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Predators, prey, and transient states in the assembly of spatially structured communities

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Abstract. Ecological theory suggests that both dispersal limitation and resource limitation can exert strong effects on community assembly. However, empirical studies of community assembly have focused almost exclusively on communities with a single trophic level. Thus, little is known about the combined effects of dispersal and resource limitation on assembly of communities with multiple trophic levels. We performed a landscape-scale experiment using spatially arranged mesocosms to study effects of dispersal and resource limitation on the assembly dynamics of aquatic invertebrate communities with two trophic levels. We found that interplay between dispersal and resource limitation regulated the assembly of predator and prey trophic levels in these pond communities. Early in assembly, predators and prey were strongly dispersal limited, and resource (i.e., prey) availability did not influence predator colonization. Later in assembly, after predators colonized, resource limitation was the strongest driver of predator abundance, and dispersal limitation played a negligible role. Thus, habitat isolation affected predators directly by reducing predator colonization rate, and indirectly through the effect of distance on prey availability. Dispersal and resource limitation of predators resulted in a transient period in which predators were absent or rare in isolated habitats. This period may be important for understanding population dynamics of vulnerable prey species. Our findings demonstrate that dispersal and resource limitation can jointly regulate assembly dynamics in multi-trophic systems. They also highlight the need to develop a temporal picture of the assembly process in multi-trophic communities because the availability and spatial distribution of limiting resources (i.e., prey) and the distribution of predators can shift radically over time.

Key words: community assembly; dispersal limitation; fragmentation; trophic interactions.

Introduction

In open ecological systems, community assembly depends on both processes that regulate colonization, and processes that affect the ability of colonists to establish and reproduce post-colonization (Tilman 2004, Hubbell 2005, McCauley 2007). Studies of terrestrial plant communities, marine invertebrate communities, and fish communities have shown that differences in assembly among sites often reflect differences in factors that limit supply rate of colonists ("dispersal limitation") or differences in factors that constrain post-colonization success such as the availability of limiting resources ("resource limitation"; Shulman 1984, Caley et al. 1996, Clark et al. 2007). The results of such studies have often been interpreted broadly, and used to develop general theories of community assembly (e.g., Tilman 2004, Hubbell 2005). However, studies that directly measure both dispersal and establishment limitation have been almost exclusively restricted to communities consisting of a single trophic level. Moreover, studies of communities containing multiple trophic levels often compare communities at a single point in time rather than documenting the time course of assembly. This approach ignores transient states, which can be vital in determining the long-term dynamics of communities (Hastings 2004). Thus, it remains unclear how dispersal limitation and post-colonization factors such as resource limitation affect the assembly of communities with multiple trophic levels.

Distinguishing effects of dispersal and resource limitation on assembly of multi-trophic communities has proven challenging in past studies, in part because the ecological and geographic factors that induce dispersal and resource limitation are often correlated. With respect to predators or prey, dispersal limitation can directly increase the time taken to colonize isolated habitats and decrease population growth rates in those habitats (Fig. 1A). Thus, isolated communities may exhibit lower abundance and species richness, on average, than communities near source habitats (McCauley 2007). However, predator and prey guilds are linked by trophic interactions. Consequently, the number of predator colonists recruiting into local populations after colonization may also depend on the availability of prey (Fig. 1B; Poulsen et al. 2007). Habitat isolation can thus have two effects on predators: a direct effect, which results from predator dispersal

