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Fish Predation Alters Community Predictability in Small Ponds

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FISH PREDATION ALTERS COMMUNITY PREDICTABILITY IN SMALL PONDS

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Abstract:

Predation can have large but variable impacts on prey species diversity. Although the effects of predation are often deterministic, stochastic processes can often influence the outcome on community assembly regardless of predator presence. Top predators can alter several properties of the community, including the abundance and richness of species, as well as the traits of species that can persist with predators. These properties, in turn, may influence the pattern of community assembly and the predictability of community structure from site to site. In this study, we investigated whether the presence of fish predators influenced the site-to-site predictability (similarity in community structure) of invertebrate and amphibian communities in small ponds. First, we surveyed a series of ponds in natural areas that varied in their presence of fish predators and examined local and regional species richness, as well as site-to-site variation in community similarity (i.e., β-diversity). Second, we established a mesocosm experiment in which we introduced fish to one-half of the arrays, and compared their community similarity. In both cases, the presence of fish reduced both local and regional species richness, but importantly, they also caused communities to become more similar in community composition. Thus, fish made communities more predictable from site to site. We conclude that the presence of top predators can alter the relative importance of stochastic versus deterministic processes in the assembly of communities.

Key Words: Community assembly, predation, beta-diversity, local richness, regional richness, fish, Green sunfish, *Lepomis cyanellus*

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Introduction:

Understanding the factors that shape the composition of a community in a given locality is central to the field of ecology (Gleason 1927; Clements 1938; Belyea and Lancaster 1999; Weiher and Keddy 1999). These processes include species responses to the abiotic environment, such as nutrient availability (reviewed in Waide et al. 1999) and disturbance (reviewed by Sousa 1984, Jackson and Fureder 2006), species responses to spatial factors, such as habitat isolation (reviewed in Leibold et al. 2004), and species responses to biotic interspecific interactions, such as competition and predation (reviewed in Chase et al. 2002). Thus, the numbers of species, or biodiversity, that can occur in a given locality is influenced by these same abiotic (productivity [reviewed by Mittelbach et al. 2001]; disturbance reviewed by [Mackay and Currie 2001]), spatial (reviewed by Cadotte 2006), and biotic factors (reviewed by Proulx and Mazumder 1998, Chase et al. 2002).

All of the above-mentioned processes that influence the composition and diversity of species in a community are deterministic, suggesting that, given a set of environmental, spatial, and/or biotic factors in a given locality, the structure of the community in that locality should be quite predictable. However, reasons often exist to expect that various random (stochastic) factors can also influence the composition of species that can occur in any given locality. Such random factors could be legacies of different histories of localities, creating multiple stable states of community composition (Samuels and Drake 1997; Chase 2003a), or at the extreme, completely neutral processes of species colonization and extinction from a given locality (Hubbell 2001, Chave and Leigh 2002). When these random factors are particularly strong, localities that are otherwise similar environmentally can differ considerably in their species composition (Sutherland 1974, Gilpin et al. 1986, Drake et al. 1993, Jenkins and Biukema 1998, Chase 2003a). Hence, examining the predictability of the composition of local communities that are otherwise similar in environment can give considerable insight into relative importance of random versus deterministic mechanisms in determining community assembly (Samuels and Drake 1997, Chase 2003a). Furthermore, because community assembly can lead to either similar or divergent communities from site to site, understanding the processes of community assembly can lead to important insights regarding the scaling of diversity from local (α-diversity) to regional (γ-diversity) scales through site to site variation in community composition (β-diversity) (Chase and Leibold 2002, Forbes and Chase 2002, Chase 2003a, Chase and Ryberg 2004).

Chase (2003a) recently synthesized a series of predictions regarding the environmental and spatial conditions in which historical effects, leading to divergent community structure, should be more prevalent, and when more deterministic effects, leading to convergent community structure should be more prevalent: (1) harsher environmental filters, such as high disturbance or low productivity, should reduce the importance of random processes, and lead to more convergent community structure (lower β-diversity with similar environmental conditions) by differentially filtering species that are unable to persist in those harsh conditions; (2) faster dispersal rates and larger habitat sizes should override the importance of random processes in determining community structure. However, the influence of biotic factors, such as predation, on the patterns of community assembly, has heretofore not been included in this synthesis.

Top predators often vary in the landscape due to deterministic factors such as habitat suitability (e.g., prey availability) and dispersal limitation. Furthermore, these predators can alter prey species' abundance and distribution in a given habitat, and reshape community composition and diversity (e.g., Brooks and Dodson 1965; Paine 1966; Shapiro 1979; Leibold et al. 1997; McPeek 1998; Chase et al. 2002). As a result, the presence or absence of top predators might also have a large influence on the assembly of their prey communities.

Top predators can alter several properties of the community that can in turn influence the pattern of assembly, and hence, the relative predictability of community structure from site to site. Two mechanisms can lead to predators creating more unpredictable communities, and two can lead to predators creating more predictable community structure (Table 1). First, top predators can reduce the number of individuals that can persist in a given locality. When community size is thus decreased, the probability of priority effects influencing final community structure, and thus producing more divergent communities, increases (Orrock and Fletcher 2005). Second, top predators can reduce the diversity of species that can live in a given habitat relative to the total number of species that persist in the regional species pool. When many more species present in the species pool than can live in any given locality, simple probabilistic priority effects will lead to more divergent community structure when predators are present (Law and Morton 1993, 1996; Fukami 2004). Third, if predators differentially influence some species from the regional species pool more than others (Wellborn et al. 1996, Leibold et al. 1997), they can limit the 'realized' number of species that can persist in a given locality, creating a deterministic filter leading to more convergent community structure with predators. Fourth, if prey trade-off in their ability to resist predation and their ability to compete with one another (Leibold 1996, McPeek 1998), species that can persist in the presence of predators are expected to be weaker interspecific competitors. As a result, their ability to create priority effects leading to multiple stable states should be weakened (Chase 2003a), and lead to more convergent community structure with predators.

Based on the above arguments, depending on a variety of mechanisms, predators can either increase or decrease the likelihood that random processes—Hubbell's (2001) concept of 'ecological drift'—will create variation in community structure among habitats that are otherwise environmentally similar. To date, only circumstantial evidence is available allowing the evaluation of the effects of predators on patterns of prey community assembly and the consequent predictability of community structure. In a comparative study taking advantage of the creation of a large reservoir, isolating once connected hilltops into islands, Terborgh et al. (2001, 2006) found that large predators (e.g., large cats) went extinct from these islands, allowing herbivore density to increase and decimate plants. At the same time, herbivore communities appeared to vary more among predator-free islands, likely due to differentially stochastic extinctions of species from different islands. Thus, predator loss may possibly have decreased the predictability of these herbivore communities. Similarly, Glenn et al. (1992) found that grazing cattle increased the similarity among local plots of tallgrass prairies relative to when grazers were excluded.

