

Effects of diversity on community assembly in newly formed pond communities

CHRISTOPHER J. HOLMES,^{1,†} STEPHANIE FIGARY,² KIMBERLY L. SCHULZ,² AND CARLA E. CÁCERES¹

¹*Department of Animal Biology, School of Integrative Biology, University of Illinois at Urbana-Champaign,
515 Morrill Hall, 505 S. Goodwin Avenue, Urbana, Illinois 61801 USA*

²*Department of Environmental and Forest Biology, College of Environmental Science and Forestry,
State University of New York, 1 Forestry Drive, Syracuse, New York 13210 USA*

Citation: Holmes, C. J., S. Figary, K. L. Schulz, and C. E. Cáceres. 2016. Effects of diversity on community assembly in newly formed pond communities. *Ecosphere* 7(7):e01377. 10.1002/ecs2.1377

Abstract. Theory suggests that in a new habitat, initial levels of genetic or species diversity can influence subsequent community assembly. Nevertheless, empirical investigations of these diversity effects in newly created habitats remain rare at both the genetic and species level, especially for animal systems. To test this theory, we conducted a field experiment in which initial stocking diversity (both intra- and interspecific) of freshwater zooplankton in newly constructed pools was manipulated in a 2 × 2 fully factorial design. Zooplankton communities were sampled every 2 weeks from May to August in 2011 and 2012, and once in May of 2013 and 2014. Estimates of overland dispersal were measured in 2012. Despite theoretical predictions, we found no difference in taxonomic richness among stocking treatments after 4 yr. A total of 24 species was recorded in the experimental pool metacommunity, with average cumulative taxonomic richness ranging from 6.1 to 7.6 species per pool. Using dispersal traps, we found that dispersal of zooplankton was rapid, with eight taxa dispersing within 7 d; we found no difference in the number of dispersed propagules based on number of neighboring source pools. Despite theoretical predictions regarding diversity and community assembly, our study suggests that initial diversity may have no effect on early successional community species richness.

Key words: biodiversity; colonization; community assembly; *Daphnia*; dispersal; ecology; genetic diversity; metacommunity; priority effects; species coexistence; species diversity; zooplankton.

Received 2 October 2015; revised 16 February 2016; accepted 16 March 2016. Corresponding Editor: J. Benstead.

Copyright: © 2016 Holmes et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** cholmes@life.illinois.edu

INTRODUCTION

Community structure results from the interaction of historical (priority effects) and ongoing processes operating at both local and regional scales. Given this complexity, generating accurate predictions for the outcome of community assembly remains difficult for most systems (MacArthur and Wilson 1967, Gadgil 1971, Titman 1976, Young et al. 2001, Dickie et al. 2012, Rajaniemi et al. 2012). The importance of both abiotic and biotic factors for establishment success is well known, yet the relative importance of these local

processes varies significantly among systems (Shurin 2000, Hubbell 2001, Jackson et al. 2001, Kennedy et al. 2002, Vanormelingen et al. 2009, Algar et al. 2011). There are also two schools of thought regarding the importance of history (timing and order of colonization) in determining final community structure. First, some models and experiments (e.g., Neill 1975, Tilman et al. 1986, Sommer 1991, Law and Morton 1996) suggest that community structure should converge on a similar state when habitats are similar, irrespective of colonization order. In contrast, other studies show that multiple equilibrium states may be a product

of colonization history (Robinson and Dickerson 1987, Drake 1991, Luh and Pimm 1993, Samuels and Drake 1997, Law 1999, Chase 2003, Allen et al. 2011). Despite extensive research on this topic, we still lack an understanding of the relative importance of local and regional factors underlying community assembly in the field. This information is necessary if restored or newly created habitats are to achieve their intended community composition and function (Loreau et al. 2001, Chase 2010).

Assembly theory has long considered how interspecific interactions (i.e., competition, predation, and parasitism) can result in resistance to biotic invasion (Tansley 1917, Hutchinson 1959, 1961, Connell 1961, Paine 1966, MacArthur and Wilson 1967, Sih et al. 1985, Case 1991, Drake 1991, Tilman 1997, Shurin 2000). However, interspecific interactions can also explain patterns of coexistence and thus determine patterns of community assembly (Brooks and Dodson 1965, Paine 1966, Connell 1980, Pacala and Tilman 1994, Morris and Knight 1996). For example, when victim species (e.g., prey or host) share a common enemy (e.g., parasite or predator), competition for enemy-free space may be intensified (Holt and Lawton 1994). On the other hand, enemies may relax competition among prey species, thereby enhancing coexistence of victims (Janzen 1970, Freeland 1983, Chase et al. 2002, Altermatt et al. 2007). As a result, context-specific details may over-ride theoretical predictions regarding assembly.

