

Experimental evidence for neutral community dynamics governing an insect assemblage

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Abstract. The high levels of species diversity observed within many biological communities are captivating, yet the mechanisms that may maintain such diversity remain elusive. Many of the phenotypic differences observed among species cause interspecific trade-offs that ultimately act to maintain diversity through niche-based coexistence. In contrast, neutral community theory argues that phenotypic differences among species do not contribute to maintaining species diversity because species are ecologically equivalent. Here we provide experimental and observational field evidence that two phylogenetically very distant *Enallagma* species appear to be ecologically equivalent to one another. Experimental abundance manipulations showed that each species gains no demographic advantage at low relative abundance, whereas manipulations of total *Enallagma* abundance resulted in large increases in per capita mortality and large decreases in growth for both species. Moreover, demographic rates and relative abundances of multiple *Enallagma* species were uncorrelated with major environmental gradients in an observational study of 20 natural lakes. These are the expected patterns if species are ecologically equivalent. However, these results do not imply that all damselflies in these lakes are ecologically identical. Previous experimental results have demonstrated the operation of strong coexistence mechanisms maintaining *Enallagma* and its sister-genus *Ischnura* in these littoral food webs. Combined with a simple theoretical model we present, these results taken together show how both neutral and niche dynamics can jointly structure communities.

Key words: coexistence; community structure; damselflies; *Enallagma* spp.; littoral zones; neutral community dynamics; New Hampshire, USA; niche; species diversity.

INTRODUCTION

The mechanisms that generate and maintain high levels of biodiversity remain elusive. Although considerable attention has focused on spectacularly high-diversity tropical systems where, for example, hundreds of beetle (Harris and Burns 2000), butterfly (DeVries et al. 1997), and tree (Condit et al. 2006) species can be found in small areas of forest, the mechanisms that maintain diversity even in less diverse areas remain enigmatic. Indeed, impressive levels of biodiversity are not restricted to the tropics or to unique “hotspots.” For example, at least 78 species in 49 genera of chironomid midges inhabit small stretches of streams in southern England (Ruse 1995), and seven to eight *Sphagnum* moss species are found in almost every bog in eastern Sweden (Rydin and Barber 2001). Regardless of the level of species diversity, the question remains the same: How can so many closely related species all coexist?

Much of ecological theory is directed at understanding how “niche” differences among species promote their coexistence. To coexist (i.e., persist together

indefinitely), the abundance of each species in a community must be regulated by different relative combinations of density-dependent ecological factors (Chesson 2000). If all species in a community coexist, each will be regulated to unique abundances (i.e., equilibrium N_i^* for species i) determined by their differential responses to density-dependent interactions with other community members (Chesson 2000). This implies that each species possesses a unique set of population dynamic parameters quantifying the strengths of interactions with other community members. These species differences in regulatory factors result from phenotypic differences that cause trade-offs in their abilities to perform in the various density-dependent interactions they face (Chesson 2000).

In contrast, the “neutral” view of community dynamics explores the consequences of communities that are composed of ecologically identical species (Hubbell 2001). If species are ecologically identical, they will have identical parameters in functions describing their population regulation. As a result, all ecologically identical species experience the same strength of density dependence determined by the total abundance of all species (i.e., $\sum_{i=1}^n N_i$), and the relative abundances of these “co-occurring” species will drift over time at a rate determined by this total abundance (Hubbell 2001, McPeck and Gomulkiewicz 2005). Species will be lost

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from such assemblages over time due to purely stochastic changes in abundances (Hubbell 2001), but species may persist for very long durations if total abundances are large, if low rates of dispersal between patches occur, and even if species are not exactly ecologically equivalent (McPeck and Gomulkiewicz 2005, McPeck 2008a).

These contrasting views of community structure have primarily been evaluated by comparing relative abundance distributions, but the results of these observational studies have been inconclusive (e.g., McGill 2003, Condit et al. 2006, Muneeppeerakul et al. 2008) and experimental tests are largely lacking (but see Fargione et al. 2003, Wootton 2005, Ellwood et al. 2009). However, the above considerations suggest a strong experimental test to discriminate these alternative perspectives by simultaneously manipulating total and relative species abundances (Leibold and McPeck 2006, Adler et al. 2007, Damgaard 2008, Levine et al. 2008). First consider an assemblage of coexisting species at their demographic equilibria (i.e., all at N_i^*). If their summed total abundance is held constant, but their relative abundances are perturbed, those species perturbed above their equilibria should do poorly (i.e., lower survival, fecundity, or growth rates because for them $(dN_i/N_i dt) < 0$), but those below their equilibria should do well (i.e., higher survival, fecundity, or growth rates because $(dN_i/N_i dt) > 0$). Regardless of whether species are at their demographic equilibria, decreasing or increasing total abundance will cause similar demographic responses in all species. However, for a given total abundance, each species should respond strongly to changes in relative abundances, because the strength of density dependence depends on the distance to its demographic equilibrium.

In addition, (1) relative abundances and density-dependent demographic rates among species should be negatively correlated, because of the necessary interspecific trade-offs inherent in coexistence mechanisms, and (2) relative abundances and demographic rates should covary along environmental gradients shaping density dependence (Chesson 2000). In contrast, in an assemblage of co-occurring, ecologically equivalent species, the demographic performance of each depends on the total abundance of all species and not on its specific abundance (Hubbell 2001, McPeck and Gomulkiewicz 2005). Thus, all species should show strong and comparable density-dependent responses to manipulations of total abundance, but no response to manipulations of relative abundance when total abundance is held constant.

