Reports

Metacommunity assembly and sorting in newly formed lake communities

MICHAEL R. ALLEN,[1] JESSICA N. VANDYKE, AND CARLA E. CÁCERES

*Program in Ecology, Evolution and Conservation Biology, School of Integrative Biology, University of Illinois, 515 Morrill Hall,
505 S Goodwin Avenue, Urbana, Illinois 61801 USA*

Abstract. When new habitats are created, community assembly may follow independent trajectories, since the relative importance of dispersal limitation, priority effects, species interactions, and environmental gradients can vary as assembly proceeds. Unfortunately, tracking community colonization and composition across decades is challenging. We compiled a multiyear community composition data set and reconstructed past communities with remains from sediment cores to investigate cladoceran assembly dynamics in six older (1920s) and two more recently formed (1950s) lakes. We found that current communities cluster along a gradient of thermal stratification that is known to influence predation intensity. Assembling communities showed evidence for a greater influence of species sorting and a reduced influence of spatial structure since the first colonizations. However, lake community trajectories varied considerably, reflecting different colonization sequences among lakes. In the older lakes, small-bodied cladocerans often arrived much earlier than large-bodied cladocerans, while the two younger lakes were colonized much more rapidly, and one was quickly dominated by a large-bodied species. Thus, by combining contemporary community data with paleoecological records, we show that assembly history influences natural community structure for decades while patterns of ecological sorting develop.

Key words: colonization; community dissimilarity; *Daphnia*; paleoecology; spatial structure.

INTRODUCTION

Metacommunity theory holds that current communities are structured by local and regional processes interacting over time (Gilpin and Hanski 1991, Holyoak et al. 2005). Dispersal is an important regional process that provides movement among patches, a set of species from which communities assemble, and potentially ongoing species turnover through extinction and recolonization. As communities assemble, local factors, such as environmental conditions and biotic interactions (predation, competition, parasitism), may influence the ability of new species to colonize habitats and the abundance or rarity of individual species within communities (Shurin 2000, Cottenie and De Meester 2004). Depending on the age of the habitat and relative influence of dispersal, the metacommunity in question may reflect history (i.e., dispersal limitation, coloniza-

tion history, and priority effects [neutral or patch dynamics]), ecological gradients (species sorting), or source–sink dynamics (mass effects) (Leibold et al. 2004). To identify these processes, metacommunity studies typically examine current community composition, ecological gradients, and contemporary dispersal rates (Holyoak et al. 2005).

The relative importance of local and regional processes to a metacommunity assemblage may also change through time (Mouquet et al. 2003). For example, in a low dispersal scenario, regional factors may be evident during initial habitat colonization when communities are unsaturated and dispersal is most limiting. Different relative abundances and dispersal abilities of potential immigrants may influence colonization history, and assembly order may produce priority effects (Mouquet et al. 2003, Price and Morin 2004). Such effects may be especially strong in systems where organisms create seed or egg banks (De Meester et al. 2002). Later in community development when the local species pool is larger, assembly history and dispersal limitation may be less important than local processes. Here, regional influences (spatial structure and priority effects) would

be most apparent early in community formation and local factors would dominate later. Thus, colonization history and temporal community dynamics may provide greater insight into the mechanisms underlying metacommunity development than simply examining contemporary dispersal rates and metacommunity composition.

Studying newly created habitats in nature is an excellent way to examine how the interaction of local and regional processes changes over time. For example, clusters of man-made lakes and the associated zooplankton metacommunities may be particularly apt for such studies, as zooplankton both vary in their dispersal abilities (Jenkins and Buikema 1998, Cáceres and Soluk 2002) and make propagules that collect in lake sediments. Consequently, paleoecological analysis of invertebrate remains in undisturbed lake sediments can allow quantification of changes in species abundance and community composition through time, providing a unique record of species colonization and extinction events (Kerfoot et al. 1999, Brendonck and De Meester 2003, Mergeay et al. 2007). Although colonization dynamics can be studied experimentally in mesocosms and ponds, little is known of the relevance of short-term findings to community assembly patterns which develop over decades (Jenkins and Buikema 1998, Cohen and Shurin 2003, Louette et al. 2008). Thus, the combination of sediment records and current community composition of recently formed lakes can provide important insights on the roles of history and inter-decadal ecological events on community assembly.