Generating accurate predictions regarding community assembly is complicated further by genetic variation in key traits (e.g., dispersal ability, competitive ability, predation defense, etc.), which may also affect the outcome of interspecific interactions (Stoll and Prati 2001, De Meester et al. 2002, Weltzin et al. 2003, Whitham et al. 2003, Hooper et al. 2005, Crutsinger et al. 2006, Steiner et al. 2007, Hughes et al. 2008, Bolnick et al. 2011). Genetic variation in early colonists may enhance colonization success and short- and long-term population persistence (Crawford and Whitney 2010; Holmes et al. 2016). When the rapid establishment of a genotype or population allows rapid numerical growth, establishment by later arriving genotypes or species may be inhibited (Boileau et al. 1992, Louette et al. 2007, Mwangi et al. 2007). Previous studies have shown that these priority effects may be enhanced when genetic variation facilitates rapid local adaptation

(De Meester et al. 2002, 2007, Urban and De Meester 2009, Ortells et al. 2014), or when sufficient variation in ecologically relevant traits increases the odds of a suitable match between genotype and environment (Holmes et al. 2016). However, understanding the relative importance of these factors and their consequences on patterns of community assembly requires manipulative experiments that examine dynamics over a long period of time.

Pond metacommunities are ideal systems for testing the mechanisms that underlie community assembly due to their discrete borders, ease of manipulation for both abiotic and biotic factors, and the plethora of coexisting species they harbor (Hutchinson 1959, Cottenie et al. 2003, Cottenie and De Meester 2004, De Meester et al. 2005). We used a set of 38 experimental pools to test the relative importance of intra- and inter-species diversity and whether priority effects (colonization history) generated by stocking would affect the outcomes of community assembly. We predicted that (1) stocking pools with regional species (high zooplankton species diversity) would relax dispersal limitation leading to (a) increased species richness and (b) communities reaching species saturation more rapidly than in pools not stocked with regional zooplankton species (Tilman 1997, Shurin 2000); and (2) “high” clonal diversity of a focal grazer species *Daphnia pulex* would decrease species richness by enhancing priority effects and inhibiting subsequent colonization events (De Meester et al. 2002, Thielsch et al. 2009). Given the importance of dispersal in metacommunity theory, we also quantified the rate of overland dispersal. We predicted that a greater number of source pools in a landscape region would provide more dispersing propagules.

MATERIALS AND METHODS

We used a field manipulation of newly created seminatural ponds to examine how initial diversity influenced patterns of community assembly over both time and space. In summer 2010, through collaboration with the Upper Susquehanna Coalition (USC), 38 experimental pools were excavated at Svend O. Heiberg Memorial Forest (Tully, New York, USA). To address questions pertaining to amphibian conservation, pools were constructed in one of three spatial layouts (nine,