In the study presented in this paper, we examined whether ecological differences among species structure *Enallagma* damselfly (Odonata) assemblages found in lakes with fish. *Enallagma* is a genus of North American origin (last common ancestor dates to ~10–15 million year ago [MYA; Turgeon et al. 2005]), with 34 of the 38 North American species found as larvae exclusively in

lakes with fish (McPeck 1998, Westfall and May 2004). All species spend almost 11 months of a 12-month life cycle as aquatic larvae in the littoral zones of lakes. Locally, five to 12 species can be found in almost every fish lake across eastern North America (e.g., Johnson and Crowley 1980, McPeck 1998). Previous field experiments have shown that fish-lake *Enallagma* experience density-dependent mortality from fish predators and density-dependent growth via competition for limiting food resources (McPeck 1998). Thus, density-dependent mechanisms clearly contribute to regulating the structure of these assemblages, but whether these mechanisms regulate individual species or the assemblage as a whole has until now been an open question.

To more concretely illustrate the above concepts for this system, we illustrate how ecological equivalence of species can be layered into a food web model. We have previously modeled the interactions among these damselflies as a keystone predation system (Holt et al. 1994, Leibold 1996, McPeck 1996). In a model assuming Lotka-Volterra predation dynamics, keystone predation can be modeled by the following system equations (Leibold 1996):

$$\frac{dP}{P dt} = \sum_{i=1}^x \alpha_i \beta_i N_i - \delta \quad (1a)$$

$$\frac{dN_i}{N_i dt} = a_i b_i R - \alpha_i P - d_i \quad (1b)$$

$$\frac{dR}{R dt} = rR \left(1 - \frac{R}{K} \right) - \sum_{i=1}^x a_i N_i \quad (1c)$$

where P , N_i , and R are the abundances of the top predator, i intermediate level consumers (*Enallagma* species in this case), and a basal resource, respectively. In this model, the basal prey has logistic population growth in the absence of the consumers, where r is the intrinsic rate of increase and K is the carrying capacity of the resource species. The top predator and all consumers have linear functional responses, where a_i and b_i are the attack rate and conversion efficiency of consumer i feeding on the resource, respectively, and α_i and β_i are the attack rate and conversion efficiency of the top predator feeding on consumer i . Additionally, the top predator has a density-independent death rate δ , and the consumers have density-dependent death rates of d_i .

If the consumers are all different from one another, meaning that the parameters quantifying the strengths of these interactions are different across species, then at most two intermediate consumers can coexist with one another at a stable equilibrium (Leibold 1996; see also Levin 1970, Holt et al. 1994, McPeck 1996 for variations of this model). Their coexistence necessitates a trade-off: one consumer must experience greater per capita mortality from the top predator, but also be poorer at converting the basal resource into new consumers (Leibold [1996] gives exact criteria for their stable

coexistence). Also, each is regulated to a unique abundance defined by the parameters of the model:

$$N_1^* = \frac{a_2 d_1 - r \alpha_2 \beta_2 \left(1 - \frac{R^*}{K}\right)}{a_2 \alpha_1 \beta_1 - a_1 \alpha_2 \beta_2}$$

and

$$N_2^* = \frac{r \alpha_1 \beta_1 \left(1 - \frac{R^*}{K}\right) - a_1 d_2}{a_2 \alpha_1 \beta_1 - a_1 \alpha_2 \beta_2}. \tag{2}$$

Now consider the case in which all the intermediate consumers (Eq. 1b) are ecologically equivalent to one another. We can accomplish this by simply dropping the subscripts on the parameters (e.g., $a_1 = a_2 = \dots = a_{x-1} = a_x = a$), which gives the following:

$$\frac{dP}{Pdt} = \alpha\beta \sum_{i=1}^x N_i - \delta \tag{3a}$$

$$\frac{dN_i}{N_i dt} = abR - \alpha P - d \tag{3b}$$

$$\frac{dR}{Rdt} = rR \left(1 - \frac{R}{K}\right) - a \sum_{i=1}^x N_i. \tag{3c}$$

From this model, we can clearly see that the top predator regulates the summed total abundance of all consumers to

$$\sum_{i=1}^x N_i = \frac{\delta}{\alpha\beta} \tag{4}$$

and all consumers are regulated by identical functions. In fact, any number of consumer species less than $\delta/\alpha\beta$ can co-occur in this system. Thus, the ecological dynamics of this system are independent of the number and abundances of individual consumer species. As far as the ecological dynamics of the food web are concerned, only one intermediate consumer is present with abundance $\sum_{i=1}^x N_i$. In other words, this group of identical consumer species operates as a functional ecological unit within the food web (i.e., a functional group).

METHODS

Experimental abundance manipulations.—We designed an experiment to test predictions from the above theoretical considerations. The experiment was performed September–November 2008 at McDaniel’s Marsh (Enfield, New Hampshire, USA, 43°31’40” N, 72°04’40” W; see Plate 1), where we placed wire cages stocked with macrophytes (*Chara vulgaris*), appropriate relative and total abundances of *Enallagma* larvae, and fish predators (pumpkinseed sunfish, *Lepomis gibbosus*) in the littoral zone of the lake. We focused on fish predators here because previous field experiments have

demonstrated that they impose substantial mortality on *Enallagma* larvae (McPeck 1990, 1998, Johnson et al. 1995). Other experiments have shown that invertebrate predators such as dragonfly larvae impose little or no mortality on *Enallagma* in fish lakes (McPeck 1998). Methods closely followed those used in previous studies (McPeck 1990, 1998, Stoks and McPeck 2003). The cages were 1.2 m high \times 0.6 m diameter cylinders of poultry netting covered with 1.2-mm mesh nylon netting. The cages were closed at the bottom with a plastic dish, extended out of the water, and were open above. Cages were placed in \sim 0.75 m deep water in the littoral zone of the lake.