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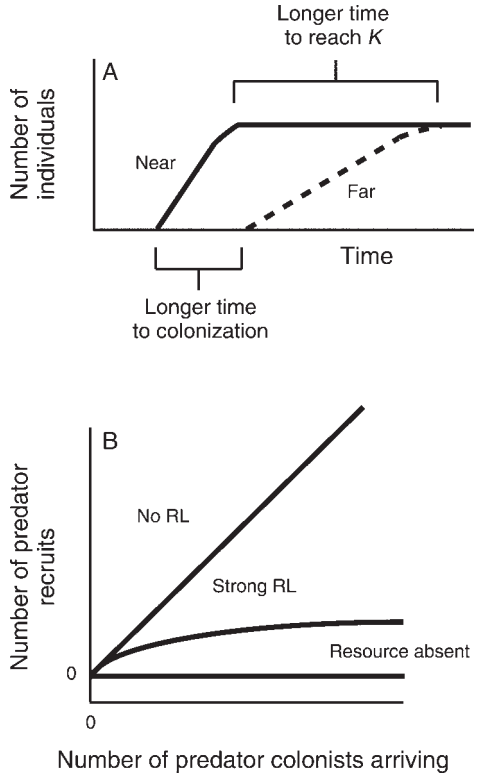

FIG. 1. Effects of dispersal limitation (DL) and resource limitation (RL) on colonization and recruitment. (A) Effects of DL on population size and time to reach carrying capacity (K) in habitats near and far from a source of immigrants. (B) RL determines the relationship between the number of predator colonists that arrive in a habitat and the number that successfully recruit into the local community.

limitation, and an indirect effect, which results when prey dispersal limitation leads to predator resource limitation.

A number of empirical studies have found that predator and prey species tend to be less abundant or less species rich in more isolated habitats (Kruess and Tscharntke 1994, Watts and Didham 2006, McCauley 2007, Shulman and Chase 2007). However, because resource availability and habitat isolation are often correlated with one another (e.g., Kruess and Tscharntke 1994), it is hard to determine whether these patterns are due to dispersal limitation, resource limitation, or both. Furthermore, studies often compare communities based on observations taken at a single, often arbitrary point in time (e.g., Kruess and Tscharntke 1994, Dubbert et al. 1998, Shulman and Chase 2007). This approach may also result in erroneous conclusions regarding the overall effect of dispersal and resource limitation if the strengths of these factors change through time.

To address these issues, we performed a large-scale field experiment to distinguish effects of dispersal and resource limitation on the assembly of aquatic invertebrate communities containing two trophic levels. We did so using a system of experimental aquatic mesocosms in the field. By manipulating prey abundance and habitat isolation, we evaluated (1) whether prey species were dispersal limited leading to low prey availability in isolated communities; (2) whether predator colonization, abundance, and species richness were affected by dispersal limitation and by resource limitation; and (3) how effects of dispersal and resource limitation on these community properties changed through time.

METHODS

We established 42 replicate aquatic mesocosms in the field at varying distances from colonization sources (permanent lakes). We inoculated half of these mesocosms with prey to create a treatment in which resources for predators were augmented at all distances (see *Results*). We then allowed inoculated and non-inoculated mesocosms to be colonized naturally for eight weeks. Eight weeks exceeds the average time period over which natural temporary ponds at our field site contain water (mean = 6 weeks; S. Coates, *unpublished data*). This interval is also roughly equal to the time required for one to two generations of the longest-lived species in our study system (i.e., small dragonflies and dytiscid beetles) and three to 10 generations of the shortest-lived species (e.g., small cladocerans and rotifers; Lynch 1980). It is thus an appropriate timescale over which to study the assembly dynamics of these communities. Abundances and richness of prey and predator species in each mesocosm were measured once every other week over the study period. Analyses were performed to determine (1) whether isolation distance and time affected prey abundance and species richness, (2) whether, distance, prey abundance, and time affected predator colonization, abundance, and richness, and (3) how effects of these variables changed through time.

Study site and experimental design

The experiment was performed at the Ordway-Swisher Biological Station (OSBS) in Melrose, Florida, USA. The OSBS consists of pine upland habitat dotted with many temporary and permanent water bodies. Natural temporary ponds in this region typically consist of three trophic levels: a basal level, which includes detritus and primary producers; a primary consumer level of saprophages and grazers, including cladocerans, rotifers, and culicid and chironomid fly larvae; and top predators including chaoborid fly larvae, larval odonates, and dytiscid beetles (A. Hein, *unpublished data*). We focused on primary and secondary consumers, henceforth referred to as prey (saprophages and grazers) and predators (species that feed on saprophages and grazers).

