

DISTURBANCE HETEROGENEITY DETERMINES FRESHWATER METACOMMUNITY STRUCTURE

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Abstract. Metacommunity theories, which consider communities as interacting species assemblages connected by dispersal, differ in their assumptions about the importance of interspecific adaptations and environmental heterogeneity as controls of assemblage composition. I assess the relative importance of regional (dispersal) and local (abiotic and biotic environmental variation) processes in explaining the structure of a freshwater pond metacommunity. Results did not support the hypothesis that dispersal was limited by interpatch distance. Instead, community diversity, composition, and trophic structure were best explained by local environmental variation associated with pond permanence. Many taxa were restricted either to temporary or semipermanent ponds, an outcome that suggests species trade off adaptations to disturbance with those to biotic interactions (species-sorting model) and that refutes the neutral model of interspecific equivalence. However, evidence for high dispersal rates, low-fitness habitats, and high temporal environmental variability indicated that interpatch dispersal also may influence local dynamics through mass effects. These results suggest that integrating the species-sorting and mass-effect niche assembly frameworks will provide a necessary step in the successful application of metacommunity theory.

Key words: *Ambystoma maculatum*; community assembly; disturbance; larval amphibians; macroinvertebrates; metacommunity; nested subset analysis; temporary pond communities.

INTRODUCTION

A community is composed of taxa from the regional species pool that can disperse to a locality, survive environmental conditions, and persist within the context of biotic interactions. Despite the recognition that assembly occurs at multiple scales, community models traditionally have emphasized either regional (e.g., colonization–extinction equilibrium) or local (e.g., interspecific interactions) processes (Mouquet and Loreau 2002). By explicitly recognizing interconnections between multispecies assemblages, the “metacommunity” concept reconciles regional and local dynamics in a more inclusive theory of community assembly (Wilson 1992, Mouquet and Loreau 2002).

Metacommunity models differ in their assumptions concerning the importance of biotic and abiotic interactions, environmental heterogeneity, and dispersal constraints in regulating local species persistence. For example, neutral models of metacommunity assembly assume that extirpation arises from stochastic processes that operate on functionally equivalent species (Hubbell 2001). In contrast, niche-assembly metacommunity models assume that species differences (both trophic and otherwise) are significant drivers of community assembly. However, niche-assembly models differ in their assumptions about the importance of local environmental heterogeneity in determining com-

munity composition (Leibold et al. 2004). Patch dynamic models often ignore environmental heterogeneity and instead emphasize regional colonization–extinction dynamics among homogeneous patches (Wilson 1992, Shurin and Allen 2001). Species-sorting models (Leibold 1998) assume that the partitioning of species among variable environments operates according to individual adaptations and that interspecific fitness varies among patches. Finally, the mass-effect framework (Mouquet and Loreau 2002) differs from species sorting models by assuming that dispersal rates exceed the rate at which environmental conditions exclude taxa such that migrants influence assemblage composition in recipient habitats.

Because species distributions are often strongly associated with environmental gradients (Whittaker 1956, McPeck 1990, Wellborn et al. 1996, Chase and Leibold 2002), I argue that adaptive tradeoffs to local environmental heterogeneity will often regulate metacommunity dynamics. In particular, local variation in disturbance regimes constitutes an important predictor of assemblage composition in many natural systems because adaptations that promote environmental tolerance often trade off against adaptations that promote fitness under conditions of intense biotic interactions (tropical forests, Connell [1978]; tallgrass prairie, Collins [2000]; intertidal, Menge and Sutherland [1987]; freshwater ponds, Wellborn et al. [1996]). The generality of disturbance gradient trade-offs suggests that species-sorting and mass-effect models will apply to the multitude of ecological systems organized along such gradients.

Manuscript received 22 September 2003; revised 15 April 2004; accepted 20 April 2004. Corresponding Editor: P. R. Leavitt.