We examined cladoceran metacommunity composition and assembly in six lakes formed during the 1920s and two lakes formed during the 1950s. We determined the current community structure for six years and used nonmetric multidimensional scaling (NMDS) and permutational MANOVA to test for species sorting along a gradient of thermal stratification. We then used paleoecological records to track how the assembly and composition of zooplankton communities varied through time in each lake, specifically contrasting assembly processes of near-century-old and more recently formed lakes. Finally, we tested the predictions that the influence of spatial structure decreased and species sorting increased through time by tracking the variance attributed to each hypothesis over each 10 year interval since the most recent lakes were formed (40–50 years before present).

METHODS

We studied eight lakes in Kickapoo State Park (Oakwood, Illinois, USA), an area once strip-mined for coal. Newly created pits rapidly filled to become spring-fed lakes varying in area, depth, and age (1926–1959; Appendix A). Based on previous research demonstrating the effect of thermal structure on the composition of zooplankton assemblages (Tessier and Welser 1991, Tessier and Woodruff 2002), we categorized lakes a priori into three groups: shallow unstrat-

ified lakes, deep stratified lakes with a well-formed hypolimnion, and moderate depth lakes with a relatively small hypolimnion (Appendix A). While some temporary ponds and farm ponds exist in the region, no natural stratified lakes are present. Thus, these lakes provided new habitats for pelagic zooplankton. Here, we focus on the colonization history and current community structure of the pelagic cladoceran assemblages. The colonization sequence of Sportsman's Lake has been previously published (Cáceres et al. 2005).

To identify current community composition, we used a 153-μm mesh Wisconsin net to collect samples from the whole water column in May 2003–2008 (spring) and in September 2003, 2004, and 2007 (fall). Samples were preserved in 95% ethanol and cladocerans later identified to family (Chydoridae) or species (*Daphnia pulicaria*, *D. dentifera*, *D ambigua*, *D. parvula*, *Ceriodaphnia lacustris*, *Bosmina longirostris*, *Diaphanosoma birgei*). To avoid the influence of extremes in raw abundance, we used relative abundance data to calculate Bray-Curtis dissimilarity matrices. Two dimensional (2D) NMDS models were fit to the spring and fall data sets with each lake-year as a unique community using the metaMDS algorithm in R 2.9.2 (R Core Development Team 2009). Species weighted average scores were added to the NMDS plots. To test for differences in community structure among lakes, we used permutational multivariate analysis of variance (perMANOVA: adonis in R). The procedure tested for differentiation in community structure among groups of lakes with different stratification regimes, a gradient known to influence zooplankton communities (Tessier and Welser 1991). A significant result suggests that communities sort along this gradient. To avoid pseudoreplication, we used mean dissimilarity matrices in which yearly dissimilarities of each lake pair were averaged for the full matrix.