Mesocosms were plastic wading pools (1 m diameter × 15 cm depth) designed to mimic small natural temporary ponds. In June 2008, we selected seven permanent lakes (experimental blocks) spread over 3000 ha to act as sources of colonists. We set up an array of six

mesocosms at each lake (7 lakes × 6 mesocosms/lake = 42 mesocosms total). Mesocosms were divided into six distance (10, 100, 400 m) by inoculation (inoculated, non-inoculated) treatments (Appendix A). We scrubbed and rinsed mesocosms; then, on 11 June 2008, we added a thin layer (1 cm deep) of sand, 70 L of well water, and 50 g of rabbit food (Small World, Manna Pro, St. Louis, Missouri, USA) to each mesocosm to provide an initial source of nutrients. To perform inoculations, we collected prey by towing a 10 cm mouth diameter, 64-μm mesh plankton net through 800 L of water in the littoral zone of each source lake. Samples were filtered through 1-mm mesh to remove top predators and scanned at 25× magnification to ensure that predators were removed. Inocula from each lake were divided into four 200-mL aliquots. An aliquot was added to one mesocosm in each distance treatment. The final aliquot was added to a control pool set up at a randomly selected distance (10, 100, or 400 m). Controls were covered with 1mm mesh to determine whether inoculation introduced predators to mesocosms. No predators were present in control mesocosms during the experiment, confirming that predators had not been added.

We sampled mesocosms two, four, six, and eight weeks after initiating the experiment. During each sampling event we counted macroinvertebrates (>1 mm in length), removed and measured the body lengths of the first 10–25 individuals of each species, and returned them to the mesocosm. We then took three 500-mL plankton samples using an integrated depth sampler. We combined plankton samples and filtered them through 64-μm nitex mesh. During the final sampling period (week 8), we sampled mesocosms as described. We then removed all macroinvertebrates by sweeping a 1-mm mesh net through the water and benthos until no individuals were captured on three consecutive sweeps. We preserved all samples in 70% ethanol.

We identified invertebrates using general and region-specific keys to the level of species in most cases, and occasionally to the level of morphospecies (henceforth "species," Appendix B). Abundance and richness estimates from field surveys did not differ from estimates based on destructive samples (paired t test; abundance $t = 0.70$, $\mathrm{df} = 41$, $P = 0.49$; $\ln(1 + \text{richness})$ $t = -1.4$, $\mathrm{df} = 41$, $P = 0.19$). Eighteen mesocosms from week 2 were excluded from abundance and richness analyses (see *Statistics*) because plankton samples from these mesocosms were damaged. These were retained in the predator colonization analysis because our ability to detect predators was not compromised.

Statistics

We used a series of analyses to determine how prey and predator abundance and richness, and predator colonization were affected by spatial isolation, inoculation, and time. We used mixed models to accommodate the spatial blocks (i.e., source lakes) and repeated measures in our study design. Linear mixed models (LMM) were used to determine whether predator and prey abundance were affected by experimental covariates. Generalized linear mixed models (GLMM) were used determine whether covariates influenced predator and prey species richness, and predator colonization (Appendix C). In all models, source lake was treated as a random effect and repeated measures were incorporated using a random-intercept model (Everitt 2005).

Effects of isolation and time on prey.—We used a LMM and a GLMM to relate prey abundance and species richness, respectively, to experimental covariates. To determine whether prey abundance declined because of dispersal limitation, we expressed log(1 + prey abundance) as a function of inoculation, distance, time, and all interactions among these variables. Abundance counts were log-transformed to reduce heteroscedasticity. To determine whether habitat isolation affected prey species richness, we used a GLMM to relate prey richness to the same covariates used in the previous model. To determine whether changes in richness were mediated by changes in abundance, we repeated the prey richness analysis after rarefying samples to a common abundance (Appendix C).

Effects of isolation, prey availability, and time on predators.—To determine whether isolation, prey availability, and time affected the colonization of predators, we expressed the proportion of mesocosms with predators in each time by treatment combination as a function of experimental covariates. We used a GLMM to express the proportion of pools that contained predators as a function of time, isolation distance, and inoculation (Appendix C).