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To evaluate the applicability of divergent metacommunity frameworks to natural communities, I assess the relative importance of local and regional community assembly mechanisms in invertebrates and amphibians inhabiting freshwater ponds in southern New England, USA. Freshwater ponds represent an ideal system in which to evaluate metacommunity predictions because of their discrete nature, isolation within terrestrial matrix, and significant variation in environmental characteristics (Wilbur 1997). I use observations of communities in 14 natural ponds to evaluate three mechanistic hypotheses.

1) Dispersal limitation. Because freshwater ponds are generally isolated within a terrestrial matrix, dispersal may influence metacommunity dynamics such that communities close to each other are more similar than distant communities. Because temporary habitats may require repeated colonization events after disturbances to maintain diversity, I predict a higher proportion of active dispersers in temporary environments, whereas passive dispersers should be found more frequently in permanent ponds.

2) Environmental limitation. Harsh conditions associated with disturbances eliminate all but the most resistant species (Southwood 1977, Connell 1978, Wiggins et al. 1980). The inability to complete ontogenetic niche shifts (e.g., metamorphosis, diapause) prior to pond drying can result in mortality (Newman 1992) or local extirpation (Jeffries 1994). If pond drying primarily determines community composition, then pond communities should be significantly nested (Patterson and Atmar 1986) due to taxa-specific extirpations along permanence gradients. If species can be considered functionally equivalent, then diversity should decrease along a gradient of increasing disturbance intensity without predictable changes in species composition.

3) Biotic limitation. The importance of biotic interactions in structuring communities is expected to increase as disturbance frequency or intensity declines (Connell 1978, Wellborn et al. 1996), especially if higher species densities increase competition for limited resources (Wilbur 1997) or longer hydroperiods promote the survival of predators (Schneider and Frost 1996). If competition limits community membership, then co-occurrences of taxa will be less common than expected by chance (Cody and Diamond 1975). If predation is an important structuring agent, I predict an increase in predator diversity and density in more permanent ponds. Because gape size often restricts the size of aquatic prey taken by predators, predation risk often decreases with increasing prey size (Werner and Gilliam 1984). To evaluate prey size effects on biotic limitation, I assessed the diversity and abundance of predators that prey on spotted salamander (*Ambystoma maculatum*) larvae, a common intermediate-sized consumer.

A combination of null models and standard statistical techniques were applied to natural distributions of pond

taxa to evaluate these hypotheses. Observational studies of this kind provide the basis for refining theoretical assumptions and offer valuable insights about the processes that underlie complex ecological patterns.

METHODS

Study site and sampling methodology

The study was conducted within a 200-ha section of the Yale-Myers Research Station in Union, Connecticut, USA. All standing water bodies within the study region were censused and located with a global positioning unit along seven (0.1×2.5 km) east-west transects during winter 1999–2000. I sampled each pond that remained inundated by 15 June ($N = 14$) every 10 m along its longest dimension (for a minimum of three samples). Linear sampling transects were chosen based on high sampling efficiencies in a pilot study. Samples consisted of stratified 17×25 cm dip net sweeps (1.4-mm mesh) inside a pipe sampler (area = 0.1 m^2 ; for method description, see Skelly et al. 1999). Supplementary timed dip net samples were used to complement estimates of amphibians to total taxa richness. Dip net effort was set proportional to pond area (5–30 min). A presence was recorded if embryos, larvae, or adults were recorded during one of three sampling periods from April through May 2000.

At each pipe sample location along the transect, I measured depth and distance to perpendicular pond edge, and classified overhead canopy cover and macrophyte structure by 10% categories. Percent substrate composition was estimated for 19 categories including sediment size, woody debris, and vegetation identity. From these data, I estimated total pond habitat diversity as the number of habitats classified by *k*-means clustering with cluster number determined objectively via iterative sums-of-squares criteria using KMEANGRP, a Matlab function developed by R. E. Strauss (*available online*).² Pond area was calculated by integrating a cubic spline fit to pond edge coordinates collected at 10-m intervals. Pond permanence was assessed as the number of weeks visible water was recorded after 22 June.