Because simultaneously manipulating the relative abundances of many species in one design would be prohibitive, we chose to include only two: *Enallagma ebrium* and *E. vesperum*. We chose these for three reasons: (1) their ranges broadly overlap in much of northeastern North America (Westfall and May 2004); (2) they commonly co-occur in lakes where their ranges overlap (McPeck 1998); (3) their last common ancestor is the basal split of the entire genus (\sim 10–15 MYA; Turgeon et al. 2005). This last criterion is critical: if ecological differences exist among *Enallagma* species, they should be most readily apparent between species that are phylogenetically most distantly separated (Webb et al. 2002). We manipulated their total and relative abundances in a 2×2 factorial design, with total abundances of 55 or 165 *Enallagma*/cage and relative abundance levels of 27% *ebrium* : 73% *vesperum* and 73% *ebrium* : 27% *vesperum*. Thus, density-dependent effects of both resource competition and fish predation contribute to any growth and mortality responses expressed in this experimental design. These two demographic rates for each species were the response variables for the experiments. We used MANOVA and ANOVA to determine the effects of total and relative abundances, as well as interactions between these factors. Our goal was not to parse the relative contributions of these mechanisms, but rather to determine whether these species respond differently as their absolute and relative abundances changed (as expected if any ecological differences among them promote their coexistence). Appendix A provides details of the experimental setup.

Enallagma demography along an environmental gradient.—To investigate how *Enallagma* demographic rates (per capita mortality and growth) and relative abundances varied across major environmental gradients, we characterized an overall environmental gradient by quantifying lake primary productivity, predator and prey abundance and diversity, and macrophyte abundance and diversity at 20 lakes throughout New Hampshire, USA (see Appendix B). This region is a center of continental species richness for *Enallagma* (Westfall and May 2004). Our approach here was to broadly estimate values for ecological parameters that might influence *Enallagma* mortality and growth in each

lake (e.g., McPeck 1998, 2008b). Here we summarize our methods; Appendix B provides greater detail.

We quantified the net primary productivity of the littoral food web of each lake by estimating the growth rates (in milligrams of C per day) of attached algae on clay tiles placed on a small floating plexiglass rack in the littoral zone of each lake in early September 2008. During August–September of 2008 we estimated the abundances and diversity of fish and newts (*Notophthalmus viridescens*), the main vertebrate predators of *Enallagma* in lakes with fish (McPeck 1998), in each lake by seining. At each lake we took four standardized seine hauls through the major vegetation types constituting the littoral zone of each lake. Sampling locations were at least 10 m apart (means were used in the analyses).

Macrophytes provide cover and are the main foraging surface for *Enallagma* larvae (Crowley and Johnson 1992), but also the primary oviposition site for adult damselflies (Butler and deMaynadier 2008). During August–September of 2008 we quantified macrophyte abundance and species composition in 0.5×0.5 m quadrats randomly placed along transects through the littoral zone of each lake. Within each quadrat all species were counted and identified to genus or species. The length of transects and the number of quadrats depended on the extent of the littoral zone in each lake and consisted of between 10 and 20 replicates.

Damselfly prey abundances in each lake were quantified by taking 10 replicate samples with a 6-L box sampler (100- μ m mesh; Downing 1986; means were used in the analyses). The sampler was placed over the macrophytes (e.g., where damselflies forage), and the invertebrates were trapped in the sampler. Prey sampling locations were stratified among the various macrophyte types present in each lake, based on the macrophyte sampling. Samples were sorted in the laboratory, and all captured prey were identified to the lowest possible taxonomic unit (family or genus in most cases). We combined all taxa that were potential prey of *Enallagma* (based on body size) and conducted a principal component (PC) analysis to reduce the dimensionality of these data. The first PC accounted for $\sim 16\%$ of the total variation, with most taxa loading positively on the first PC. Thus, we considered PC1 as an overall measure of prey abundance.

During September–November of 2008 we sampled *Enallagma* larvae to estimate relative and total abundance, species diversity, and mortality and growth rates. At the beginning and again near the end of this period, we sampled *Enallagma* larvae using standardized 1 m long sweeps with a D-frame dip-net (28-cm net opening, mesh size 1×1 mm) at a depth between 0.25 and 0.50 m; this method gives highly repeatable estimates of odonate abundances (Stoks and McPeck 2003). On each sampling date we took 10 replicate sweeps from throughout the macrophytes within the littoral zone of each lake. *Enallagma* larvae were measured for body length using a

dissecting microscope fitted with an ocular micrometer. Per capita mortality and growth rates for each species were calculated as follows: mortality rate = $-\ln(\text{number individuals of the } i\text{th species in the second sample} - \text{number of individuals of the } i\text{th species in the first sample}) / (\text{time between first and second sample})$; growth rate = $\ln(\text{mean body length of the } i\text{th species in the second sample} - \text{body length of the } i\text{th species in the first sample}) / (\text{time between the first and second sample})$. The time between the first and second samples was typically ~ 30 d.