To determine whether isolation distance, prey availability and time affected predator abundance, we expressed ln(1 + predator abundance) as a function of distance, time, and ln(1 + prey abundance). We used a separate model to express predator richness as a function of the same covariates. To account for the possibility that predators might respond to prey biomass rather than abundance, we re-ran all predator models using ln(1 + prey biomass) as a covariate. Finally, we analyzed rarefied predator species richness as a function of covariates (Appendix C).

We fitted all LMMs using maximum likelihood (nlme package) and all GLMMs using the Laplace approximation (lme4 package; both code packages *available online*).[2,3] We estimated P values in GLMMS using Monte Carlo simulations (1000 iterations) to build distributions of parameter estimates for each model and comparing these to the null hypothesis of no effect (Appendix C). We simplified each model by removing the highest order interaction with an F (LMMs) statistic with probability > 0.05, or with parameter estimates with probability > 0.05 under the null hypothesis

[2] ⟨http://cran.r-project.org/src/contrib/Archive/nlme/⟩
[3] ⟨http://cran.r-project.org/src/contrib/Archive/lme4/⟩

(GLMMs). We removed fixed effects until all interactions were significant or only main effects remained. Analyses were performed using R (R Core Development Team 2009).

Results

During the course of the experiment, we identified a total of 95 species (72 prey and 23 predators; Appendix B). The percentage of these species encountered at each distance declined with distance, from 71% in mesocosms at 10 m, to 67% and 61% in mesocosms at 100 and 400 m. An increasing percentage of the total species pool was present in each successive time period. We found 32%, 52%, 67%, and 74% of all species in weeks 2, 4, 6, and 8, respectively.

Effects of isolation, inoculation, and time on prey

Prey abundance decreased with increasing distance in non-inoculated mesocosms but was independent of distance when prey were added (Fig. 2; distance by inoculation, $F_{2,30} = 7.77$, $P = 0.002$; Appendix C). Prey abundance also increased with time in all treatments ($F_{3,102} = 49.5$, $P < 0.001$). Non-inoculated mesocosms at 400 m, in particular, contained no individuals in week 2, but an average of 5.4×10^3 individuals (95% CI = 1.78×10^3 to 2.63×10^4) in week 8. When data from week 8 were analyzed separately, only inoculation had a significant effect on prey abundance ($F_{1,34} = 6.08$, $P = 0.019$) and there was no evidence of a distance effect ($F_{2,32} = 0.06$, $P = 0.94$). Prey species richness decreased with increasing isolation distance in non-inoculated mesocosms (400 m: $P < 0.001$) but was unaffected by distance in inoculated mesocosms (Fig. 2; distance by inoculation in 400 m treatment: $P = 0.007$). The effect of distance on prey richness persisted through the experiment (400 m distance by inoculation treatment in week 8: $P < 0.001$). In week 8, inoculated mesocosms at 400 m contained an average of eight more species (95% CI = 3.1–20.9) than non-inoculated mesocosms at the same distance. When we repeated the analysis on rarefied richness, distance by inoculation interactions were no longer significant (all weeks, $F_{2,102} = 1.22$, $P = 0.3$; week 8, $F_{2,30} = 0.35$, $P = 0.71$); however, main effects of distance and inoculation over the whole study were still detectable (distance, $F_{2,32} = 6.4$, $P = 0.005$; inoculation, $F_{1,32} = 4.5$, $P = 0.04$), as was the effect of inoculation in week 8 ($F_{1,32} = 4.4$, $P = 0.04$).

Effects of isolation, prey abundance, and time on predator colonization

Predator colonization approached 100% in all treatments by the end of the experiment indicating a strong effect of time (Fig. 3; $P = 0.034$, 0.004, and <0.001, in weeks 4, 6, and 8, respectively). Additionally, fewer mesocosms at 400 m contained predators ($P = 0.001$). The effect of distance was most apparent in non-inoculated mesocosms at 400 m, where the proportion of mesocosms colonized increased from 0 in week 2 to 0.86 in week 8, but differences between inoculated and non-inoculated mesocosms were not distinguishable (inoculation: $P = 0.459$), suggesting that prey abundance exerted a minimal effect on predator colonization. When only data from week 8 were considered, the effect of distance on predator colonization was no longer present ($P = 0.84$ and 0.55 at 100 and 400 m, respectively).