Invertebrate samples were preserved in 70% EtOH. Amphibians were identified to species in the field (adults and embryos) or preserved for laboratory identification (larvae). Invertebrates were identified using a 7–50 \times stereoscope and standard literature (Peckarsky et al. 1990, Merritt and Cummins 1996). Chironomidae (Diptera) were wet mounted and identified using a 70–350 \times compound microscope. Taxa were categorized into trophic and dispersal categories based on standard texts (Merritt and Cummins 1996, Petranka 1998), applicable literature (Wiggins et al. 1980, Schneider 1997), and field observations. In a few cases, functional classifications for congeners were necessary. Predators were defined as taxa predominantly feeding on meta-

² (<http://www.biol.ttu.edu/Strauss/Matlab/matlab.htm>)

zoans (Warren and Gaston 1992). Passive dispersers were defined as taxa that depend on the movements of other species for dispersal. For example, Hydrachnidia and Gastropoda taxa generally depend on animal vectors for dispersal, thus leading to their classification as passive dispersers. A predator list for *A. maculatum* was constructed from literature (Schneider 1997, Petranka 1998) and personal observations (M. Urban, unpublished data).

Statistical analyses

Variance inflation factors (VIFs) for the six environmental variables revealed moderate (range = 2.7–7.8), but not excessive (>20) collinearity that would recommend the removal of highly redundant variables from the model (Hall et al. 1999). Due to this collinearity, I used principal components analysis (PCA) to extract orthogonal measures of site heterogeneity. Only those principal components that explained significantly non-random variation were retained for further analysis (broken stick model; Jackson 1993). The significance of variable loadings was assessed via 10 000 runs of a bootstrapped broken-stick model (Peres-Neto et al. 2003).

Total taxa richness was calculated as the number of taxa recorded from both pipe and dip net samples. Sampling efficiency was calculated as observed total taxa richness divided by the asymptote of species accumulation curves using EstimateS, version 6.0.b1 (available online).³ Because I detected a marginally significant positive relationship between sampling effort and efficiency ($P = 0.06$), I analyzed sample-invariant Fisher's alpha diversity in addition to total taxa richness.

Mantel tests were used to test the hypothesis that community dissimilarity, measured as 1-Jaccard's coefficient, was spatially autocorrelated. In addition, partial Mantel tests were applied such that the relationship between community and geographic distance was conditioned on site heterogeneity (factor scores of PC1). Nonrandom patterns of species co-occurrence were evaluated via comparison to *C*-scores of 5000 permutations of the original matrix with fixed-row and column constraints using Ecosim version 7.0 (available online).⁴ I evaluated the effect of decreasing permanence on selective extirpation with nested subset analysis. For a matrix ordered by an environmental variable, a species was considered maximally nested when it occurred at every site with an environmental value of higher rank.

Because alternate methods for nested subset analysis returned qualitatively similar results to the simpler and widely used number of unexpected absences from maximal nestedness (hereafter N_0 ; Patterson and Atmar 1986), I only report results for N_0 . I used fourth-corner

statistics to concurrently evaluate relationships among traits, environmental variation, and community composition (Legendre et al. 1997). Detrended canonical correspondence analysis (DCCA) was used to visualize species trait–environment relationships following detection of long (>4 SD) community gradients (ter Braak 1996). Simulations were used to assess whether taxa found only in the seven most temporary or semipermanent ponds were more common than expected by random permutations. Nestedness, fourth-corner statistics, and gradient specialization were evaluated via 5000 Monte Carlo permutations of the random (1) model (Patterson and Atmar 1986). The random (1) model was chosen over alternate methods based on its incorporation of ecological detail by preserving site diversity and relative species incidences during permutations.

RESULTS

Environmental and community variation

Environmental characteristics varied significantly among ponds (Appendix A). Several ponds dried soon after the final sampling period, while others retained water for the year's duration. Total taxa richness ranged from 1 to 39 (Appendix B). The first principal component (PC1) explained 64% of environmental variation (Fig. 1) and was the only axis that explained more variation than was expected by chance. Only permanence ($P = 0.001$), vegetation structure ($P = 0.005$), and pond area ($P = 0.022$) explained significant variance in PC1 according to bootstrapped broken stick simulations. Of the six pond variables used to construct PC1, only permanence was retained in a stepwise multiple regression model for predicting Fisher's alpha diversity (Splus, version 3.0; Insightful Corporation, Seattle, Washington, USA; $F_{1,12} = 13.2$, $R^2 = 0.54$, $P < 0.005$). Ranked environmental scores explained 73% of the variation in the rank hydroperiod of the same ponds sampled two years later ($F_{1,12} = 32.9$, $P < 0.001$), suggesting that relative permanence and associated environmental variation remained constant over time.