We used simple pairwise correlation analyses to determine whether (1) relative abundances and demographic rates among species were negatively correlated and (2) relative abundances and demographic rates were correlated with environmental variables. While this is an unsophisticated analysis it nevertheless provided a strong test to detect any of the associations from the above predictions. Because of low densities of *Enallagma* in some lakes, we limited our analyses of mortality and growth rates to those lakes where we obtained an initial abundance estimate of ≥ 20 *Enallagma*. This criterion was important for obtaining reliable estimates of mortality and growth rates. We performed the former analysis for each species separately and by combining all species together (e.g., total *Enallagma* abundance and mortality and growth rates). In addition, for the total abundance comparisons we also conducted a canonical correspondence analysis with matrices of the demographic parameters and the various environmental variables.

Null model comparison of species co-occurrence.—We used a null model approach to determine whether patterns of species co-occurrence differed from what we would expect by random chance. In brief, if interspecific interactions shape patterns of species co-occurrence, some species would be expected to co-occur less frequently than by random chance (e.g., Stone and Roberts 1990). We compared patterns of species co-occurrence among lakes with that of 5000 randomly generated matrices using an algorithm that generated matrices with the same number of species and number of samples as the original matrix. Statistical comparisons between the original data and that of the random matrices were made using the *C* score, which is an index of species co-occurrence that measures the mean number of checkerboard units between all possible pairs of species in a co-occurrence matrix (Stone and Roberts 1990). Implementation of the simulation was performed in the program Ecosim (Gotelli and Entsminger 2009).

RESULTS

Experimental study.—For both species, per capita mortality rates in the high total abundance replicates were on average double those in the low total abundance replicates (MANOVA including per capita mortality rates of the two species as response variables, $F_{2,7} = 5.14$, $P < 0.04$), and mean per capita growth rates in the high

total abundance replicates were on average 15% lower than those in the low total abundance replicates (MANOVA, $F_{2,7} = 9.51$, $P < 0.02$; Fig. 1). However, the species showed no responses to the relative abundance manipulation (mortality MANOVA, $F_{2,7} = 2.57$, $P > 0.14$; growth MANOVA, $F_{2,7} = 0.03$, $P > 0.95$) or an interaction between total and relative abundance treatments (mortality MANOVA, $F_{2,7} = 1.16$, $P > 0.37$; growth MANOVA, $F_{2,7} = 2.01$, $P > 0.20$; Fig. 1). Moreover, the two species showed a strong positive correlation across replicates for mortality rate ($r = 0.81$, $P < 0.002$), and the mortality rates of the two species were not different from one another (paired t test, $t_{11} = 1.20$, $P > 0.25$; Fig. 1a). The two species' growth rates were, however, uncorrelated ($r = 0.42$, $P > 0.15$). *Enallagma ebrium* had a slightly higher growth rate than *E. vesperum* (paired t test, $t_{11} = 3.48$, $P < 0.01$; Fig. 1b). Individual species ANOVAs showed similar patterns, indicating that the experimental effects were not driven by a single species (Appendix C).

We combined these mortality data with the data from previous manipulations we have performed using similar methods in experiments done in 1987, 1994, and 1995 in Michigan, USA (McPeck 1990, 1998), to determine whether these per capita mortality results are general across a range of total *Enallagma* densities, a third species (*E. hageni*), and considerable temporal and spatial environmental heterogeneity (see Appendix A). These results all show a strong common pattern: *Enallagma* per capita mortality is strongly density-dependent (ANCOVA total *Enallagma* density term, $F_{1,49} = 43.81$, $P < 0.0001$), and the relationships for the three species are not different (test for heterogeneity of slopes among the three species, $F_{1,49} = 1.71$, $P > 0.19$; ANCOVA test for differences in elevation of regression lines, $F_{2,49} = 0.41$, $P > 0.65$; Fig. 2a).

Observational study.—Our field observational study was designed to test the two ancillary coexistence predictions outlined in the *Introduction*. In our survey of 20 lakes we found that per capita mortality and growth rates and relative abundances of individual *Enallagma* species were not correlated among species or with any of a set of environmental variables that should influence per capita mortality and growth rates; this statement is true even before any Bonferroni correction is applied for multiple comparisons (Fig. 3, Appendix D).

However, consistent with our experimental results, the per capita “mortality rate” of the entire assemblage (i.e., the per capita change in total *Enallagma* abundance) of *Enallagma* species increased with increasing total *Enallagma* abundance (Fig. 2b). The total assemblage mortality rate also increased with increasing fish density (Appendix D). Per capita total growth rate (i.e., the per capita change in mean size of all *Enallagma*) was not correlated with total *Enallagma* abundance, but was positively correlated with prey abundance (Appendix D).