To determine colonization sequences of cladocera into all lakes, we collected sediment cores (6.5-cm inner diameter) by SCUBA with a hand-held corer in May 2003 and June 2004. Cores were sliced into 1-cm intervals (corresponding to ~0.5–2 yr), and all diapausing egg cases (ephippia) were removed by sieving and density centrifugation of the sediment. Ephippia were identified to species (except *D. ambigua* and *D. parvula* ephippia which were indistinguishable and pooled). All lakes except Emerald had multiple cores that reached the sediment base, which represents the date of lake formation. As gamma spectroscopy cannot accurately measure sediment age on lakes with high sedimentation rates (D. Engstrom, *personal communication*), we calculated each species' colonization year based on its first appearance in the sediment, assuming an equal sedimentation rate through time within each lake. Sedimentation rates likely decreased as the surrounding terrestrial communities developed, meaning the calculated colonization year is relative rather than exact. Nevertheless, these relative dates distinguish among rapidly colonizing species vs. those that colonized much later, allowing
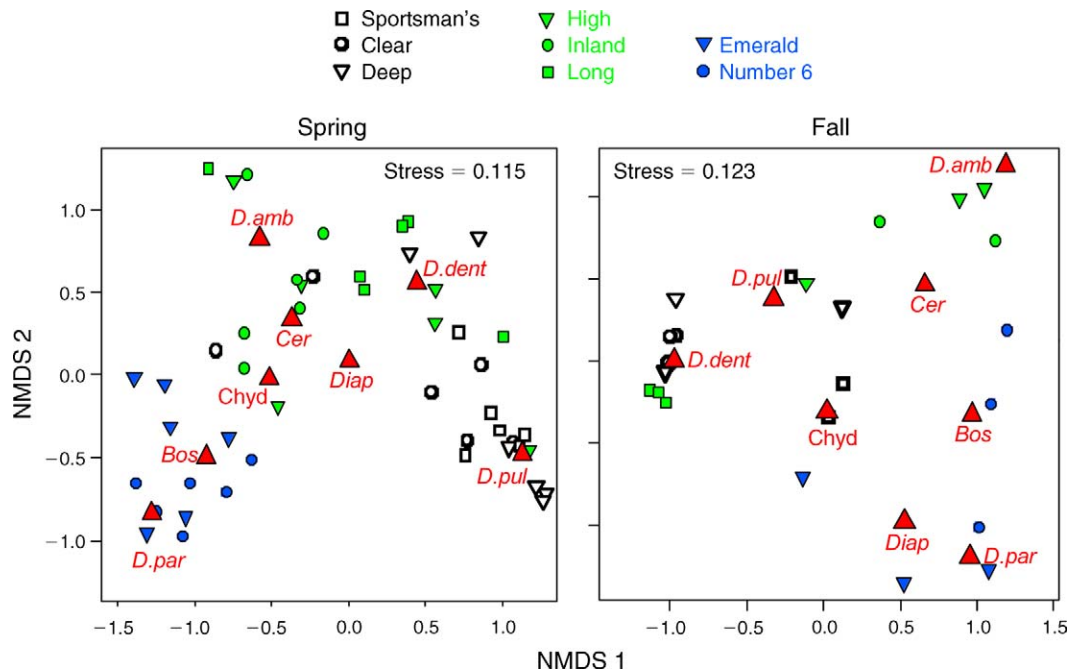
FIG. 1. Nonmetric multidimensional scaling plot of recent cladoceran community structure among eight lakes from spring (2003–2008) and fall (2003, 2004, and 2007). Deep lakes are black, moderate-depth lakes are green, and shallow lakes are blue. Red triangles represent the species position in the ordination. Abbreviations are: Chyd, Chydoridae; *D.pul*, *Daphnia pulicaria*; *D.dent*, *D. dentifera*; *D.amb*, *D. ambigua*; *D.par*, *D. parvula*; *Cer*, *Ceriodaphnia lacustris*; *Bos*, *Bosmina longirostris*; *Diap*, *Diaphanosoma birgei*.

interpretations of relative community trajectories (see next paragraph) and colonization sequences.

We quantified the influence of spatial structure and species sorting on community compositions through time using sedimentary time series of approximately decadal resolution. Metacommunity theory predicts that new communities should be structured more by random colonization processes with evidence of stronger spatial structure (e.g., dispersal limitation), while older communities may be structured by local processes and exhibit species sorting. To quantify these predictions, we tracked community composition changes by calculating the average density of ephippia for 10-yr sediment intervals (four to seven intervals per lake). This effectively smoothed interannual variability in ephippial production, while preserving community changes through time. We calculated the Bray-Curtis dissimilarity on the relative abundance matrix among all lake–interval pairs. We used the mean community dissimilarity matrix (water-column data) and the ephippial dissimilarity matrices for each time interval. Changes in spatial structure through time were measured as the Mantel correlation between these matrices and a matrix of minimum Euclidian distances among lakes. The magnitude of species sorting through time was calculated as the partial R^2 attributed to stratification class in a perMANOVA model for each time interval. We then used NMDS to visualize community structure changes by plotting each community trajectory from 70 years

ago to the present, highlighting the first time point where all lakes were represented. For the statistical analysis, we excluded the shallow lakes due to low abundances of ephippia (or none) which led to unstable estimates of species relative abundance, especially for NMDS analysis of shallow lakes (see *Results*).