Dispersal limitation

Although the mean distance between ponds was more than 0.5 km, Mantel tests suggested that interpatch distance was unrelated to community composition ($r = -0.05$, $P = 0.58$). This relationship remained nonsignificant when the relationship between community and geographic distance was conditioned on environmental distance (PC1 scores; $r = 0.01$, $P = 0.43$). As well, community distance as a function of dispersal traits was not associated with pond proximity (active dispersers, $r = -0.01$, $P = 0.46$; passive, $r = -0.06$, $P = 0.58$). Dispersal traits were unrelated to PC1 using fourth corner statistics (Appendix C, Table C1; $F = 2.19$, $P > 0.05$). A DCCA biplot of taxa,

³ <http://viceroy.eeb.uconn.edu/estimates>

⁴ <http://homepages.together.net/~gentsmin/ecosim.htm>

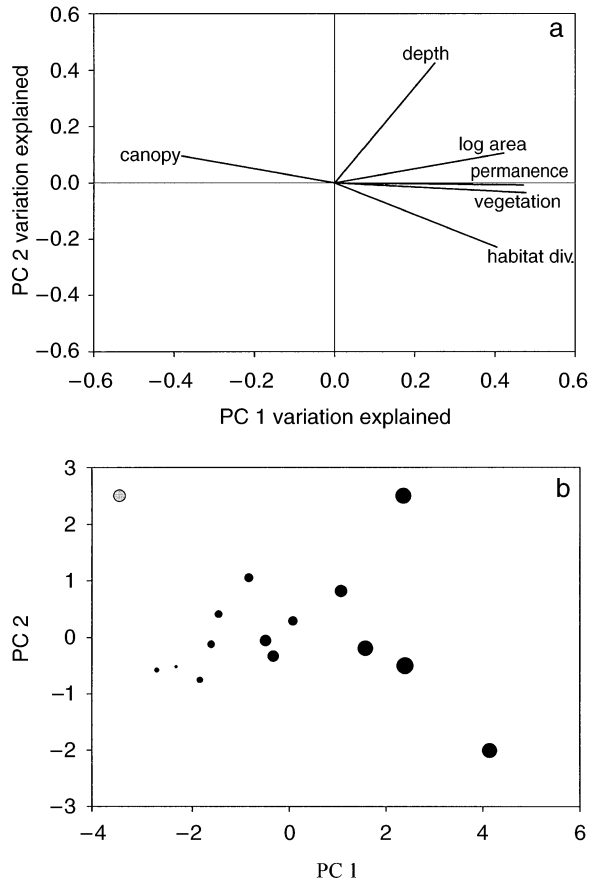


FIG. 1. (a) Factor loadings for original variables on the first two principal components. (b) Total taxa diversity per pond plotted with respect to the first two principal component scores. Circle area is proportional to taxa diversity. The gray circle in the upper left corner indicates the symbol area associated with a total taxa richness of 20.

environmental scores, and dispersal traits also indicated that dispersal traits were not associated with environmental variation (Fig. 2). The proportion of active dispersers was independent of the environmental variation and was not significantly different from the local species pool.

Environmental limitation

PC1 explained 85% of the variation in total taxa richness (Fig. 3; $F_{1,12} = 69.0, P < 0.00001$) and 46% of the variation in Fisher's alpha diversity (Fig. 3; $F_{1,11} = 9.3, P = 0.01$). The significant relationship between Fisher's alpha and environmental variation suggests that observed increases in diversity along PC1 were not an artifact of passive sampling, but represent biologically relevant patterns (Rosenzweig 1995). Communities were not significantly nested when compared to simulated communities ($P = 0.31$). Instead, taxa were more likely to be restricted to either end of the permanence gradient than expected by chance (Fig. 4).