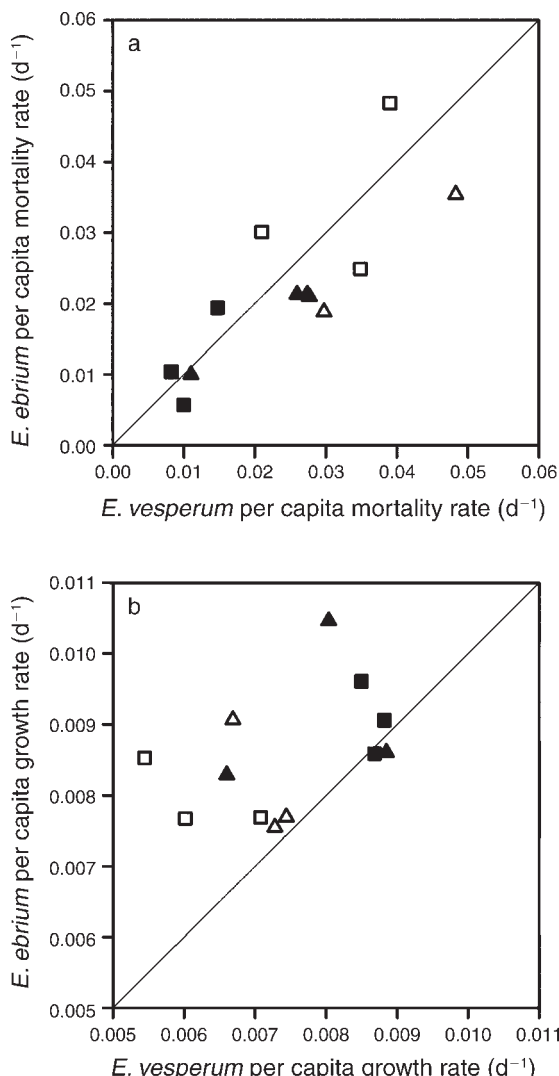


FIG. 1. Two damselfly species, *Enallagma ebrium* and *E. vesperum*, showing strong responses to the manipulation of total abundance for per capita (a) mortality and (b) growth rates but no effects of relative abundance manipulations. Each symbol represents the responses of the two species in an experimental replicate. The symbols identify total abundance (open symbols, high total abundance; solid symbols, low total abundance) and relative abundance (squares, *E. vesperum* high relative abundance; triangles, *E. ebrium* high relative abundance) treatment replicates. The experiment was performed September–November 2008 at McDaniel’s Marsh, Enfield, New Hampshire, USA.

Finally, we evaluated whether the co-occurrence of *Enallagma* species among lakes is nonrandom. Results from this analysis confirm that co-occurrence of taxa among the lakes does not differ from that of randomly assembled communities ($P = 0.102$).

DISCUSSION

From these results, we conclude that *Enallagma* in fish lakes are effectively ecologically equivalent species, or at

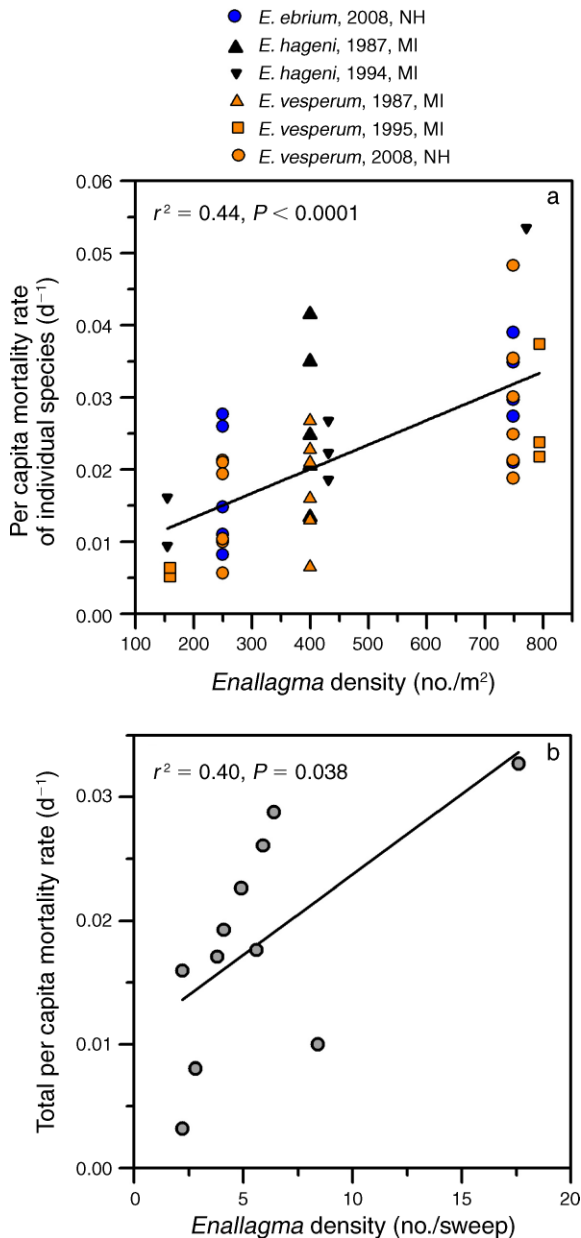


FIG. 2. *Enallagma* per capita mortality increases as total *Enallagma* abundance increases (a) in density manipulations in field experiments performed in New Hampshire (NH) and Michigan (MI), USA, across 20 years and (b) in 20 natural lakes in New Hampshire in 2008. In panel (a), each symbol represents a replicate cage in a field experiment. Replicates for 2008 are the experimental results presented in Fig. 1. All other experimental replicates were performed in Palmatier Lake, Barry County, Michigan, USA. In panel (b), each symbol represents the total per capita mortality rate of all *Enallagma* species in each of 20 lakes sampled in the present study. The abscissa gives the mean number of total *Enallagma* larvae in 10 standardized sweep net samples taken in the lake.

least nearly so, and that neutral dynamics should dominate their patterns of relative abundance across lakes (Hubbell 2001). Strong density-dependent regulatory mechanisms imposed by fish predation and resource

competition shape *Enallagma* larval mortality and growth rates within these lakes, but total *Enallagma* abundance is the variable determining these demographic rates instead of each species' own abundance. Species responded strongly to manipulations of total abundance, but showed no responses to relative abundance manipulations when total abundance was held constant (Fig. 1). Moreover, mortality and growth of individual species across lakes were not correlated with any underlying environmental factor, but the mortality and growth rates calculated for the entire assemblage of *Enallagma* species changed with total *Enallagma* abundance. Finally, local diversity appears to be essentially a random draw from the regional species pool, a pattern that would readily be generated given no associations between demographic rates and major environmental factors (Fig. 3, Appendix D) and the ability to disperse among lakes (McPeck 1989).