RESULTS

Recent community structure varied substantially among the lakes (perMANOVA: $F_{7,40} = 8.57$, $P = 0.001$). Some lakes exhibited consistent spring community structure from 2003 to 2008, while others were more variable (Appendix B). Averaged over years, spring communities grouped into the three clusters we defined based on lake stratification: deep stratified lakes, moderate-depth lakes, and shallow unstratified lakes ($R^2 = 0.69$, $F_{2,5} = 5.65$, $P = 0.002$; Fig. 1). These groups were highly separated from one another (deep vs. shallow $R^2 = 0.76$, $P = 0.001$; deep vs. moderate $R^2 = 0.46$, $P = 0.07$; moderate vs. shallow $R^2 = 0.66$, $P = 0.001$). Large-bodied *D. pulicaria* dominated deep stratified lakes, while small-bodied *D. ambigua* and *D. parvula* were abundant in moderate depth and shallow lakes, respectively (Fig. 1; Appendix B). *Daphnia dentifera*, a medium-bodied species, was common in both moderate and deep lakes. We found similar segregation among lake types for the fall community data ($R^2 = 0.61$, $F_{2,5} = 3.85$, $P = 0.016$), but seasonal succession in the dominant species resulted in greater
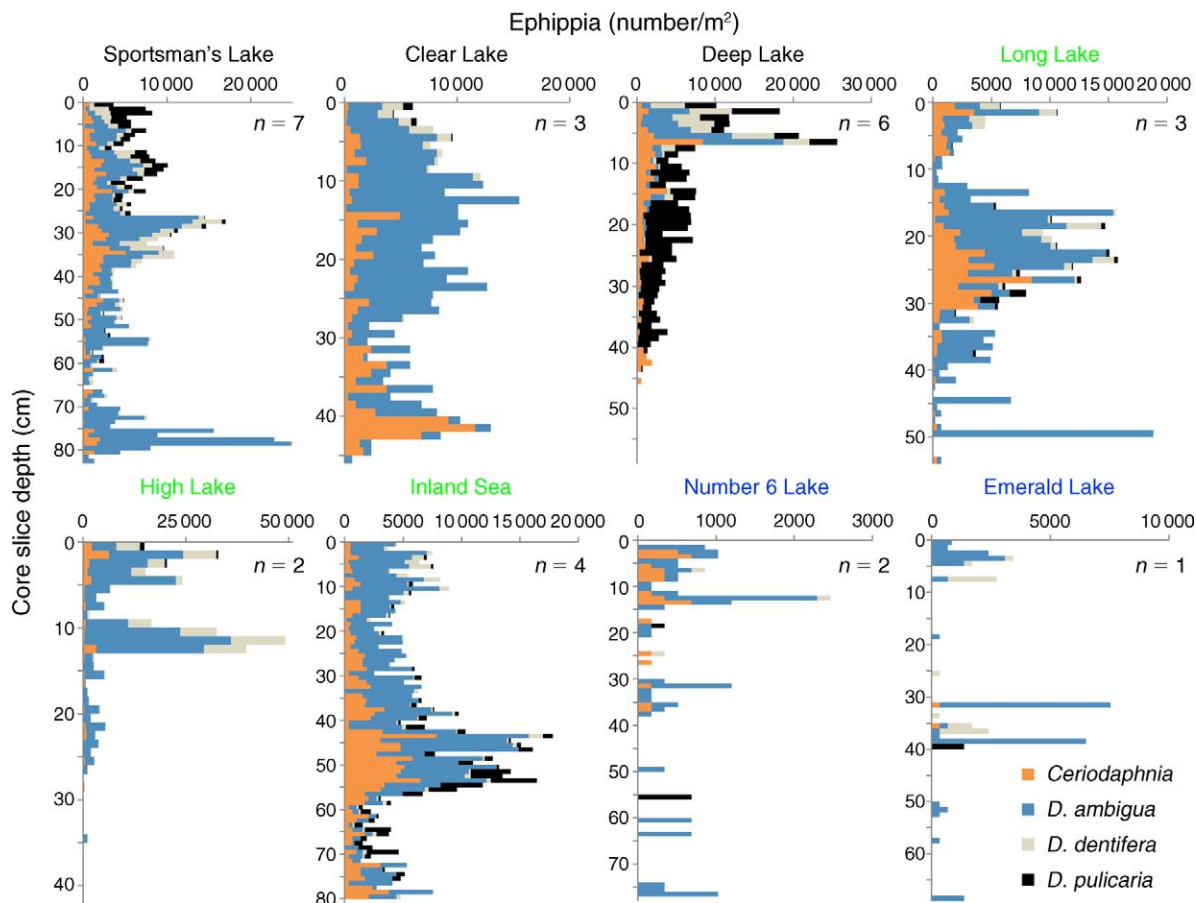
Reports