Biotic limitation

Species did not occur in significantly nonrandom (checkerboard) patterns ($P > 0.1$). Although total predator diversity significantly increased with pond permanence ($R^2 = 0.68, F_{1,12} = 26.0, P < 0.001$), the trophic composition of taxa was unrelated to permanence (Appendix C, Table C1; fourth-corner global F statistic = 0.01, $P > 0.9$). The ratio of predator to nonpredator diversity remained constant across the permanence gradient and did not significantly differ from that found in the local species pool (Appendix C, Table C2). The ratio of predator to nonpredator densities was approximately 1:2 and did not differ significantly from the ratio obtained by analysis of pooled species samples. Trophic density ratios were strongly related to site diversity ($F_{1,11} = 13.1, R^2 = 0.54, P < 0.005$) and weakly related to PC1 ($P = 0.09$). The former pattern occurs because predator densities increase disproportio-

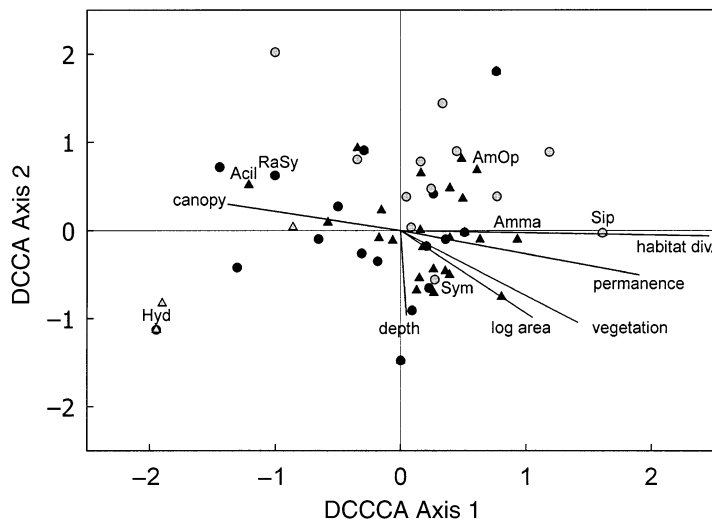


FIG. 2. DCCA biplot of species and environmental scores. Environmental variation was significantly related to canonical axes (Monte Carlo test; 10000 simulations; $P = 0.01$). Active dispersers are indicated by black symbols, passive dispersers by gray symbols. Predators are symbolized by triangles, and nonpredators by circles. The following taxa characteristic of ponds of varying hydroperiod are identified: Acil = *Acilius* sp.; Amma = *A. maculatum*; Amop = *A. opacum*; Sip = *Siphonurus* sp.; Hyd = *Hydrachnidia*; RaSy = *Rana sylvatica*; Sym = *Sympetrum* sp. Environmental scores were multiplied by a factor of 2 for interpretative purposes.

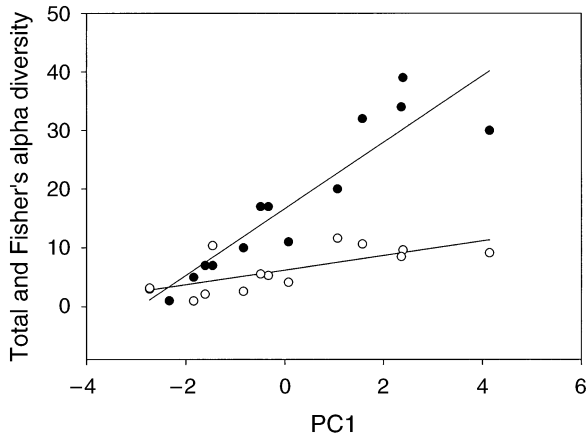


FIG. 3. Pond total taxa richness (black) and Fisher's alpha diversity index (white) in relation to PC1.

tionately to nonpredator densities in more diverse ponds ($F_{1,11} = 6.8$, $R^2 = 0.38$, $P < 0.05$). For larger-bodied *A. maculatum* larvae, total diversity of potential predators increased with permanence ($F_{1,12} = 16.5$, $R^2 = 0.58$, $P < 0.005$). Contrary to community patterns, the density of *A. maculatum* predator taxa did not increase in more permanent or diverse ponds.