In this study, we explored the effects of top predatory fish on community assembly and site-to-site predictability in community structure among a diverse array of aquatic invertebrates and amphibians in small pond ecosystems. The distribution of fish across landscapes is often deterministic because fish cannot persist in ponds that periodically dry or are highly anoxic. However, fish are also limited to where they can and cannot disperse, so they are not present in many ponds and lakes that could support them (Magnuson et al. 1998; Knapp et al. 2001; Scheffer et al. 2006). Fish often have dramatic, but variable impacts on the structure of freshwater fauna (Brooks and Dodson 1965; Hall et al. 1970; Eriksson 1979; Zaret 1980; Crowder and Cooper 1982; Wellborn et al. 1996; McPeek 1998). The presence of fish often reduce the richness of many groups of pond dwelling invertebrates and amphibians (Sexton and Phillips 1986, Hansen and Riggs 1995, Hecnar and McLoskey 1997), although in some instances, fish can increase local species richness by differentially reducing the dominant competitor (Werner et al. 1983, Gilinsky 1984, Sih 1985, Shurin 2001). More importantly, fish often a strongly selective filter on which species can and cannot coexist with them (Wellborn et al. 1996). Finally, many species of a variety of taxa that are able to persist with fish are inferior competitors when compared to closely related species that persist without fish (Werner and McPeek 1994, McPeek 1998, Tessier and Woodruff 2002, Wellborn 2002, Stoks and McPeek 2003, Johansson et al. 2006).

Small ponds and experimental microcosms and mesocosms have been used to show large compositional site to site variation in a variety of taxa, much of which can be attributed to historical or random factors leading to multiple community states (Robinson and Dickerson 1987; Robinson and Edgemon 1988; Drake 1991; Drake et al. 1993; Weiher and Keddy 1995; Jenkins and Buikema 1998; Shurin 2001; Chase and Leibold 2002; Chase 2003a,b,c; Chase and Ryberg 2004). Further, the importance of these historical effects leading to variable community structure in otherwise similar habitats varies with pond productivity (Chase and Leibold 2002, Chase 2003a,b,c), permanence (Chase 2003a), and habitat isolation (Chase 2003a, Chase and Ryberg 2004). To date, these studies have only considered ponds deliberately chosen to be fish-free.

Thus, whether top-predatory fish would increase or decrease the similarity (β-diversity) among ponds relative to fish-free ponds remains unclear. If the selective effects of fish on the realized pool of species that can persist in those ponds and/or the selection of prey species that are poorer competitors dominate the assembly process, then we would expect that the presence of predatory fish would increase the similarity among ponds (decrease β-diversity) (Table 1). Alternatively, if the effect of fish on the reduction of local diversity and/or overall community size dominates the assembly process, then we would expect that the presence of predatory fish would decrease the similarity among ponds (increase β-diversity) (Table 1).

We used a two-pronged approach to test among these hypotheses. First, we surveyed the composition of amphibians and invertebrates in ponds that were otherwise similar in spatial and environmental conditions, but varied in whether top predatory fish were present or absent. Second, in order to provide more control for environmental factors that might vary among natural ponds, we established a series of mesocosm arrays at Washington University's Tyson Research Center, where we varied the presence of fish and measured the community structure and similarity among mesocosms within arrays.

Methods:

Pond Surveys:

Pond surveys were performed in 4 natural areas (see Map 1) located near St. Louis, MO (USA): the Tyson Research Center, a ~800 ha biological field station run by Washington University in St. Louis; the Shaw Nature Reserve, a ~1100 ha reserve run by the Missouri Botanical Garden; and two areas operated by the Missouri Department of Conservation, Reifsneider State Forest (~500 ha) and Busch Conservation Area (~2800 ha). Although natural ponds are rare in this region, each natural area had 10-90 ponds created as borrow pits, livestock and wildlife watering ponds, wetland mitigation ponds, and/or small fishing, recreation ponds (Smith et al. 2002) (Table 2). Natural areas were dominated by terrestrial habitats typical of the region, including Oak-Hickory forest, prairie, and old-fields.

We considered a pond to be fishless if no fish were found after seining 10-20% of a pond's surface area with a mesh seine. For fish ponds, we included only ponds that had one or more species of Centrarchidae sunfishes (*Lepomis cyanellus*, *Lepomis macrochirus*, and *Micropterus salmoides*), though many had several other species as well; ponds that had only smaller fish (e.g., Cyprinidae, Poeciliidae) were not sampled. At each site, we chose 6 ponds—three with fish and three fishless—to sample invertebrates and amphibians. To ensure that any community compositional differences were most likely to be due to fish, and not other covarying factors, we specifically chose ponds so that there were no systematic differences (paired t-tests among sites; all P>0.3) in several important factors, including area, average depth, canopy coverage, and water chemistry (Table 2).

Each pond was sampled twice, once early in the growing season (May 15-June 5), and once later (August 15-Sept 3), in order to capture much of the natural phenology of species presence in the ponds (e.g., both early and late breeding amphibians and Odonates, zooplankton with seasonal succession). A species was marked as present in a pond if it was found in either of the sampling periods.

Macroinvertebrates and amphibians were sampled in two ways. First, using methods similar to a box sampler (Macan 1958, O'Connor et al. 2004) and chimney sampler (James and Nicholls 1961, O'Connor et al. 2004), we used a 75 cm-diameter by 73 cm tall plastic cylinder deployed by pushing the bottom in the substrate. After placing the sampler, we pulled a 0.33 mm mesh hand net through the area within the sampler to collect all encountered specimens (except for those large amphibians which could be readily identified to species, which were released after being counted). We continued sampling until no new individuals were encountered in five sweeps. We preserved all collected individuals in 70% ETOH which were then taken back to the laboratory for identification and enumeration (see below). We repeated this procedure three times in each pond. Second, to sample rare species and those that are not readily collected using the above methods (e.g., those which are fast swimmers), we used a second technique wherein we pulled a 5-mm mesh D-net with a 1.5 m handle through the water for 3-5 m at a time. We collected and preserved any individual from a species that was not encountered in the previous sampling and/or when identification was difficult to do in the field (e.g., some Dytiscidae, Coenagrionidae, Libellulidae). We repeated this procedure 20 times, and spread samples vertically and horizontally through the pond.

In the laboratory, with a few notable exceptions, we identified individuals to species (or in rare cases to taxonomic unit) using a variety of keys (for insects, Merritt and Cummins eds. 1996; for zooplankton, Balcer et al. 1989, Pennak 1989; for snails Wu et al. 1997; for invertebrates Thorp and Covich eds. 2001) or in some cases, comparisons to a library of collected specimens identified to species by taxonomic experts (Table 3). Exceptions to this specific identification, where possible groups of very similar species were lumped into a single category due to the difficulty in distinguishing them, included: (1) members of the *Rana pipiens* species complex (*Rana sphenocephala* and *Rana blairi* in these sites) (Anura: Ranidae), (2) members of the *Hyla versicolor*/*chrysocelis* species complex (Anura: Hylidae), (3) members of the *Anopheles quadrimaculatus* species complex (Diptera: Culicidae), (4) members of the *Hyalella azteca* species complex (Amphipoda: Hyalellidae), (5) members of the Chironomidae (Diptera), which we identified only to subfamily, and (6) members of the Ostracoda, which we identified only to family. Despite our efforts, particularly cryptic species of some difficult to distinguish taxa (particularly some genera of Coleoptera, Odonata, and Diptera) may have been lumped together. Nevertheless, such minimal lumping should not alter our qualitative results comparing the community structure and predictability of fish versus fishless ponds, unless those difficult to distinguish species were more likely to be associated with one pond type over the other, which is unlikely.