Effects of isolation, prey abundance, and time on predator abundance and richness

Unlike predator colonization, predator abundance was not directly affected by distance ($F_{2,33} = 1.4$, $P = 0.26$). Time ($F_{3,104} = 6.9$, $P < 0.001$) and prey abundance ($F_{1,104} = 36.5$, $P < 0.001$), on the other hand, were strong predictors of predator abundance. Fig. 2 shows that mean predator abundance increased at all distances through time and that predator abundance declined with distance only when prey abundance declined with distance. Results were the same when ln(1 + prey biomass) was substituted for ln(1+ prey abundance), except that there was marginal evidence for an effect of distance (time, $F_{3,104} = 12.2$, $P < 0.001$; prey biomass, $F_{1,104} = 6.9$, $P = 0.01$; distance, $F_{2,33} = 2.7$, $P = 0.08$). By week 8, predator abundance was similar in all treatments (prey abundance, $F_{1,32} = 0.14$, $P = 0.74$; distance, $F_{2,32} = 0.78$, $P = 0.47$).

Predator species richness remained fairly low throughout the experiment (Fig. 2). Despite this, we detected a dependence of predator richness on prey abundance ($P < 0.001$) and distance (400 m, $P = 0.036$), but not on time (all $P > 0.298$). Results were similar when ln(1+ prey biomass) was substituted for ln(1 + prey abundance) (Appendix C). Predator richness increased by 0.12 ln units (95% CI = 0.05–0.2) per ln-unit increase in prey abundance. When data from week 8 alone were analyzed, none of the covariates affected predator richness (all $P > 0.557$). Fig. 2 shows that predator richness was relatively uniform across all treatments by the end of the experiment (mean = 2.1, 95% CI = 1.7–2.7). Rarefied predator richness increased with time ($F_{3,104} = 20.9$, $P > 0.001$) but was unaffected by distance or prey abundance (all $P > 0.11$).

Discussion

Our results show that assembly dynamics of experimental pond communities are jointly regulated by dispersal and resource limitation. We found that dispersal limitation exerted direct effects on predator and prey species. Yet, at the level of the whole community, these factors were not independent of one another because prey dispersal limitation led to predator resource limitation. The effects of dispersal and resource limitation on abundance, richness, and colonization varied substantially through time and were diminished by the end of the experiment as communities at all distances became similar in predator and prey abundance and richness. Because the length of our experiment and spatial distribution of our mesocosms were