One concern with any study attempting to evaluate hypotheses of ecological equivalence is whether important environmental factors shaping population regulation and coexistence have been measured. In our observational study we explicitly focused on factors that prior studies of *Enallagma* have shown to be important, namely the abundances of predators and food (Pierce et al. 1985, Blois-Heulin et al. 1990, McPeck 1990, 1998). Our comparisons of total *Enallagma* abundance do show that these are important environmental factors. However, niche dimensions are multifarious so that trade-offs along a few readily observable dimensions may not be apparent, but instead occur along multiple axes (e.g., Clark et al. 2007). A strength of two of our tests was that they did not require that we have measured any environmental variables. First, we detected no evidence of negative correlations of demographic rates among species across lakes, and in fact some indication of positive correlations (Appendix D), a pattern consistent with neutral processes (e.g., Hubbell 2001, see also Houlihan et al. 2007). If coexistence mechanisms shape community structure, the negative correlations among the demographic rates of species should be apparent regardless of the specific coexistence mechanism. Second, our null model approach was blind to whether important ecological factors are measured and revealed that co-occurrence of taxa among lakes was no different from that of randomly created communities. Such a pattern is consistent with stochastic, not deterministic processes (e.g., Ellwood et al. 2009). Obviously, the studies we present here do not include processes acting in the adult life stage, but no density-dependent factors have been identified to act in the adult stage (McPeck 2008b), and individuals live on average for four days as adults (Fincke 1984). Also, although the experiment covered much of the larval phase of the life cycle (from approximately the fourth to the penultimate instar [*Enallagma* has 11 larval instars]), these results do not include very early or the latest instars.