Zooplankton were sampled by pulling a 10 cm diameter 80 μm zooplankton net through the water column for ~ 5 m (e.g. Harris et al. 2000). This was repeated 5 times at haphazardly varying locations and water depths throughout each pond. Samples were concentrated to 50 ml, preserved in Acid Lugols solution, and brought back to the laboratory for identification and enumeration under a dissecting microscope. Cladocerans and copepods were identified to species and rotifers were identified to species in most cases, but sometimes to operational taxonomic units within genera (using Stemberger 1979, Balcer et al. 1984, Smith 2001). Protists and other single-celled organisms were not examined because of the difficulty to morphologically distinguish between species.

Experimental Mesocosms:

Even though we attempted to maintain everything equal other than fish presence in our surveys, fish presence may have been non-random with respect to ponds. As a result, to examine experimentally the effects of fish presence on patterns of community assembly, as part of a larger project (J. M. Chase, unpublished), we established 24 experimental mesocosms at Washington University's Tyson Research Center (see Map 2). Despite their similarity in environmental conditions, slight variations in initial conditions, even if unintended, could lead to large and long-term variation in species composition in these mesocosms (e.g., Forbes and Chase 2002, Chase 2003b, J. M. Chase unpublished).

In May 2005, we established ~1000 L experimental mesocosms (cattle tanks; see Picture 1) in arrays of three (actually 4, but one was included in a different experiment) spread across the 800 ha facility. Sites for mesocosm arrays were selected to be similar in forest canopy opening (10-20% canopy), and were situated in open forest gaps and old-field edges and each was a minimum of 200 m from other experimental units or existing ponds. Each mesocosm was initiated with 2 cm of topsoil and nutrient-poor well water (from the same well). After the water and topsoil were allowed to settle, the nutrient levels were tested in all mesocosms to find they were intermediate relative to surrounding pond habitats (25±4 μg/L P: 625±43 μg/L N). For this experiment, we had 8 arrays of three mesocosms; four arrays were randomly assigned to examine community composition without fish, and four to examine composition with fish.

Because submerged plants, many algae, zooplankton, and some invertebrates (snails and amphipods) cannot readily colonize these habitats in a reasonable amount of time, we inoculated those species at the initiation of the experiment using a standardized protocol. Several species of macrophytes and macroalgae were collected from nearby ponds, sorted to species, and inoculated into each pond in a standardized amount. Microorganisms and zooplankton (more than 40 species) were inoculated by collecting water concentrated with an 80 µm zooplankton net from 10 nearby ponds that were known to vary considerably in their species composition; 100 ml aliquots of homogenized water were introduced to each mesocosm. Snails (5 species) and amphipods (1 species) were collected from nearby ponds, and 10-15 individuals of each species were introduced to each mesocosm. In addition, a majority of the species that occur in ponds in the area are highly effective colonizers, and readily establish in newly created mesocosms, albeit in a somewhat stochastic manner. In this experiment, more than 40 taxa colonized independently, including Coleoptera (Dytiscidae, Haliplidae, Hydrophilidae, Noteridae), Diptera (Culicidae, Chironomidae, Chaoboridae, Tipulidae), Ephemeroptera (Baetidae), Hemiptera (Corixidae, Notonectidae, Pleidae), Odonata (Aeshnidae, Libellulidae, Coenagrionidae, Lestidae), and amphibians (Anura: Hylidae).

In the early spring (April) of the second year of the experiment, after most species had ample opportunity to establish within, and go extinct from, mesocosm arrays, we introduced predatory green sunfish (*Lepomis cyanellus*) (see Picture 2) to each of the (3) mesocosms in one-half (4) of the experimental arrays. This allowed us to examine whether fish presence in an array would alter the similarity among each mesocosm relative to the fishless mesocosms. *L. cyanellus* is one of the most widespread and abundant fish species in Missouri (Perry 1989) and throughout the Midwest (Werner et al. 1977) because of their wide habitat tolerances, and their broad diet that includes zooplankton, macroinvertebrates, and amphibians (Werner and Hall 1976, 1977; Werner 1977). Additionally, *L. cyanellus* is a relatively small fish (10-20 cm), which makes it an ideal species to use in these mesocosms. For each mesocosm identified to receive fish, we introduced three medium-sized (30-40 mm) individuals, representing an approximately average density of this species (mean=0.36/m^2) in nearby ponds where this species exists in monoculture (J. M. Chase unpublished). Fish used in this experiment were collected from a single pond with a very dense population at Tyson Research Center, and were monitored monthly to ensure individuals were still present. No individuals died over the course of the experiment, and although not intended, many of these fish reproduced, so that ending fish density included many juveniles and was somewhat variable among mesocosms.

We sampled mesocosms during July 2006, in order to capture the majority of species (early and late breeding species) present in the pond. We sampled only once because of the potential destructiveness of our methods, and the time intensiveness of the sampling, identification, and enumeration. Benthic macroinvertebrates and amphibians were sampled in three ways to ensure that we were able to capture a majority of the species in the mesocosm. First, we used a 0.2m^2 x 1 m tall cylinder sampler similar to that used in the pond surveys above. We deployed the sampler in three haphazard locations in each mesocosm and collected, preserved, and identified organisms as above (Table 3). Second, because these mesocosms have steep sides, many organisms preferentially use the sides, and are less likely to be captured in the above methodology. Thus, we used a 25 cm wide 0.33 mm mesh rectangular net; the net was pressed firmly against the side of the tank at the bottom, and rapidly pulled up towards the surface, effectively catching most of the individual organisms on the sides. This was repeated 4 times in each mesocosm, equally spaced around the circumference. Individuals were collected, preserved, and identified as above. Finally, to discover any rare species and/or fast swimming species that might have eluded our quantitative surveys, we pulled a 1 mm mesh D-net 5 times through the water column in opposite directions at varying locations and depths, and collected and preserved any taxa not encountered using the other two methods.

Zooplankton were sampled using a modified integrated tube sampler (5-cm diameter PVC pipe x 1 m tall) (Leibold and Wilbur 1992, Paggi et al. 2001, Shurin 2001, Forbes and Chase 2002). The entire water column was sampled at five haphazard locations within each mesocosm to sample a total of 15 L, which were combined in a large bucket and concentrated to ~50 ml with an 80μm mesh zooplankton net. Samples were preserved in Acid Lugols solution and later identified and counted under a dissecting microscope as above.

Statistical Analyses:

For the pond survey data, we used paired t-tests to compare fish and fishless ponds paired within sites. We compared average local richness as the mean of the 3 ponds from fish and fishless ponds, and regional richness as the total richness observed in all 3 fish or fishless ponds. We further calculated the species compositional similarity among the three ponds with fish and the three fishless ponds for each site using EstimateS software (Colwell 2005). Although we calculated several incidence-based (Jaccard’s, Sorenson’s) and abundance-based (e.g., Bray-Curtis) similarity metrics, we discuss only the results from the Jaccard’s incidence-based metric here. This is because all of the incidence and abundance-based metrics showed qualitatively similar results, and Jaccard’s index is one of the most frequently used similarity metrics in ecological studies. We arcsine square-root transformed Jaccard’s similarity values to meet the assumptions of normality, and with a paired t-test compared fish and fishless ponds by pairing pond types within sites.

For the mesocosm data, we calculated local richness within each array as the average number of species from the 3 mesocosms in an array, regional richness as the total number of species in all 3 mesocosms, and Jaccard's similarity among the 3 mesocosms. We compared the average local, regional, and Jaccard's similarity (after arcsine-square root transformations) among mesocosm arrays with and without fish using two-sample t-tests.