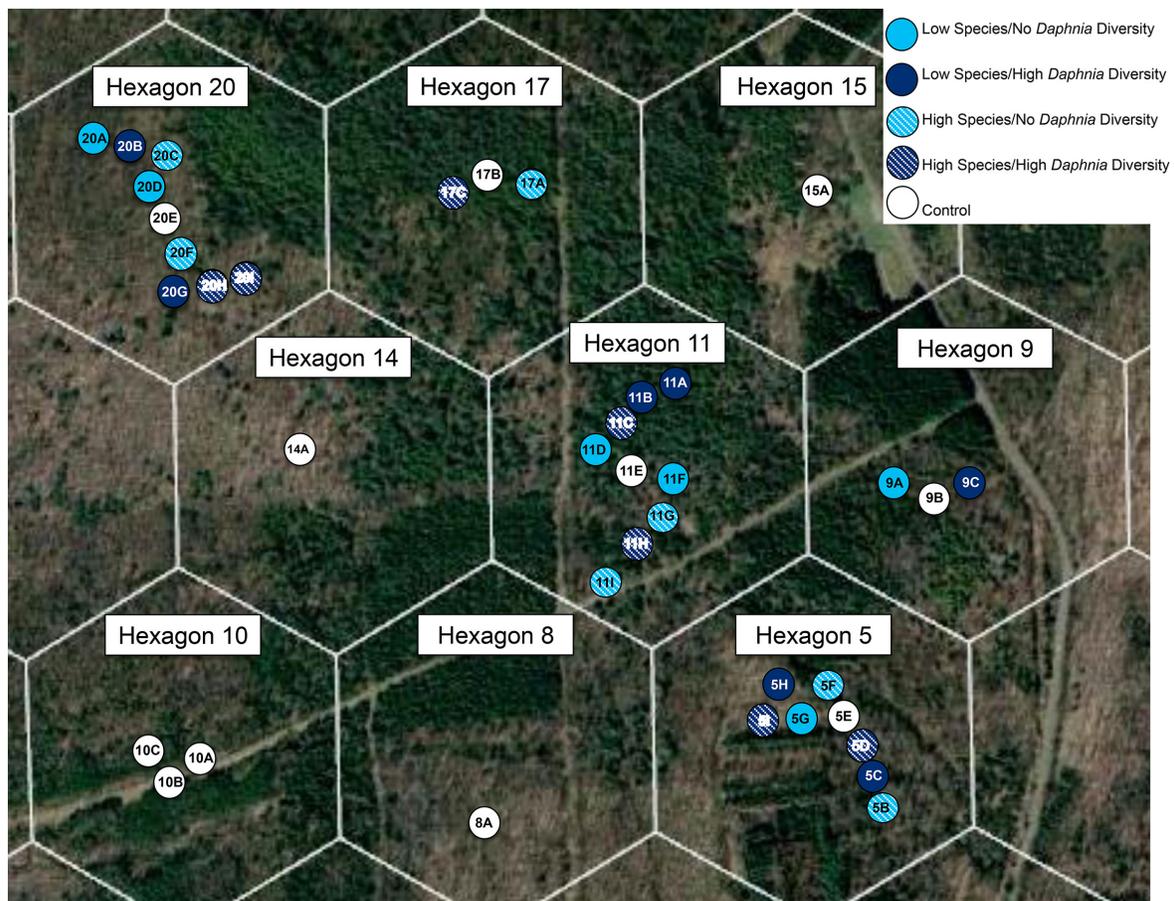


Fig. 1. Spatial pattern of experimental pool infrastructure at Svend O. Heiberg Memorial Forest (Tully, New York, USA, 42.774310, -76.085746). The pools reside in a 9.1-ha forested plot, part of a larger 1578-ha forest. Each experimental pool is uniquely labeled by hexagon number and letter. Pool 5A failed to hold water and was excluded from the field manipulation.

three, or one pool per cluster) and delimited into arbitrary landscape “hexagons” that were 330 m in width (Fig. 1 for spatial arrangement). Pools were designed to be circular, roughly 10 m in diameter, but because they were constructed in a forest, to leave large trees intact as much as possible, the actual diameters of the filled pools varied from 4.5 to 11 m and their shapes ranged from ovate to circular. Most pools failed to drain during the time of this study. In an initial survey of the region, 29 preexisting natural ponds were found near or within the experimental pool infrastructure that may have served as sources for potential colonists.

We used the crustacean zooplankton *D. pulex* as the focal species for manipulating clonal

diversity because it is a dominant species in many temporary ponds and exerts considerable grazing pressure on algal resources (Shapiro et al. 1975, Persson et al. 2007). From an initial survey of 59 *Daphnia* individuals collected from 12 regional ponds located in or within 2 km of Heiberg Memorial Forest, we found no more than three multilocus genotypes per pond. Six obligately asexual clones were isolated for use in manipulations of clonal diversity. Additional information on the genetic methods is provided in Holmes et al. (2016).

In May 2011, we manipulated initial community diversity using a 2×2 fully factorial design (Fig. 1) with two *D. pulex* diversity treatments in 27 pools (no clonal diversity or “high” clonal

Table 1. Zooplankton community composition (indicated by X) and relative taxa abundance (values in parentheses) in the experimental pool metacommunity over four years (2011, 2012, May 2013, and May 2014), as well as the composition of the high species diversity stocking aliquots.