DISCUSSION

I was able to reject the hypothesis that terrestrial habitats imposed a significant barrier to dispersal in freshwater taxa in this study. Although dispersal limitations have figured prominently in other systems (e.g., Tofts and Silvertown 2002), pond communities were not significantly affected by interpatch distance at the scale of this analysis (200 ha). This result is in accordance with predictions for freshwater zooplankton provided by Shurin et al. (2000), where dispersal affected community patterns at coarse (>100 km²) regional scales rather than at local landscape scales. Contrary to predictions, dispersal was unaffected by the mode of species dispersal (active, passive) or pond permanence. Instead, results from this study suggest that pond taxa were well adapted to overland dispersal.

Environmental heterogeneity among ponds was associated with a single nonrandom principal component. Specifically, PC1 was significantly correlated with longer hydroperiods, greater vegetation structure, and larger pond area—factors that were themselves collinear. However, because pond size need not be associated with permanence (Snodgrass et al. 2000) and because increased aquatic macrophyte structure and decreased tree canopy cover can both result from hydroperiod-induced tree mortality (Relyea 2002), habitat permanence is likely the main factor explaining environmental and community variation among ponds. Concordant with this prediction, permanence was the only variable selected in a stepwise regression model predicting taxa diversity.

Evidence presented here suggests that environmental heterogeneity places important constraints on community diversity, composition, and trophic relationships. Most strikingly, diversity decreased from more than 30 taxa in semipermanent habitats to only a few in temporary habitats. Over 54% of the variation in Fisher's alpha diversity was attributed to variability in pond permanence. In conjunction with similar studies (Schneider and Frost 1996, Spencer et al. 1999, Snodgrass et al. 2000), these analyses suggested that failure to reach particular developmental stages (metamorphosis or drought-resistant stage) prior to drying constitutes an underlying constraint on species persistence in temporary ponds. As well, the highly nested distribution of *A. maculatum* with respect to habitat permanence provided strong evidence for such developmental constraints. In this example, *A. maculatum* larvae require a minimum of 11 weeks to develop from eggs to terrestrial juveniles (Petranka 1998). Based on oviposition date (2 April; M. Urban, unpublished data) and developmental rate, successful *A. maculatum* larvae should be restricted to ponds that remained inundated until late June. As expected, *A. maculatum* occurred in all ponds that retained water after 29 June, but were absent from four of five ponds that dried by 22 June. The only unexpected presence occurred in Pond Z-5, where high *A. maculatum* mortality was observed in 2001 when the pond dried prior to any individuals in the population reaching metamorphosis. *A. maculatum* did not lay eggs in Pond Z-5 the following year, providing evidence for a low-fitness habitat that might also function as a population sink. In general, these results agree with a growing number of studies that suggest the importance of colonization and extinction dynamics in temporary pond communities (Hecnar and M'Closkey 1996, Skelly et al. 1999, Trenham et al. 2003). Thus, habitat permanence appears to

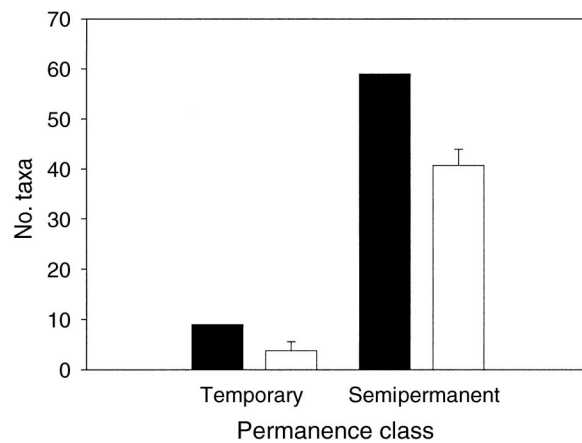


FIG. 4. Expectations of gradient specialization under the R1 null hypothesis. Bars show the number of taxa only inhabiting either the seven most temporary or seven most permanent ponds (black bar) and the predicted number of taxa under the R1 (white bar) null hypothesis. Error bars represent +1 SD.

constitute a particularly important agent of community assembly in freshwater habitats.