To further understand the distribution of species between the fish and fishless ponds and mesocosms, we examined the proportion of the total number of pond/mesocosms with and without fish that were occupied by each species. This method allowed us to determine whether species occurring in one of the pond/mesocosm types were more (occurring in a higher proportion of the total ponds) or less (occurring in a lower proportion) predictable than in the other pond/mesocosm type. We then performed a one-sided paired t-test (after arcsine-square root transformations) to determine whether any differences seen were significant between fish and fishless for both the ponds and mesocosms.

Results:

Pond Survey:

The presence of fish significantly reduced both local and regional richness, while increasing the similarity among those ponds in their community structure. Local richness with fish (27-31 species) was ~70% that of local richness without fish (36-47 species) (paired *t*-test: $df = 3$; $t = 4.315$, $P < 0.023$) (Figure 1a). Regional richness (the total number of species found in all 3 ponds at each site) with fish (34-41 species) was ~45% that of regional richness without fish (68-94 species) ($df = 3$; $t = 8.464$, $P < 0.003$) (Figure 1b). The Jaccard's indices of similarity among ponds were considerably lower in fishless ponds (0.23 - 0.29) than in fish ponds (0.55 to 0.65) ($df = 3$; $t = 26.765$, $P < 0.0001$) (Fig. 1c). Overall, 45 species occurred only in fishless ponds, while 7 species occurred only in fish ponds; the remaining species were observed in both pond types.

The proportion of the total number of pond/mesocosms that were occupied by each species was significantly different between fish and fishless ponds. Proportionally, a higher amount of species occur at a lower amount of fishless ponds, while a higher amount of species occur at a higher number of fish ponds ($df = 124$, $t = 4.043$, $P < 0.0001$) (figure 3 a).

Mesocosm Experiment:

The results of the mesocosm experiment mirrored the results for the survey data. The presence of *L. cyanellus* significantly reduced the local and regional richness, while increasing the similarity of those tanks in community structure. The local richness of the fish treatments (10 to 15 species) was ~60% that of local richness of the no fish treatments (17-26 species), ($df = 6$; $t = 3.939$; $P < 0.013$) (figure 2a). Regional richness of the fish mesocosms (16-22 species) was ~50% that of fishless mesocosms (28-46 species)($df = 6$; $t = 4.589$; $P < 0.012$) (figure 2b). When comparing the similarity of the two different treatments, with and without fish, we found that treatments with fish had a significantly higher Jaccard's index (0.401 to 0.583) than the treatments without fish, (0.248 to 0.38) ($df = 6$, $t = 3.644$ $P < 0.011$) (figure 2c). Here, 33 species were observed only in fishless mesocosms, whereas 4 species occurred only in fish mesocosms; the remaining occurred in both type of treatments of mesocosms.

The proportion of the total number of pond/mesocosms that were occupied by each species was significantly different between fish and fishless mesocosms. Species in fish treatments were more likely to occur at a higher number of mesocosms, while species in fishless treatments were more likely to occur at a lower number of mesocosms ($df = 65$, $t = 7.760$, $P < 0.0001$)(figure 3b).

Discussion:

Comparisons of the faunal assemblages between fish ponds and fishless ponds, as well as in the experimental mesocosms, reveal dramatic differences in the structure of the invertebrate and amphibian community. Specifically, we found that both local (α) and regional (γ) species richness declined with fish, but that site-to-site similarity increased with fish (lower β-diversity)(Fig. 1 and 2). The fact that fish reduced local diversity is not necessarily surprising, and the same result has been found in several studies (Hanson and Riggs 1995, Batzer et al. 2000; but see Sih 1985, Shurin 2001). However, fish are sometimes thought to be able to increase regional diversity by allowing niche opportunities for species that are less susceptible to predation (but often weaker competitors) to coexist regionally (McPeek 1998, Shurin and Allen 2001, others).

The perspective that predators can enhance regional diversity by allowing different species to coexist in each habitat (Shurin and Allen 2001) does not, however, take into account: (1) the fact that communities are often highly divergent from site to site, leading to high β-diversity, as a result of stochastic factors, and (2) predators may alter this site-to-site predictability through one or more mechanisms (Table 1). Indeed, we found that sites with fish predators were considerably more similar to one another in community composition than sites without fish predators (Fig. 1c and 2c). Fish had a larger effect on regional species diversity, by making species composition from site to site more similar, than on local species diversity.

Our results show that fish predators increased the community compositional similarity among habitats that were similar (in the surveys) or close to identical (in the mesocosms). This suggests that predators altered the assembly process, taking communities that were assembled more stochastically, and making them more deterministic. Indeed, in the experimental mesocosms, although individuals of many species were introduced into every mesocosm in an identical manner, small variations in survivorship and population growth likely led to large variations in community structure. This combined with the stochastic colonization of other species in the regional species pool led to considerable variation among communities in fishless mesocosms. However, the addition of fish to one-half of the mesocosm arrays in the second year of the experiment created a precipitous increase in the similarity of the communities.

Overall, our results suggest that fish imposed a deterministic filter onto these communities and erased the importance of the stochastic assembly process, making them more predictable. In that context, Jaccard's index, as a unit of similarity, is somewhat confounded because it varies with species richness (Rice and Belland 1982; Real and Vargas 1996). As local species richness declines (but the regional pool remains the same), the null expectation would be that communities would become on average more different from one another. This is because when fewer species are present in a locality with the same regional pool, by random probability alone, those communities are likely to share fewer species than when more species are present in the locality (J. M. Chase et al. unpublished). Since the presence of fish reduced the local richness of ponds and mesocosms, the null expectation would be that the presence of fish should cause communities to become more different from one another. But because fish increased community similarity, this result was not due to random chance alone, and instead, fish created more predictable communities.

The four hypotheses by which predators might alter patterns of community predictability (Table 1) predict opposing patterns. The first two hypotheses (1 and 2) predict that top predators will cause communities to diverge, thus making them less predictable. The other two hypotheses (3 and 4) make the prediction that predators will cause communities to converge and be more predictable. Since our results found that top predators cause the community composition to converge, we can immediately conclude that even if the mechanisms inherent to hypothesis 1 and 2 are occurring, they are overridden by the mechanisms in hypotheses 3 and 4. This does not mean that the mechanisms are not occurring, as both stochastic and deterministic processes can occur simultaneously. For example, predators in our study did reduce overall prey biomass (unpublished data), and this result has been found often (Hall et al. 1970, Eriksson 1979, Zaret 1980, Crowder and Cooper 1982, Morin 1984; Townsend 1996, Batzer et al. 2000). Such reductions could increase the likelihood of stochastic processes by reducing the community size (Orrock and Fletcher 2005), even though these processes seem to be overridden by factors that increase the likelihood of deterministic processes (e.g., reductions in the realized species pool).

Both hypotheses 3 and 4 predict that predators should increase the predictability of community structure, however, we cannot necessarily discern the relative importance of these hypotheses, even though both are likely occurring simultaneously. Hypothesis 3 (Table 1) states that if predators differentially influence some species from the regional species pool relative to others (Wellborn et al. 1996, Leibold et al. 1997), they can restrain the 'realized' number of species that can persist in a given locality. We found this in our study, whereby fish lowered the realized pool of species that could persist in fish ponds, which likely created a deterministic filter leading to more convergent community structure. Hypothesis 4 (Table 1) states that prey trade-off in their ability to resist predation and their ability to compete with one another (Leibold 1996, McPeek 1998), such that species that can persist in the presence of predators are expected to be weaker interspecific competitors. As a result, their ability to create priority effects leading to multiple stable states should be weakened (Chase 2003a), and lead to more convergent community structure with predators. Although, we could not test this hypothesis directly, this trade-off does indeed seem to be important in our system (Werner and McPeek 1994, Leibold 1996, McPeek 1998, Tessier and Woodruff 2002, Wellborn 2002, Chase 2003b, Stoks and McPeek 2003, Johansson et al. 2006).

