.D.). University of Chicago Press, Chicago, IL, pp. 374–398.
- Ryberg, W.A. & Chase, J.M. (2007). Predator-dependent species-area relationships. *Am. Nat.*, 170, 636–642.
- Samuels, C.L. & Drake, J.A. (1997). Divergent Perspectives on community convergence. *Trends Ecol. Evol.*, 11, 427–432.
- Schoener, T.W. & Spiller, D.A. (1996). Devastation of prey diversity by experimentally introduced predators in the field. *Nature*, 381, 691–694.
- Shurin, J.B. & Allen, E.G. (2001). Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.*, 158, 624–637.
- Turner, A. & Trexler, J.C. (1997). Sampling invertebrates from the Florida Everglades: a comparison of alternative methods. *J. North Am. Benthol. Soc.*, 16, 694–709.
- Wellborn, G., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.*, 27, 337–363.
- Werner, E.E. (1977). Specific packing and niche complementary in three sunfishes. *Am. Nat.*, 111, 553–578.
- Whittaker, R.H. (1972). Evolution and measurement of species diversity in plant communities. *Taxon*, 21, 213–251.
- Wilbur, H.M. & Travis, J. (1984). An experimental approach to understanding pattern in natural communities. In: *Ecological Communities: Conceptual Issues and the Evidence* (eds Strong, D.R., Jr, Simberloff, D., Able, L.G. & Thistle, A.B.). Princeton University Press, Princeton, NJ, pp. 113–122.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Physio-chemical properties of the ponds surveyed. In all cases, there were no systematic differences between fish and fishless ponds.

Table S2 Results from univariate tests comparing any differences among ponds in several physical, chemical and biological variables. Sites are the four regions sampled, and pond type is fish or fishless.

Table S3 List of species found in fish (F) and fishless (NF) ponds and mesocosms.

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