If pond desiccation is the primary source of mortality, then taxa should select habitats based on predictable cues of pond hydroperiod. The correlation of environmental diversity (e.g., canopy cover, area, macrophytes) with pond permanence argues for the existence of such visual cues. For example, Odonata use macrophyte cover in addition to other cues to determine habitat suitability (Bernáth et al. 2002). Both odonates found in the study, *Sympetrum* and *Lestes*, only occurred in ponds containing high (>45%) macrophyte cover. Thus, habitat selection by mobile taxa may be an important means through which species track changes in pond permanence over time.

Because taxa were not significantly nested with respect to pond permanence, I was able to reject the hypothesis that community composition was predictable solely on the basis of developmental constraints. Instead, a significant number of taxa were restricted to either temporary or permanent ponds, suggesting that species trade off adaptations to pond disturbance with those associated with other control factors. For example, five of the nine temporary specialists in the study were Hydrachnidia, which can survive pond drying in moist microhabitats (Wiggins et al. 1980). The three beetles restricted to temporary ponds belonged to beetle families (Histeridae, Hydraenidae, and Staphylinidae) that inhabit littoral zones and can survive terrestrial conditions. Taken together, these patterns argue for the non-equivalence of species and suggests that assumptions of the neutral model are not appropriate for this metacommunity.

The occurrence of temporary pond specialists provides evidence of mechanisms that may exclude taxa from more permanent ponds. Competition and predation have been proposed to limit taxa adapted to harsh environmental conditions in more moderate habitats (Connell 1978, Wellborn et al. 1996, Wilbur 1997). Cody and Diamond (1975) predicted that species co-occurrence in natural communities would be less than expected by chance if competitive exclusion was an important determinant of community composition. However, species co-occurrences in this study were not significantly different from the random expectation, suggesting that competition was not an important driver of community composition.

A trade-off between predation risk and growth can also limit the fitness of fast-developing taxa in more permanent ponds (Wellborn et al. 1996). An increase in predation risk due to greater total predator diversity in permanent ponds has been attributed to a release from developmental constraints on slower developing predators (Schneider and Frost 1996). In this study, total predator diversity increased with permanence in agreement with previous studies (Skelly 1996, Spencer et al. 1999). An increase in total predator diversity can impose biotic limits on community membership if

adaptive defenses are predator specific and trade off among each other (Sih et al. 1998).

Despite increases in total predator diversity, the predator to nonpredator (trophic) diversity ratio did not change with pond permanence or within-site habitat diversity. The finding that trophic ratios are often independent of species richness may be a general feature of community assembly (Warren and Gaston 1992). However, such patterns could also be explained if the predator to non-predator diversity ratio reflects random draws from the local species pool (Warren and Gaston 1992). In this study, the ratio of predator to nonpredator diversity did not differ significantly from that found in the local species pool. Whether such constancy results from long-term evolutionary dynamics or random draws from a wide-dispersing species pool remains a subject for future study.

Another measure of trophic structure, per capita predator density, increased with pond diversity and permanence. An increase in per capita predation risk due to abundance rather than diversity in more permanent ponds suggests that the short time scale for predator-prey interactions prior to drying may lead to greater changes in prey abundance rather than diversity (Schneider and Frost 1996). Predators can have a positive indirect effect on prey persistence by limiting intraspecific competition (Abrams and Rowe 1996). In addition, prey composition may remain unaffected by increased predation within a focal community due to an immigration subsidy from source habitats within the metacommunity (Mouquet and Loreau 2002).

Predation risk can depend on body size if larger prey experience a rarified subset of gape-limited predators (Werner and Gilliam 1984). Contrary to community-wide results, the per capita density of potential predators for the intermediate-sized consumer, *A. maculatum*, did not increase in more permanent ponds. This result indicates that relative body size and ontogenetic trajectory can determine the degree to which biotic limits affect species distributions among pond habitats. Therefore, body size may provide an additional axis for producing interspecific tradeoffs among patches that differ in predation risk.