Predation can have significant consequences on the local, regional and β-diversity of communities. In this study, we find that an increase in predictability among pond communities with predatory fish, suggesting more deterministic community assembly, whereas in the absence of fish, communities are less predictable and thus assembled more stochastically. Several mechanisms may contribute to the observed pattern, and we suggest that future research should focus on testing these mechanisms directly. Investigating how communities assemble in the presence of certain conditions (i.e. predation, productivity, disturbance, and spatial isolation) is central not only to community ecology but also restoration ecology (Keddy 1999). Understanding the patterns and mechanisms that naturally shape the composition of a community will help to focus restoration efforts to maximize species diversity at different spatial scales.

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Table 1. General predictions from the four hypotheses on how local communities can either converge or diverge when top predators are present.

Property of Community	Mechanism	Predictability	References
1. Community size	The probability of priority effects influencing final community structure increases.	**Divergent**	Orrock and Fletcher 2005
2. Diversity of species	When many more species are present in the species pool than can live in any given locality, the probability of priority effects increases.	**Divergent**	Law and Morton 1993, 1996; Fukami 2004
3. Regional species pool	Predators create a deterministic filter, which can limit the 'realized' number of species that can persist in a given locality.	**Convergent**	Wellborn et al. 1996, Leibold et al. 1997
4. Traits of prey	Prey species that can persist in the presence of predators are expected to be weaker interspecific competitors and their ability to create priority effects is weakened.	**Convergent**	Leibold 1996, McPeek 1998; Chase 2003a

Table 2. Characteristics of the ponds surveyed.

Site	Pond	Area (m^2)	Ave. Depth (m)	Canopy	pH	Conductivity
Tyson Research Center (Washington University)						
Fishless	Twin 1	1886	2.6	15%	8.24	235
	New	290	0.4	4%	9.15	387
	310 Lagoon	789	0.7	9%	7.89	183
Fish	Twin 2	1963	2.9	12%	8.54	229
	South field	314	0.5	1%	8.13	361
	Railroad	907	0.8	3%	7.74	467
Shaw Nature Reserve (Missouri Botanical Garden)						
Fishless	Wildflower 2	962	1.1	11%	7.87	119
	Wetland 3	868	0.3	2%	9.01	292
	Education	1257	0.2	8%	8.38	397

Fish	Mirror	1294	0.5	0%	8.14	421
	Turtle	3019	1.4	8%	9.54	134
	Wetland 4	1134	0.6	12%	8.87	283
Augustus Busch Conservation Area (Missouri Department of Conservation)						
Fishless	Triangle	3848	0.7	15%	7.94	243
	Fork	1320	0.5	5%	8.42	129
	West Field 1	1863	0.3	22%	8.23	354
Fish	West Field 2	1886	0.9	18%	8.27	249
	Lily Pond	1576	1.1	17%	7.76	198
	East Forest	1499	0.2	11%	8.68	367
Reifsneider State Forest (Missouri Department of Conservation)						
Fishless	RF 1	962	0.7	13%	7.71	191
	RF 4	451	0.4	22%	7.95	237
	RF 5	988	1.1	8%	8.16	145

Fish						
	RF 2	1160	0.4	15%	7.69	233
	RF 3	1128	0.7	24%	7.99	187
	RF 6	754	0.8	4%	8.34	344

Table 3. List of species found in fish and fishless ponds for the survey and mesocosm experiment.

Survey Species Present:

Order	Species	Fish Pond	Fishless Pond
Caudata	*Notophthalmus viridescens*	Y	Y
	Ambystoma maculatum	Y	Y
	Ambystoma annulatum	Y	Y
Salientia	*Pseudacris crucifer*	Y	Y
	Pseudacris triseriata	Y	Y
	Acris crepitans	Y	Y
	Hyla versicolor	Y	Y
	Rana clamitans	Y	Y
	Rana catesbeiana	Y	Y
	Rana sylvatica	Y	N
	Rana sphenocephala	Y	Y
	Bufo americanus	Y	Y
Decapoda	Cambarus	Y	Y
	Orconectes virilis	Y	Y
	Orconectes punctimanus	Y	Y
	Orconectes immunis	Y	N
Veneroida	Sphaeriidae	Y	Y
Euhirudinea	Erpobdella	Y	Y
	Plecobdella	Y	Y
Isopod	Isopod	Y	Y
Amphipoda	Hylalla	Y	Y
	Gammarus	Y	Y
Mesogastopoda	Campanula	N	Y
	Amnicola	Y	Y
Lymnaeidae	*Physa gyrina*	Y	Y
	Gyralus parvus	Y	Y
	Helisoma trivolvis	Y	Y
	Helisoma aceps	Y	N
	Pseudosuccinea columella	Y	Y
	Lymnea elodes	Y	Y
	Ferrisea	Y	Y
	Lymnea stagnalis	Y	Y
Coleoptera	*Acilius fraternus*	Y	Y
	Acilius mediatus	N	Y
	Agabus 1	N	Y
	Agabus 2	N	Y
	Hydroporus 1	N	Y
	Hydroporus 2	N	Y
	Hydroporus 3	Y	Y
	Hygrotus 1	N	Y
	Hytgrotus 2	N	Y
	Laccophilus maculosa	N	Y

	Laccophilus mediatus	N	Y
	Peltodytes literalis	Y	Y
	Berosus 1	Y	Y
	Berosus 2	Y	N
	Tropisternus lateralis	N	Y
	Tropisternus blatchleyi	Y	Y
	Dytiscus hybridus	Y	Y
	Suphisellus bicolor punctipennis	Y	Y
	Suphisellus puncticollis	N	Y
	Hydrocanthus iricolor	N	Y
	Hydrobiomorpha	Y	Y
	Hydropchara	N	Y
	Hydrophilius	Y	Y
	Paracymus confluens	N	Y
	Lioproeus	N	Y
	Thermonectus basillaris	N	Y
	Uvarus lacustris	N	Y
	Hydrovatus pustulatus	N	Y
	Copleatus glyphicus	Y	Y
	Dyticus hybridus	Y	Y
	Heterosternulta pulcher	N	Y
	Hydaticus	N	Y
Diptera	Chaoborus	N	Y
	Mochlonyx	N	Y
	Anopholes quadrimaculatus	Y	Y
	Culex territans	Y	Y
	Culiseta impatiens	N	Y
	Anopheles punctulatus	Y	Y
	Culex pipiens	Y	Y
Ephemeroptera	Callibaetis	Y	Y
Hemiptera	*Belostoma flumineum*	Y	Y
	Buenoa	N	Y
	Notnecta irrorata	N	Y
	Notonecta undulata	Y	Y
	Neoplea plea	N	Y
	Hesperocorixa	N	Y
	Sigara	Y	Y
	Pelocoris	Y	Y
	Ranatra	N	Y
	Lethocerus	N	Y
Odonata	*Anax junius*	N	Y
	Aeshna	N	Y
	Epiaeschna	N	Y
	Epitheca	Y	Y
	Erythemis simplicicollis	Y	Y
	Libellula cynaea	Y	Y
	Libellula incesta	Y	Y