Ephippia (number/m²)

FIG. 2. Average cladoceran ephippial abundance in sediment cores from eight Kickapoo State Park Lakes (Illinois, USA). Each 1-cm interval represents the average number of ephippia per square meter of four cladoceran taxa, and core length represents the entire colonization sequence for the lake. The maximum numbers of ephippia collected in each lake are recorded in Appendix B. Differences in core length among lakes reflect different terrestrial sediment inputs. We examined 1–7 cores per lake (*n*). *Daphnia ambigua* ephippia are indistinguishable from *D. parvula* ephippia and were thus pooled. Note the different axes on each graph.

overlap between moderate and deep lakes ($R^2 = 0.38$, $P = 0.10$; Fig. 2). During fall, *D. pulicaria* exhibited reduced densities, and *D. dentifera* showed higher densities. Moderate depth lakes were dominated by *D. dentifera* or *D. ambigua*. Shallow communities continued to be characterized by *D. parvula* presence, and were distinctly different from deep ($R^2 = 0.70$, $P = 0.001$) and moderate-depth communities ($R^2 = 0.54$, $P = 0.001$; Fig. 1).

Colonization sequences varied substantially among the eight lakes (Fig. 2; Appendix A). The five oldest lakes took an average (± SE) of 48 ± 12 yr to be colonized by all four cladoceran species, with Inland Sea exhibiting the most rapid complete colonization. In general, *D. ambigua/parvula* and *C. lacustris* were the first colonists of older lakes. In contrast, the two lakes created in the 1950s were colonized by all species more rapidly (20 ± 7 yr).

The influence of spatial structure and species sorting changed substantially through time (Fig. 3). Historical-

ly, the influence of spatial proximity on community composition was high; however, its influence decreased to zero for both the most recent decade and the contemporary water column data. Additionally, the variance attributed to species sorting between moderate and deep lake clusters increased approximately fourfold since Deep Lake was first formed, suggesting initially disparate communities became more similar within and more distinct between their clusters.

Multivariate community trajectories further demonstrated the role of history and sorting among the lakes (Fig. 4). Within the deep and moderate clusters, lake trajectories started from unique initial conditions, but became more similar through time. For example, deep lakes were initially highly dissimilar (0.66), with Sportsman's Lake dominated by *D. ambigua/parvula*, Deep Lake by *D. pulicaria*, and Clear Lake by *C. lacustris*. However, trajectories converged over time and dissimilarity decreased substantially (0.26) in recently deposited sediments. Moderate lakes likewise decreased in
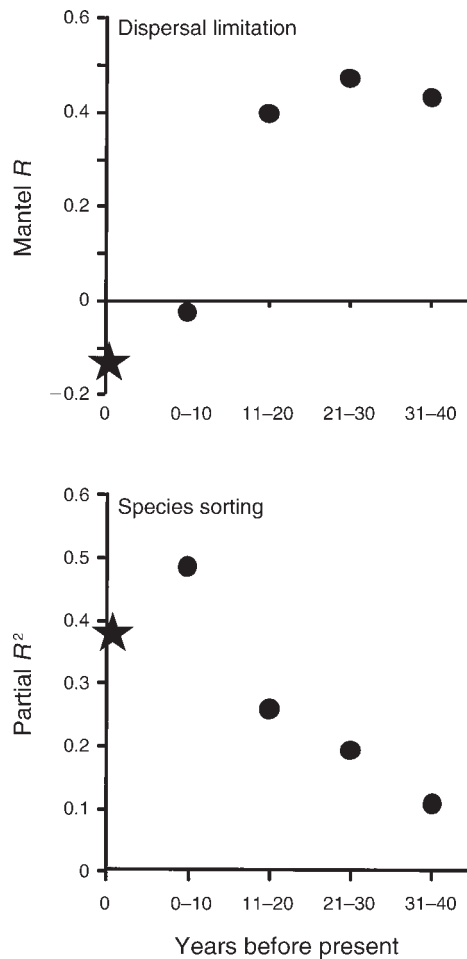
FIG. 3. The effect of dispersal limitation and species sorting over time for deep and moderate-depth lakes. Correlation coefficients represent variation attributable to community dissimilarity vs. geographic distance and the sorting model among lakes over time. Each point represents an approximately 10-year average egg bank composition. The 31–40 years before the present decade (YBPD) interval is the first where all lakes were represented. Time 0 (stars) uses the mean dissimilarity matrix from water column samples.