Significant variation in community structure associated with local conditions indicates that environmental heterogeneity may be an important control of metacommunity dynamics at landscape scales. While species richness was best explained by environmental limitation, species composition appears to be mediated by individual adaptations to abiotic and biotic interactions. However, contrary to an assumption of most metacommunity theories, competitive interactions did not figure prominently in determining species composition. Instead, evidence suggested that diverse predator assemblages limit the abundance and composition of species in more permanent ponds.

Accurate predictions of metacommunity dynamics depend on reconciling spatial scales of research with

system-specific scales of environmental heterogeneity, interspecific variation, and dispersal limitation. The degree to which environmental heterogeneity influences the fitness of community members will likely determine the applicability of traditional niche and emerging neutral theories to natural communities. An integrated view suggests that joint processes of local niche assembly among heterogeneous environments and regional dispersal lead to fitness equivalence at regional, rather than local scales (Mouquet and Loreau 2002). Thus, determining the spatial scale(s) over which fitness equivalence is likely to be manifested should play a prominent role in the future development and integration of neutral and niche assembly metacommunity theories.

Strong species-environment relationships and evidence for interspecific trade-offs among divergent habitat types detected at the scale of this study argue for the application of a species-sorting (Leibold 1998) or mass-effect (Mouquet and Loreau 2002) framework. Compelling evidence for niche assembly in these temporary pond communities was likely the product of the strong disturbance gradients and trophic interactions. In light of these results, I suggest that niche assembly metacommunity models will often be applicable to natural communities at landscape scales because of the multitrophic nature of most communities and widespread evidence for interspecific tradeoffs between conditions in disturbed and undisturbed habitats.

The species sorting framework suggests that local diversity can be maintained when dispersal rates are sufficient to distribute potential species among variable habitats, but not too fast that species sorting processes cannot selectively eliminate unfit taxa prior to recolonization (Leibold et al. 2004). However, evidence for high local dispersal rates and sink-source dynamics (e.g., *A. maculatum*) in this system suggest that the local persistence of some taxa will depend on immigration from other patches, i.e., mass effects (Mouquet and Loreau 2002). Thus, evidence presented here supports the integration of species sorting and mass effect metacommunity frameworks based on species- or system-specific dispersal rates. This integration could have important consequences for predictions of local species diversity and composition. For example, metacommunities assembled from the same species pool along similar environmental gradients could exhibit strikingly different dynamics if mass effects occur in one but not the other due to variation in interpatch distances.

This study indicates the importance of environmental heterogeneity for maintaining community diversity. Ponds differed significantly in absolute permanence among years, even though rank permanence remained similar from year to year. Consequently, a source habitat for a species in one year may become a sink habitat in the next year. This shifting mosaic of habitat suitability over time suggests that metacommunities may be resilient to spatially synchronous disturbance as

long as inter-patch connectivity and environmental heterogeneity are maintained. However, the loss of a specific habitat type or a decrease in landscape connectivity could lead to significant declines in both local and regional biodiversity.

ACKNOWLEDGMENTS

I thank C. Burns, K. Freidenburg, A. Halverson, E. Palokovacs, and D. Skelly for field assistance. Research was supported by a Carpenter/Sperry/Mellon grant and manuscript preparation was supported by a National Science Foundation Graduate Fellowship. The manuscript was greatly improved by comments provided by D. Skelly, O. Ovadia, P. Leavitt, and two anonymous reviewers.

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APPENDIX A

A table documenting among-pond environmental variation is available in ESA's Electronic Data Archive: *Ecological Archives* E085-096-A1.

APPENDIX B

A presence and absence matrix for pond communities is available in ESA's Electronic Data Archive: *Ecological Archives* E085-096-A2.

APPENDIX C

Results from nested subset, fourth-corner, and functional composition analyses are presented in ESA's Electronic Data Archive: *Ecological Archives* E085-096-A3.