	Libellula pulchella	Y	Y
	Pachydiplax longipennis	Y	Y
	Pantala hymenea	Y	Y
	Perithemis tenera	Y	Y
	Plathemis lydia	Y	Y
	Sympetrum rubicundulum	N	Y
	Sympetrum corraculatum	N	Y
	Tramea lacerata	Y	Y
	Lestes 1	Y	Y
	Lestes 2	Y	Y
	Ischnura	N	Y
	Enallagma A	N	Y
	Enallagma B	Y	N
	Argia	Y	Y
	Eurycercus	Y	Y
Cladocera	Kurzia	N	Y
	Macrothrix	Y	Y
	Moina	N	Y
	Pleuroxus	N	Y
	Scapholeberis	Y	Y
	Simocephalus	N	Y
	Sida	N	Y
	Ceriodaphnia quadrangula	Y	Y
	Diaphansoma birgei	Y	Y
	Chydorus	Y	N
	Bosmina	N	Y
	Daphnia pulex	Y	N
	Daphnia ambigua	Y	Y
	Daphnia rosea	Y	Y
	Daphnia mendotae	N	Y
	Mesocyclops edax	Y	Y
	Diaptomus oregonensis	Y	Y
	Tropocyclops parsinus	Y	Y
Copepoda	Diacyclops	N	Y
	Diaptomus 2	N	Y
	Cyclopoid	Y	Y
Ostracoda	*Ostracod cypricercus*	Y	Y

Mesocosm Experiment Species Present:

Order	Species	Fish Pond	Fishless Pond
Salientia	*Hyla versicolor*	N	Y
Amphipoda	Hylalla	Y	Y
Lymnaeidae	*Physa gyrina*	Y	Y
	Gyralus parvus	Y	Y
	Helisoma trivolvis	Y	Y
	Lymnea elodes	N	Y
Coleoptera	*Acilius mediatus*	N	Y
	Acilius fraternus	N	Y
	Agabus	Y	Y
	Berosus	N	Y
	Peltodytes literalis	Y	Y
	Tropisternus lateralis	N	Y
	Laccophilus maculosa	N	Y
	Laccophilus mediatus	N	Y
Diptera	Anopheles A	N	Y
	Anopholes quadrimaculatus	N	Y
	Culex territans	Y	Y
	Charborous A	N	Y
	Charborous B	Y	N
	Chironomid A	Y	Y
	Chironomid B	Y	Y
Ephemeroptera	Callibaetis	N	Y
Hemiptera	*Notonecta irrorata*	Y	Y
	Notonecta undulata	N	Y
	Buenoa	N	Y
	Neoplea plea	N	Y
	Sigara	N	Y
Odonata	*Pantala hymenea*	N	Y
	Plathemis lydia	N	Y
	Libellula puchella	N	Y
	Libellula luctuosa	Y	Y
	Libellula A	N	Y
	Libellula B	Y	Y
	Pachydiplax longipennis	Y	Y
	Erythemis simplicicollis	N	Y
	Archilestes grandis	N	Y
	Ischnura	N	Y
Rotifera	Rotifer B	N	Y
	Lecane A	Y	Y
	Lecane B	N	Y
	Trichocerca	N	Y
	Platyias patalus	Y	Y
	Brachionus quadridentata	Y	N

	Brachionus angularis	Y	Y
	Monostyla bulla	Y	Y
	Habrotrocha	N	Y
	Tintinnid	Y	Y
	Difflugia oblonga	N	Y
	Difflugia	N	Y
	Difflugia elegans	N	Y
Cladocera	*Ceriodaphnia quadrangula*	Y	Y
	Cladoceran A	Y	Y
	Chydorus sphaericus	Y	Y
	Diaphanosoma birgei	N	Y
	Daphnia	Y	Y
	Bosmina longirostris	Y	Y
	Macrothrix laticornis	Y	N
	Diaphanosoma brachyurum	N	Y
	Cladoceran B	Y	Y
Copepoda	*Mesocyclops edax*	Y	Y
	Copepod A	Y	Y
	Diaptomus oregonensis	Y	Y
	Tropocyclops	Y	N
Ostracoda	*Ostracod cypricercus*	Y	Y
Hydrachnida	Hydrovolziodea	Y	Y
Oligochaetes	branchiodellida A	Y	Y

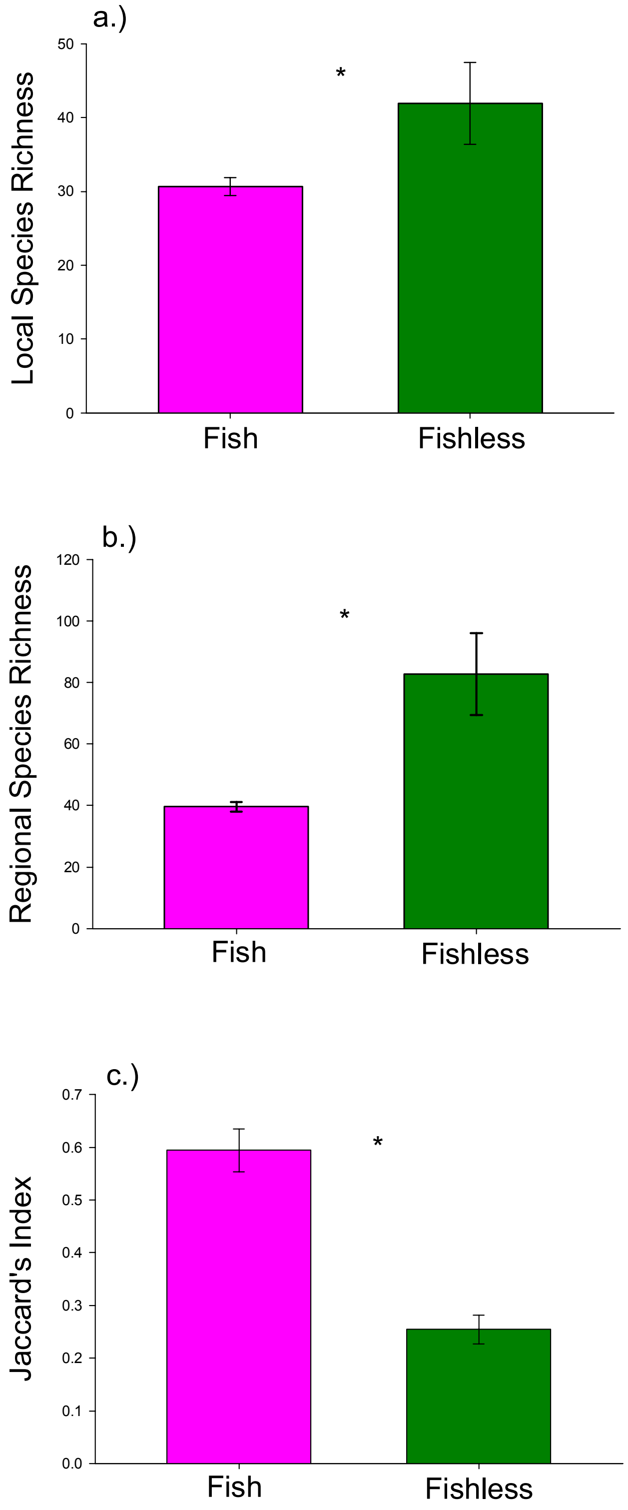


Figure 1. (a) Local species richness ($P < 0.023$), (b) regional species richness ($P < 0.003$), and (c) similarity (Jaccard's index) ($P < 0.0001$) of fish and fishless ponds for survey data. Asterisk indicates values are significantly different.