dissimilarity and converged through time (0.72–0.10), such that all four species were present in each lake during the most recent decade. Finally, lake community trajectories exhibited temporal autocorrelation, although this was less the case for the shallow lakes.

DISCUSSION

Our data indicate that current cladoceran communities are similar to those observed in other Midwestern kettle lakes (e.g., Tessier and Welser 1991). After 50–80 years, our deep stratified lakes with a hypolimnetic summer refuge are dominated by the largest cladoceran species, *Daphnia pulicaria*, while smaller-bodied species are more frequent in moderate-depth and shallow lakes (*D. dentifera*, *D. ambigua*, *D. parvula*, and *C. lacustris*). However, paleolimnological evidence suggests this
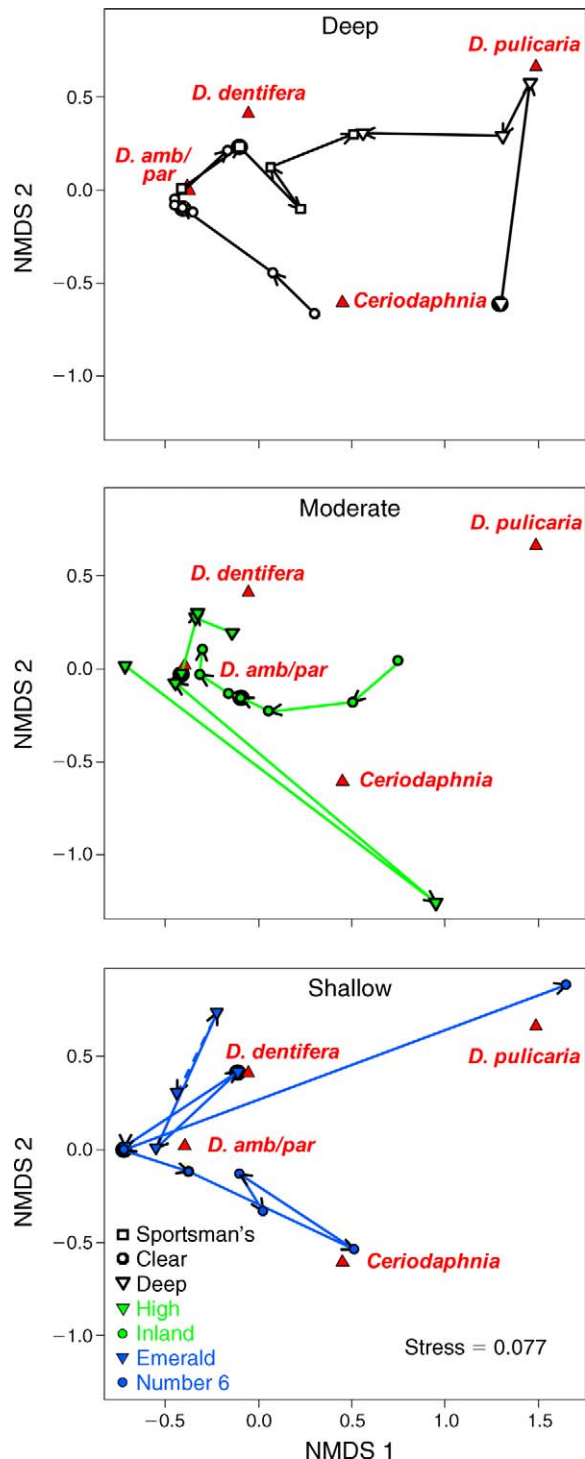