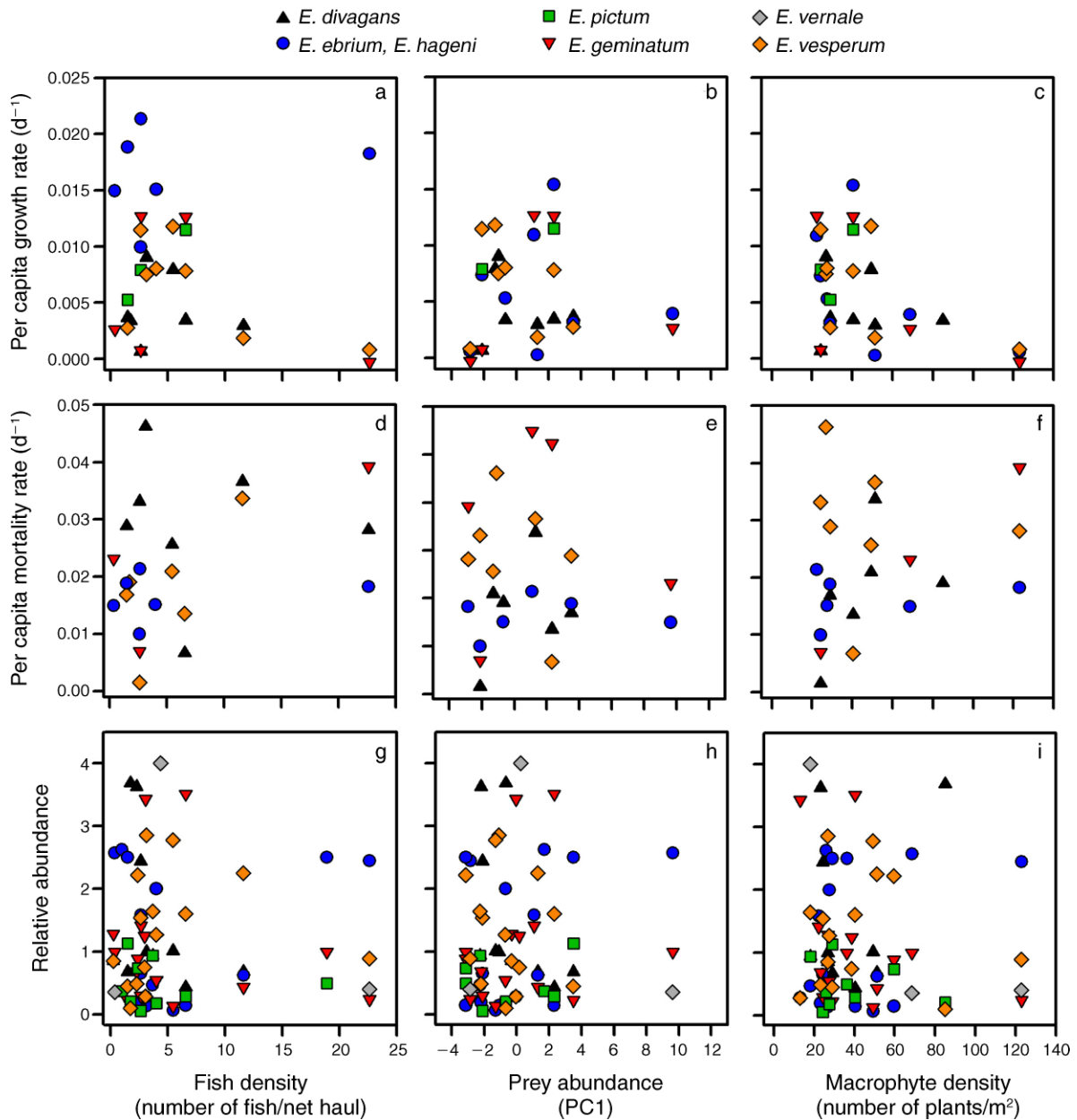


FIG. 3. Per capita (a–c) growth and (d–f) mortality rates and (g–i) relative abundance of *Enallagma* species under different environmental factors (density of predators, prey [principal component 1], and vegetation). No significant relationships (Appendix D) were found, suggesting that each species is not regulated by different density-dependent ecological factors. Each data point represents given species in a different lake.

Even if *Enallagma* species are not exactly ecologically equivalent, the relative importance of neutral dynamics in shaping patterns of community structure should dominate any subtle niche differences among species. This arises because the extent to which coexistence mechanisms are operating is determined by the combined effects of fitness similarities and density-dependent ecological differences (Chesson 2000, Adler et al. 2007). The density-dependent mortality imposed by fish predation can account for at least 75% of total mortality

in the larval stage of *Enallagma* (McPeck 1990, 1998), and so fish predation is a predominant ecological agent regulating *Enallagma* abundances. We could find no difference in mortality rate between the two species we included in the experiment, even though these species commonly co-occur and their last common ancestor was the basal split in the genus 10–15 MYA. They did differ in growth rates, but density-dependent growth rates play an inconsequential role in population regulation in *Enallagma* because larval growth rates do not influence

adult fecundity (McPeck and Peckarsky 1998). We can also use a retrospective power analysis of our experimental results to provide an indirect measure of the extent of ecological differences among *Enallagma* species. We would have needed a total of 72 and >480 replicates to detect differences in mortality and growth rates, respectively, in the relative abundance treatments at $\alpha = 0.05$ for the species (see Appendix C). In addition, more extreme manipulations of relative abundance may have been able to detect subtle effects, but the relative abundances we used were constrained to ensure an adequate number of larvae surviving to the end of the experiment (see also Levine et al. [2008] for additional comments on such issues). Thus, any possible niche differences that would promote their coexistence must be extremely small, and so the dynamics of the *Enallagma* assemblage should be influenced primarily by the consequences of their ecological similarity; i.e., ecological drift (Hubbell 2001).

The fact that the multiple *Enallagma* species found together are ecologically equivalent, or nearly so, does not, however, imply that all littoral-dwelling species within this trophic level are similarly equivalent. In fact, consideration of the food web in which *Enallagma* are embedded suggests a general framework for how niche and neutral processes may simultaneously influence community structure (Leibold and McPeck 2006). The model presented in the *Introduction* is easily extended to have two coexisting functional groups with a number of ecologically equivalent species comprising each. In this case, the two functional groups are regulated to the abundances given in Eqs. 2, but each can be composed of many ecologically equivalent species, and what is regulated for each is their summed total abundance:

$$\sum_{i=1}^x N_{1i}^* = \frac{a_2 d_1 - r \alpha_2 \beta_2 \left(1 - \frac{R^*}{K}\right)}{a_2 \alpha_1 \beta_1 - a_1 \alpha_2 \beta_2}$$

and

$$\sum_{j=1}^y N_{2j}^* = \frac{r \alpha_1 \beta_1 \left(1 - \frac{R^*}{K}\right) - a_1 d_2}{a_2 \alpha_1 \beta_1 - a_1 \alpha_2 \beta_2}. \quad (5)$$

In this case, the “niche” structure is clearly evident at the consumer trophic level, but embedded in each functional group are some number of ecologically equivalent species. The number of species in each will be determined by the rate of speciation in the component taxa that occupy that functional group and the rate of species loss due to ecological drift in their relative abundances, which will be governed by the summed total abundance of the functional group.

Our previous work has shown that *Enallagma* species are ecologically differentiated from *Ischnura* species (the sister genus to *Enallagma*) exactly in ways that should promote their coexistence as predicted by this model of keystone predation (Holt et al. 1994, Leibold 1996,

McPeck 1996, 1998): *Enallagma* species are substantially better at avoiding predators, whereas *Ischnura* species are substantially better at converting prey into their own biomass (McPeck 1998). However, species within each genus are very similar to one another. Each genus thus represents a functional group of ecologically equivalent (or nearly equivalent) species embedded in the food web. In these damselflies, the trade-offs that promote coexistence seem to be manifested at the level of genus, but other functional groups that comprise a food web need not break at any specific taxonomic level or necessarily correspond to taxonomic affinities at all. Mechanisms of coexistence promote the persistence of each functional group and regulate the total abundance of all species in each functional group, but ecological drift dominates the dynamics of species’ relative abundances within each group (Leibold and McPeck 2006).