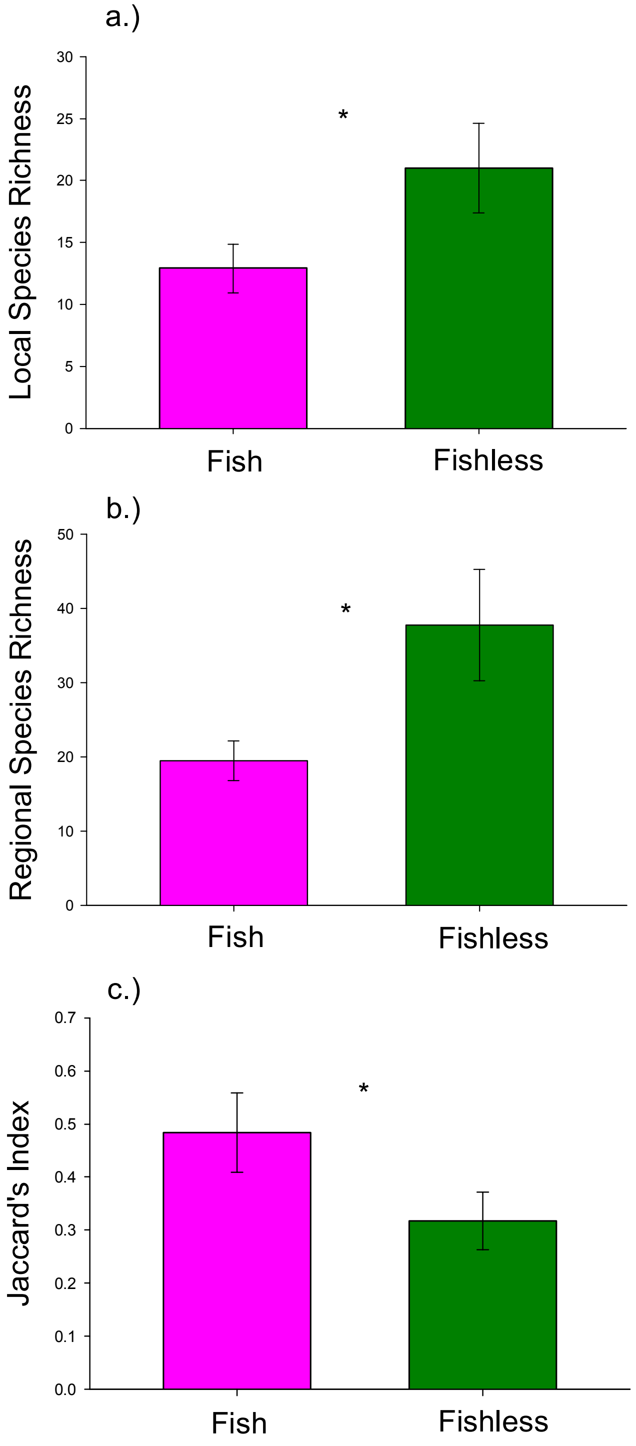


Figure 2. (a) Local species richness ($P < 0.013$), (b) regional species richness ($P < 0.012$), and (c) similarity (Jaccard's index) ($P < 0.011$) of fish and fishless ponds for mesocosm experiment data. Asterisk indicates values are significantly different.

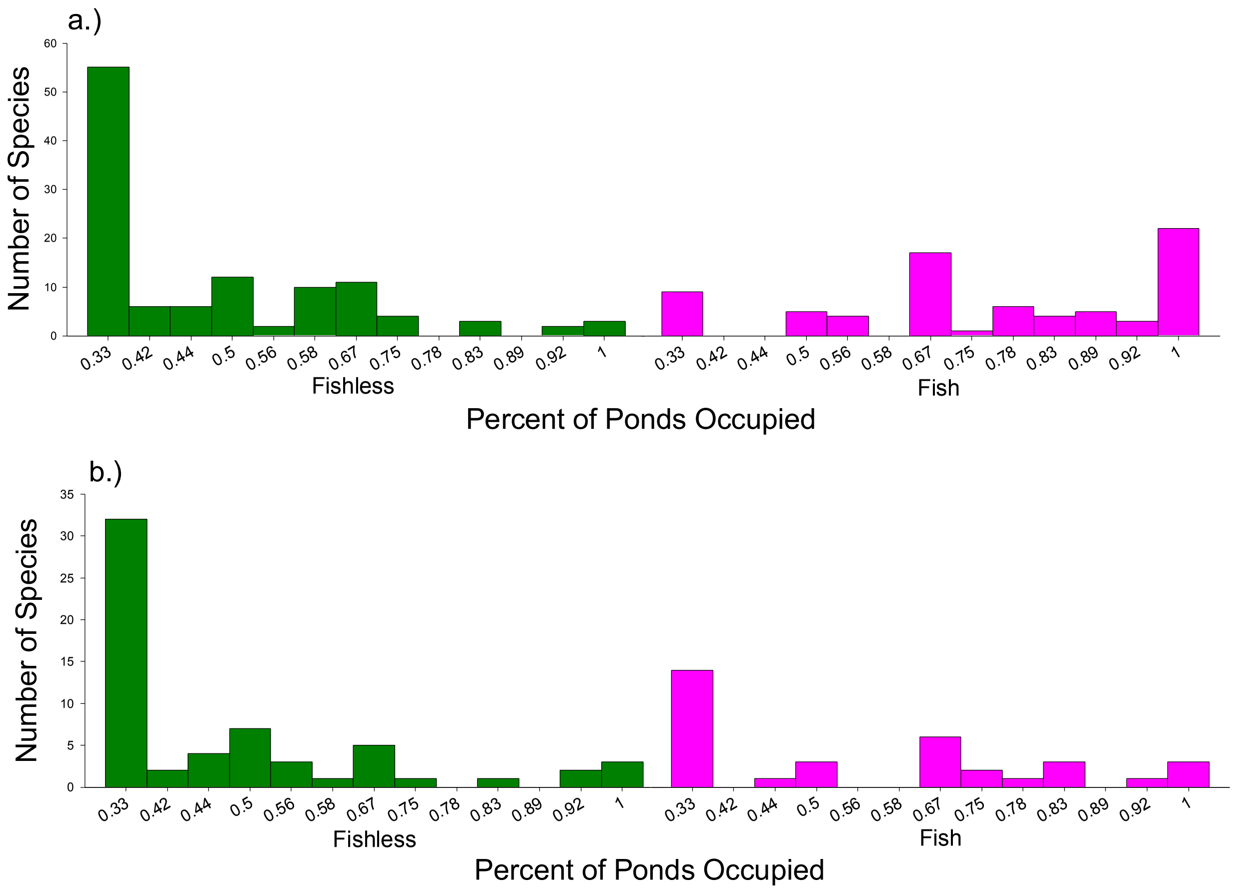
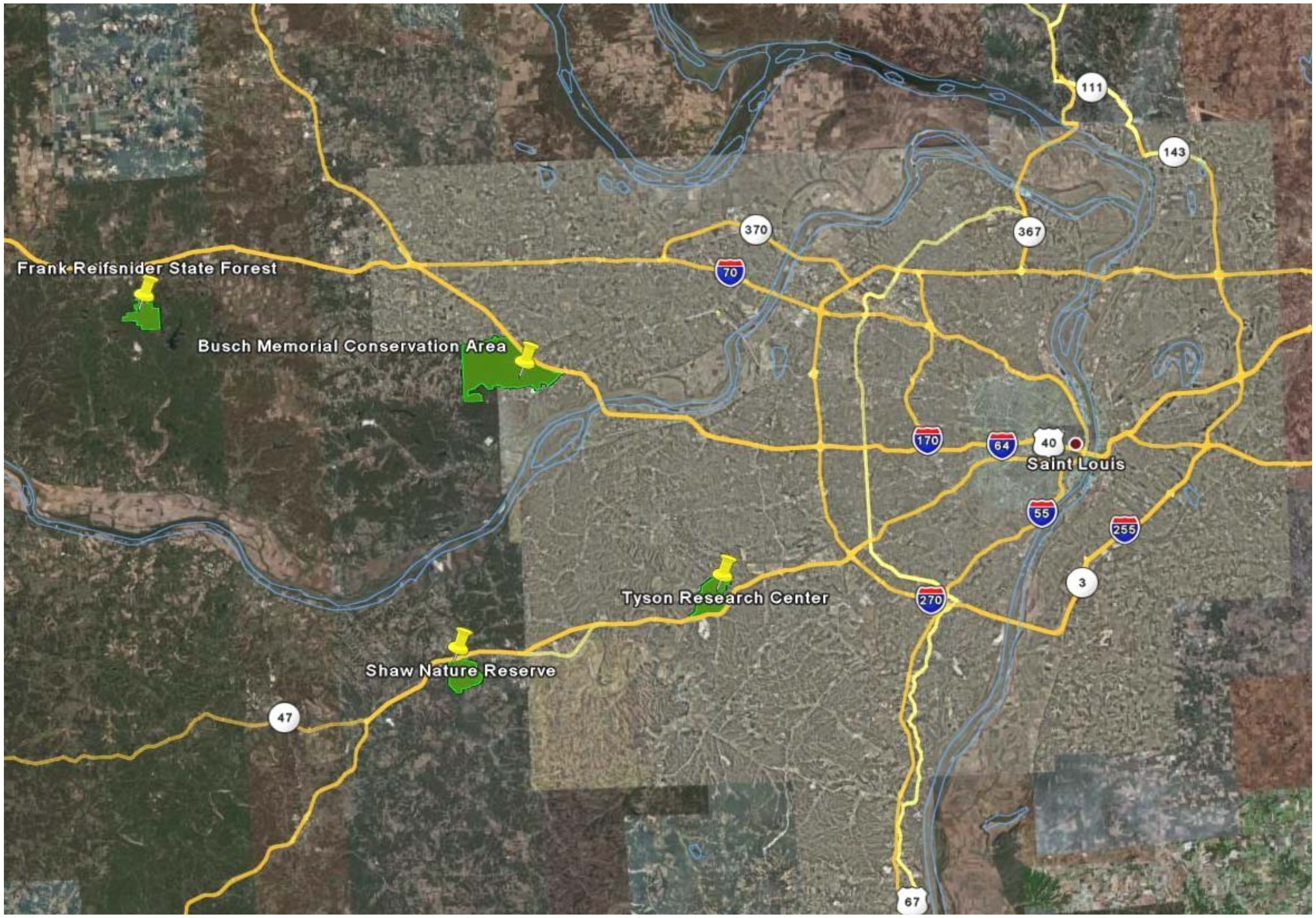