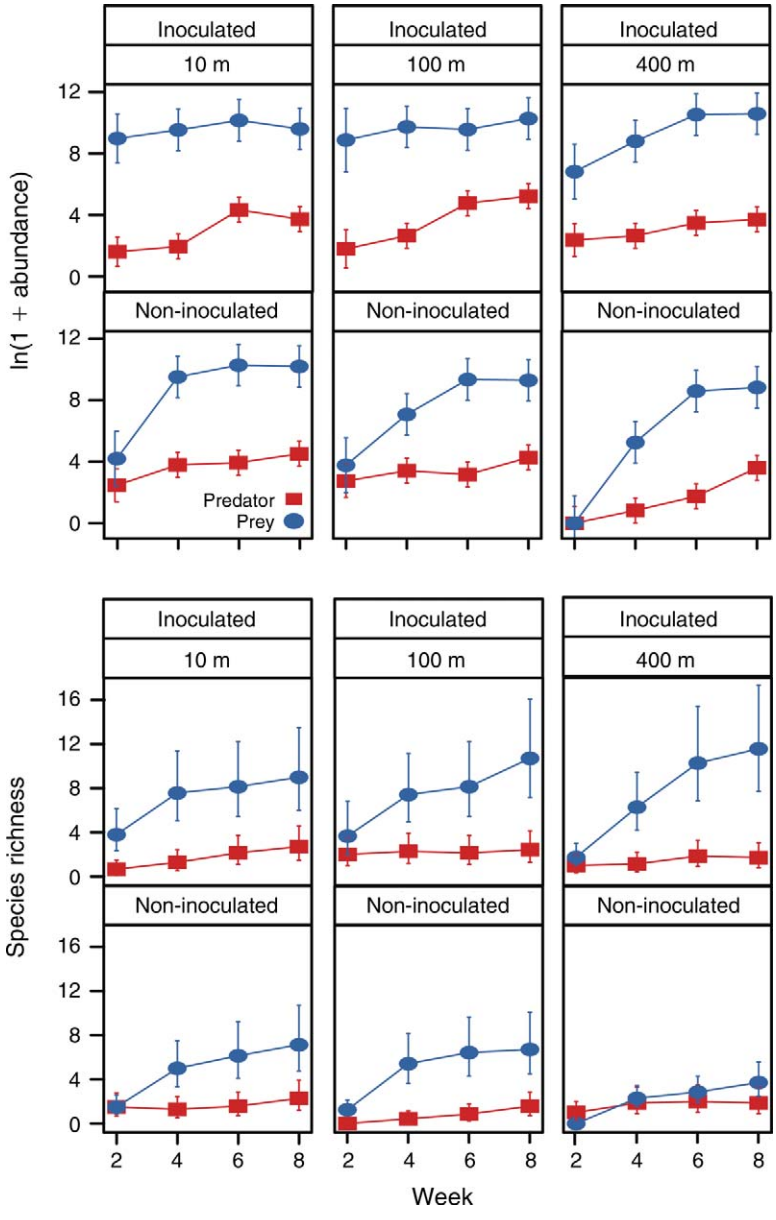

FIG. 2. Mean prey and predator abundance and richness as functions of experimental variables (distance, inoculation). Upper panels show data from inoculated mesocosms. Lower panels show data from non-inoculated mesocosms. Error bars represent ±2 SE.

similar to the length of the hydroperiod and the spatial distribution of natural ponds at our study site, it is likely that the mechanisms revealed by our experiment also regulate assembly dynamics in natural habitats.

Determining how assembly dynamics are regulated by both dispersal limitation and post-colonization factors like resource limitation is vital to inform basic ecological theory (Clark et al. 2007). Our experiment revealed several important results that aid in understanding how these factors regulate assembly in natural multi-trophic communities. Early in the experiment, prey abundance and richness decreased with increasing distance in non-inoculated mesocosms but was independent of distance in inoculated mesocosms indicating that this effect was caused by dispersal limitation. We also observed strong effects of distance on predators in the earlier stages of the experiment. Predator colonization declined with increased isolation in early weeks in inoculated and non-inoculated mesocosms (Fig. 3), suggesting that predators failed to colonize isolated mesocosms not because of limited prey availability, but because they were unable to reach isolated sites early in the study. While predator abundance also decreased with increasing distance in non-inoculated mesocosms, this effect was driven by the

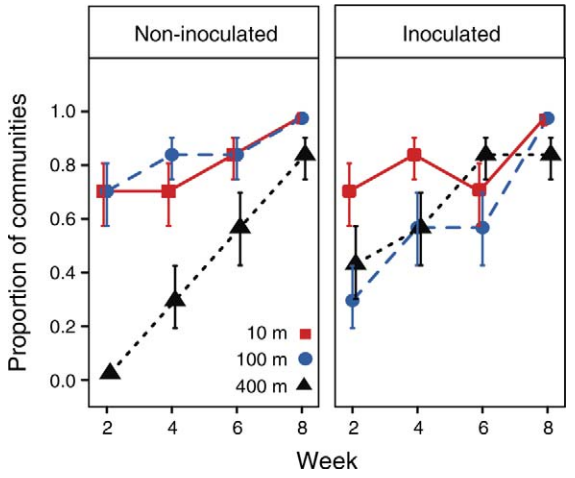

FIG. 3. Proportion of mesocosm communities that contained predators as a function of distance, time, and inoculation. Symbols represent different distance treatments. Error bars represent ±2 SE.

effect of distance on prey rather than by a direct effect of distance on predators. Thus, habitat isolation affected predators directly, by reducing predator colonization rate in isolated habitats, and indirectly, by reducing the availability of prey in isolated habitats.