FIG. 4. Nonmetric multidimensional scaling plots of community trajectories based on ephippial abundances through time. All lakes were included in one analysis and subsequently plotted by category. The point corresponding to 30–40 YBPD in each lake (Deep Lake created) is shown by a heavier black outline. Species are plotted as red triangles (*Daphnia ambigua/parvula*, *D. pulicaria*, *D. dentifera*, *Ceriodaphnia lacustris*). The last Emerald connection is dotted, as no ephippia were found in the 11–20 year interval. Long Lake (moderate depth) is absent, as recent human alterations of the lake basin disrupted sedimentation rates.

Reports

pattern of sorting along a stratification gradient developed over multiple decades, with changing metacommunity dynamics shaping community assembly, trajectories, and composition through time.

The slow colonization rate of older lakes by large cladocerans is consistent with the effects of dispersal limitation early in community assembly. For example, older lakes were initially colonized and dominated by small-bodied species, with large-bodied species usually appearing much later as composition and dominance hierarchies changed within these lakes. This pattern is reinforced by a stronger correlation between species composition and distance early in assembly. We hypothesize that the slow colonization by large cladocerans reflects the paucity of naturally deep lakes in the region and, therefore, a relative scarcity of colonist sources, although variation in dispersal rates among cladoceran taxa may also contribute to slower colonization by some species (Cohen and Shurin 2003). Such differences in the colonization rate of species from the regional species pool into newly created communities are common (Cohen and Shurin 2003, Louette et al. 2008) and often contribute to ecological succession (e.g., Tilman 1990).

Analysis of sedimentary time series suggests that the predominant mechanisms structuring zooplankton communities varied with the age and history of the ecosystem. For example, as lakes became enriched with taxa, the influence of spatial structure on species composition in each lake decreased as the influence of local processes (stratification regime) increased. This pattern was particularly striking in the colonization sequences of the younger deep lakes (Deep and Sportsman's), as initially divergent community compositions converged rapidly over a few decades. In principle, these sequences could result either from simple dispersal limitation or from priority effects of initial colonizers early in assembly (Shurin 2000, Louette et al. 2008), followed by a shift to control by local processes later in the time series. However, we recognize that additional experimental studies will be required to distinguish between dispersal limitation and priority effects (e.g., Steiner et al. 2007).

Mechanisms regulating community assembly may also have been influenced by the establishment of older lakes as sources of colonists to younger systems. Consistent with this hypothesis, both young lakes were colonized more rapidly by all species, and *D. pulicaria* was rapidly established in Deep Lake: an event that did not occur in any other system. It could be argued that the apparently rapid colonization of younger sites resulted instead from much lower sedimentation rates in the two younger lakes, which would influence inferred dates of colonization. However, under this scenario we would expect much shorter cores in the younger lakes, which we did not find. Hence, we infer that the establishment of additional local sources of colonists is a more consistent mechanism to explain the rapid colonization of younger lakes.

It is unlikely that historical changes in lake community composition arose from directional changes in environmental conditions during the 20th century. For example, although we lack complete historical records, current productivity (range ~10–45 µg P/L), Secchi depth, pH, and temperature profile measurements are similar to the 1960s (Horner and Brummett 1972). Similarly, because these lakes have been stocked continually with largemouth bass (*Micropterus salmoides*), bluegill sunfish (*Lepomis macrochirus*), and other fish species (Horner and Brummett 1972; R. W. Larimore, *personal communication*), we infer that predation regimes have been comparatively stable during the study period, and that shifts in the size-structure and species composition of pelagic invertebrates do not arise from historical variation in size-selective vertebrate predation.

There are caveats to the use of paleoecological records to infer changes in species composition (Jankowski and Straile 2003). Specifically, although cladocerans are well represented in sediments, rotifers and copepods are rarely preserved. Moreover, sedimentary banks of diapausing eggs only reflect those individuals that reproduced sexually during a given year, and that frequency can vary over time. In addition, the production of diapausing eggs can vary following environmental shifts (e.g., predator and trophic structure changes) and differences in ephippial buoyancy can affect settling rates, both potentially influencing estimates of absolute and relative density derived from sediment records. Finally, the low density of ephippia in sediments (e.g., shallow lakes) hampers our ability to determine whether species went locally extinct and later recolonized, or were present but numerically undetectable. Fortunately, the importance of many of these issues can be reduced through the use of low-resolution (decadal) time series which average out the effect of such short term variation in sexual reproduction. Similarly, while water-column data provided better resolution of community clusters, sedimentary records still contained all four modern predominant taxa needed to quantify major transitions in community structure through time.