One substantial criticism of neutral community theory is how ecologically similar species can arise and persist in systems (Hubbell 2001). Although many species come into existence through niche diversification (Schluter 2000), speciation often proceeds with little or no ecological differentiation (e.g., speciation via sexual selection and mate recognition, chromosomal rearrangements, polyploidization [Coyne and Orr 2004, Price 2008]), and these speciation modes are common in many taxa; for example, sexual selection has played a substantial role in the diversification of many speciose taxa (e.g., Hawaiian *Drosophila* [Boake 2005], African lake cichlids [Salzburger 2009], birds [Price 2008]). Furthermore, the widespread existence of sympatric cryptic species complexes (e.g., Bickford et al. 2006) further belies the argument that substantial ecological divergence need accompany speciation. While some speciation events in *Enallagma* were the result of ecological speciation (e.g., habitat shifts to colonize lakes with dragonflies as top predators [McPeck and Brown 2000, Stoks and McPeck 2006]; endemism on the Atlantic coastal plain [Turgeon et al. 2005]), the vast majority seem to have been driven primarily by sexual selection for differentiation in reproductive structures and little else (McPeck et al. 2008). Indeed, previous studies have found little difference among fish lake *Enallagma* species in phenotypes that shape both predator susceptibility and competitive ability (Stoks and McPeck 2006). Given that *E. ebrium* and *E. vesperum* are derived from the different clades emanating from the basal split in the genus 10–15 MYA and phylogenetic reconstructions indicate that this last common ancestor lived in fish lakes (Turgeon et al. 2005), this diversification to produce the 34 extant North American species in fish lakes appears to have resulted in little ecological differentiation among species that would promote local coexistence. These considerations lead to the prediction that, like *Enallagma*, taxa in which non-ecological speciation modes predominate should be those that also display the greatest signatures



PLATE 1. McDaniel's Marsh, Enfield, New Hampshire, USA. Photo credit: M. A. McPeck.

of neutral community dynamics, and they frequently do just that (McPeck 2008a).

Although ecologically similar species may readily arise, a more general framework for how they become established in a system is lacking (Hubbell 2001). Coexistence requires that a species can increase when rare to invade an otherwise intact community (MacArthur 1965, 1972). Ecologically equivalent species have, by definition, no such demographic advantage to promote their invasion. However, our phylogeographic and phylodemographic studies of recent *Enallagma* radiations suggest that invasion of intact ecological systems is an inappropriate metaphor for understanding community assembly. Like many taxa (e.g., Jansson and Dynesius 2002), *Enallagma* species show the demographic signatures of major bottlenecks, range fragmentations, and range expansions caused by Pleistocene glacial cycles (Turgeon et al. 2005). For example, *E. ebrium* shows the genetic signature of arising somewhere in the area of eastern New York, Vermont, and southern Quebec at the end of the last glacial maximum and rapidly expanding to its present range (Atlantic coast to British Columbia) (Turgeon et al. 2005). Thus, *E. ebrium* did not have to invade an intact ecological community as theoretical analyses of coexistence demand, but rather arose and expanded its range to colonize lakes along with all the other species that chased the retreating glacier north. Presumably, repeat-

ed glacial cycles throughout the Pleistocene caused periodic disruptions to many biological communities across the globe (Jansson and Dynesius 2002, Hewitt 2004). New species that came into existence during these brief cycles of community disassembly and reassembly would have had limited impediment to invasion, because they would have been colonizing new areas along with already existing species (Turgeon et al. 2005).

These cycles of species production coincident with the dismantling and reassembling of local communities on a continental scale means that new species would almost immediately exist at substantial local abundances over large areas of the continent, and the ensuing process of species loss through ecological drift would take an astronomical amount of time. At the end of each cycle, old and new species alike may have had ranges that covered millions of square kilometers, with each species present in most local assemblages. For example, because total *Enallagma* abundance in any particular pond or lake is typically on the order of 10^4 – 10^7 , stochastic changes in species relative abundances, both locally and regionally, would proceed at exceedingly slow rates, and low levels of dispersal among lakes would retard the loss of any species (McPeck and Gomulkiewicz 2005). Even if species are not identical, but merely very similar, those that were (and are) being driven deterministically extinct would still take an exceedingly long time to do so (McPeck 2008a). Moreover, slight ecological differences

among species may mean that each is in fact best adapted to a particular subset of local patches within its range, but these differences are not strong enough to prevent any species from excluding others in the face of even a trickle of dispersal (i.e., mass effects within a metacommunity; Schmid and Ellner 1984). These dynamics are by no means unique to *Enallagma*, but may be most relevant for taxa in which diversification is predominantly by non-ecological means and communities prone to recurrent assembly and disassembly.

In sum, our results suggest an important conceptual unification of both neutral dynamics and niche-based processes of coexistence for understanding the structure of biological communities. This more nuanced view of community structure does not pit “niche” vs. “neutral” processes, but rather layers the contributions of these processes to community structure (e.g., Leibold and McPeck 2006, Ellwood et al. 2009). As a result, their relative importance cannot be evaluated by simply searching for evidence of niche structure to negate the importance of neutral dynamics (e.g., Fargione et al. 2003, McGill 2003, Wootton 2005, Condit et al. 2006, Muneeppeerakul et al. 2008). Obviously, food webs are comprised of interacting functional groups, which means that niche structure will always be apparent. However, the evolutionary dynamics of the taxa that fill a functional group may have as much influence on patterns of species diversity as the ecological regulation of food web structure. Understanding the interplay between the ecological processes structuring relationships between functional groups and the evolutionary processes driving the diversification of taxa filling each functional group are necessary for a more synthetic understanding of the structure of biological communities.

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APPENDIX A

Details of the experimental design (*Ecological Archives* E091-061-A1).

APPENDIX B

Details of the observational study (*Ecological Archives* E091-061-A2).

APPENDIX C

ANOVA results of the experimental study (*Ecological Archives* E091-061-A3).

APPENDIX D

Detailed results from the observational study (*Ecological Archives* E091-061-A4).