Past studies in both single and multi-trophic systems have emphasized testing whether dispersal or resource limitation has a significant effect on some measure of community structure (e.g., Shulman 1984, Kruess and Tscharntke 1994, references in Clark et al. 2007). Yet, here we show that these two types of limitation can both have important effects on assembly and that trophic dependencies among species cause them to be correlated. We also show that it is possible to separate effects of resource limitation from those of dispersal limitation to understand how assembly depends on these two processes (i.e., dispersal limitation slows predator colonization but has little effect on abundance post-colonization, resource limitation regulates predator abundance post colonization but does not influence initial colonization) and how these dependencies change through time. This approach moves beyond simply determining whether effects of dispersal or resource limitation are statistically distinguishable from zero (Clark et al. 2007), and explicitly incorporates the dynamic nature of community assembly and the nonequilibrium nature of systems commonly studied by community ecologists (Hastings 2004).

Effects of dispersal and resource limitation on the structure of individual communities were largely transient on the timescale of our entire experiment. However, the transient dynamics we observed are likely to have important consequences for the richness and abundance of species at the level of our entire study system. For example, predators were absent from most communities at 400 m for at least four weeks, whereas the mean hydroperiod of small temporary ponds at our field site is only six weeks. This is a significant period of time considering that larval development times of species like *Culex* mosquitoes can be as short as seven days (Henn et al. 2008). Indeed, we observed large numbers of mosquito and chironomid pupal exuvia in isolated, predator-free mesocosms indicating that these species were able to complete development and recruit into the adult population before predators arrived. Similarly, Chase and Shulman (2009) found that isolated artificial and natural aquatic habitats supported higher larval mosquito abundances than more proximate habitats because of the low abundance of predators in these habitats. Our results suggest that the location of predator-free habitats has not only a spatial component, but also a temporal component. This may be important for understanding population booms of species that exploit predator-free habitats. For example, Chase and Knight (2003) posited that mosquito population booms are more likely to follow drought years because droughts eliminate predators, thereby creating large amounts of predator-free habitat when rains return. Our results confirm that such predator-free habitats do indeed occur in a landscape-scale experiment, but also that they are most likely to occur in regions that are far from permanent water bodies. The observation that this pattern was diminished by the end of the experiment supports the notion that drying is important in re-setting predator–prey dynamics in these habitats (Chase and Knight 2003). We suspect that many systems, including agricultural landscapes (Kruess and Tscharntke 1994), phytotelmata communities (Pimm and Kitching 1987), and small islands (Schoener and Spiller 2006) may be characterized by periodic loss and re-establishment of predator–prey interactions, and also by dynamic spatial gradients in resource availability and predation pressure.

Our findings demonstrate the importance of evaluating the combined effects of dispersal and resource limitation on community assembly through time. In the temporary pond communities studied here, dispersal and resource limitation are strongly linked. In the future, researchers should attempt to include both sources of limitation into their study designs. It will also be important to develop a temporal picture of the assembly process in multi-trophic communities because the availability and spatial distribution of limiting resources (i.e., prey) and the distribution of predators can shift radically over time. A richer and more dynamic view of the roles of dispersal and resource limitation and their interactions will emerge as ecologists continue to study assembly of multi-trophic communities.

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APPENDIX A

A schematic of a mesocosm array (*Ecological Archives* E092-046-A1).

APPENDIX B

Species encountered and number of occurrences by treatment (*Ecological Archives* E092-046-A2).

APPENDIX C

Results of statistical analyses, Monte Carlo simulations, and rarefaction (*Ecological Archives* E092-046-A3).