Metacommunity studies are often constrained to contemporary patterns of abundance, estimates of dispersal, and small-scale experiments (Holyoak et al. 2005). Here, we demonstrate that paleoecological studies can provide a unique opportunity to track the development of communities over multiple decades, a time frame which appears essential to understanding the mechanisms regulating community assembly. By combining current community data from a diverse set of lakes with such sedimentary records, we have shown that spatial effects may dominate natural communities for decades while broader patterns of ecological sorting develop. Thus, the importance of regional and historical processes relative to abiotic factors and species interac-

tions can change substantially during metacommunity development.

Literature Cited

Brendonck, L., and L. De Meester. 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia 491:65–84.

Cáceres, C. E., S. L. Mulvany, K. A. Paczolt, and C. F. Steiner. 2005. Cladoceran community assembly in a recently created lake. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 29:1020–1024.

Cáceres, C. E., and D. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408.

Cohen, G., and J. B. Shurin. 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103:603–617.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: Synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85:114–119.

De Meester, L., A. Gomez, B. Okamura, and K. Schwenk. 2002. The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecologica 23:121–135.

Gilpin, M. E., and I. Hanski. 1991. Metapopulation dynamics: empirical and theoretical investigations. Academic Press, New York, New York, USA.

Holyoak, M., M. A. Leibold, and R. D. Holt. 2005. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Horner, R. W., and K. L. Brummett. 1972. Vermilion County surface water resources. Illinois Department of Conservation, Division of Fisheries, Springfield, Illinois, USA.

Jankowski, T., and D. Straile. 2003. A comparison of egg-bank and long-term plankton dynamics of two *Daphnia* species, *D. hyalina* and *D. galeata*: potentials and limits of reconstruction. Limnology and Oceanography 48:1948–1955.

Jenkins, D. G., and A. L. Buikema. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. Ecological Monographs 68:421–443.

Kerfoot, W. C., J. A. Robbins, and L. J. Weider. 1999. A new approach to historical reconstruction: Combining descriptive and experimental paleolimnology. Limnology and Oceanography 44:1232–1247.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Louette, G., L. De Meester, and S. Declerck. 2008. Assembly of zooplankton communities in newly created ponds. Freshwater Biology 53:2309–2320.

Mergeay, J., J. Vanoverbeke, D. Verschuren, and L. De Meester. 2007. Extinction, recolonization, and dispersal through time in a planktonic crustacean. Ecology 88:3032–3043.

Mouquet, N., P. Munguia, J. M. Kneitel, and T. E. Miller. 2003. Community assembly time and the relationship between local and regional species richness. Oikos 103:618–626.

Price, J. E., and P. J. Morin. 2004. Colonization history determines alternate community states in a food web of intraguild predators. Ecology 85:1017–1028.

R Core Development Team. 2009. R 2.9.2. R project for Statistical Computing, Vienna, Austria. ⟨www.r-project.com⟩

Shurin, J. B. 2000. Dispersal limitation, invasion resistance and the structure of pond zooplankton communities. Ecology 81:3074–3086.

Steiner, C. F., C. E. Cáceres, and S. D. P. Smith. 2007. Resurrecting the ghost of competition past with dormant zooplankton eggs. American Naturalist 169:416–422.

Tessier, A. J., and J. Welser. 1991. Cladoceran assemblages, seasonal succession and the importance of a hypolimnetic refuge. Freshwater Biology 25:85–93.

Tessier, A. J., and P. Woodruff. 2002. Cryptic trophic cascade along a gradient of lake size. Ecology 83:1263–1270.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3–15.

APPENDIX A

Additional description of the study system (*Ecological Archives* E092-022-A1).

APPENDIX B

Additional data from the water column and sediment cores (*Ecological Archives* E092-022-A2).

Reports