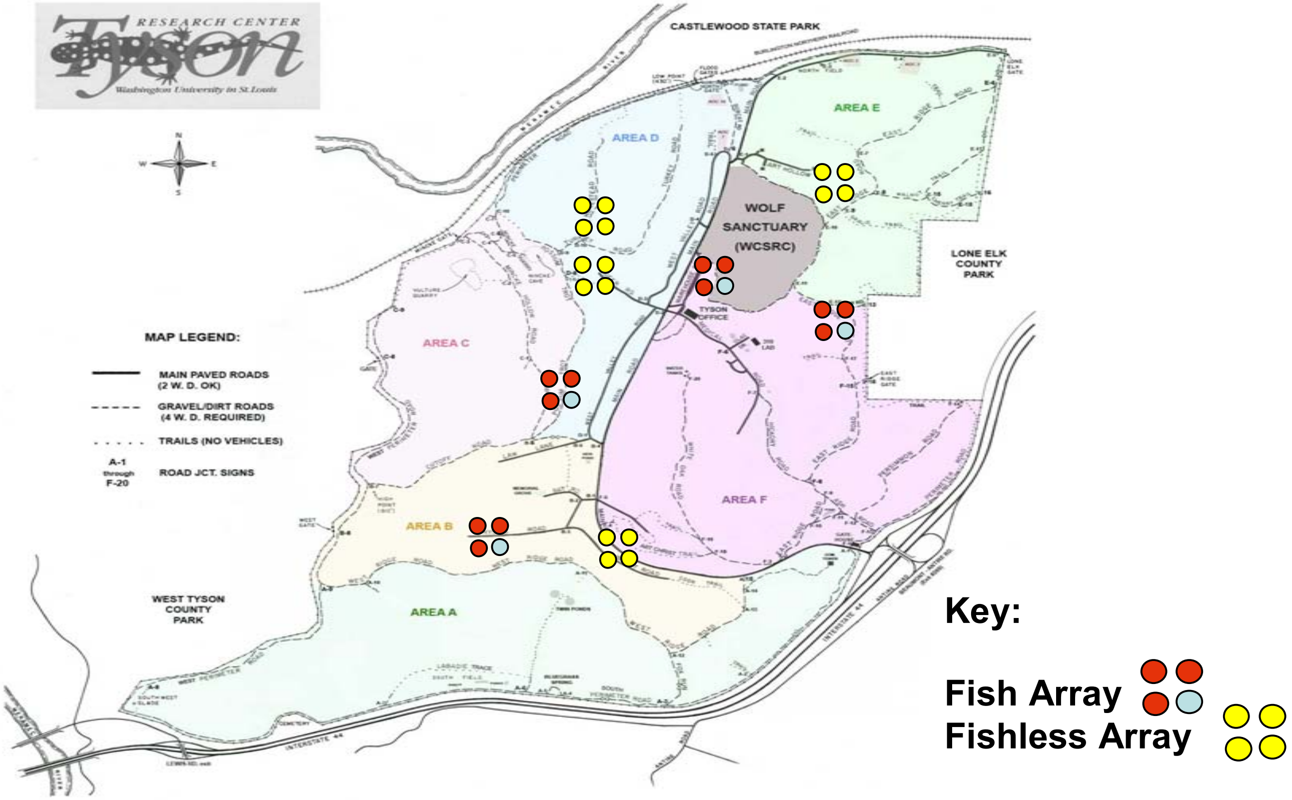
Figure 3. The percentage of ponds (fish and fishless) occupied by species in the regional species pool for the (a) survey data ($P <$ 0.0001) and (b) mesocosm data ($P < 0.0001$).

Picture 1. Array of mesocosms at Tyson Research Center.

Picture 2. Green sunfish (*Lepomis cyanellus*)



Map 1. Location of natural area survey sites in the St. Louis, MO area. Three fish and fishless ponds were sampled at each natural area.



Map 2. Location of fish and fishless mesocosm arrays at Tyson Research Center.