Species	Regional taxa initially stocked (14) (%)	Taxa found in 2011 (17) (%)	Taxa found in 2012 (19) (%)	Taxa found in May 2013 (13) (%)	Taxa found in May 2014 (12) (%)
Cladocerans					
<i>Daphnia pulex</i>		X (11.7)	X (7.8)	X (17.5)	X (11.1)
<i>Chydorus sphaericus</i>	X (7.2)	X (0.4)	X (11.2)	X (25.1)	X (10.9)
<i>Acroperus harpae</i>	X (0.2)				
<i>Daphnia ambigua</i>					
<i>Sida crystallina</i>	X (0.2)				
<i>Eurycerus</i> spp.	X (0.2)				
<i>Bosmina longirostris</i>	X (0.4)				
Macrothricidae spp. or Ilyocryptidae spp.	X				
<i>Ceriodaphnia</i>	X				
<i>Daphnia dubia</i>					
<i>Alona</i>				X	
<i>Scapholeberis mucronata</i>					X
<i>Simocephalus vetulus</i>					X
Copepods					
Immature cyclopoids	X (69.7)	X (40.3)	X (33.8)	X (33.7)	X (59.8)
<i>Tropocyclops prasinus</i>	X (13.2)	X (12.8)	X (34.7)	X (2.7)	X (3.6)
<i>Microcyclops rubellus</i>	X (3.2)	X (9.0)	X (0.3)	X	X (0.3)
<i>Eucyclops elegans</i>	X (3.2)	X (0.4)	X	X (0.2)	
<i>Harpacticoid</i>	X (1.4)	X	X	X (0.2)	X (0.2)
<i>Skistodiaptomous oregonensis</i>		X	X		
<i>Eucyclops agilis</i>		X (19.3)	X (6.0)	X (6.0)	X (1.6)
<i>Orthocyclops modestus</i>		X (0.2)	X (1.7)	X (0.2)	
<i>Ectocyclops phaleratus</i>		X (0.2)	X		
<i>Acanthocyclops</i> spp.		X (0.9)	X (4.0)	X (10.4)	X (1.7)
Unknown cyclopoid		X (2.6)	X		
<i>Microcyclops vicarians</i>		X			
Immature calanoid		X			
<i>Macrocyclus albidus</i>			X	X	X
<i>Diacyclops bicuspidatus odessanus</i>			X		
<i>Cyclops scutifer</i>			X		
<i>Diacyclops thomasi</i>			X		
<i>Macrocyclus fuscus</i>			X		
Other					
<i>Ostracod</i>	X (0.9)	X (2.2)	X	X (3.9)	X (10.8)

Notes: For each year, relative abundance values were obtained by summing across all zooplankton samples collected. Taxa without a relative proportion indicated were found to constitute <0.1% of total.

diversity) crossed with the addition of no other zooplankton species (no species diversity) or the addition of a regional zooplankton species inoculum consisting of 13 species after *Daphnia* were removed (high species diversity). Zooplankton were collected from 25 regional ponds and all individuals pooled in a common container. *Daphnia* were removed under a dissecting microscope, and 750 individual zooplankton were added to

half (13) of the experimental pools (high species diversity—see Table 1 for taxa in initial inoculum and relative proportions added). Half of all experimental pools (13 pools) received no clonal diversity (monoclonal), which was represented by one *D. pulex* genotype, whereas the other half (14 pools) were stocked with “high” clonal diversity and received either four or five unique genotypes of *D. pulex*. To replicate “high” clonal diversity,

only a subset of the six isolated clones was stocked to those “high” clonal diversity pools. All pools were stocked with the same number of laboratory reared *D. pulex* adults (either 750 of one clone for monoclonal treatment, or 750 individuals divided between four or five focal clones) to ensure that the effects of clonal diversity stocking on population persistence was not confounded with differing numbers of colonists. However, an error in genotyping was discovered after the pools were stocked, resulting in some pools having been stocked with twice as many individuals of one clone (Holmes et al. 2016). The remaining 11 pools were left un-stocked and served as controls.

Following stocking in 2011, experimental pools were sampled for zooplankton twice per month (May to August) in 2011, 2012, and once in both May 2013 and 2014. We expected 4 yr would be adequate to capture temporal dynamics in aquatic zooplankton, as other studies have found community saturation on a similar timescale (Cáceres and Soluk 2002, Louette et al. 2008). To sample zooplankton communities, 3 L of pond water was taken from the center of each pool, filtered using an 80- μ m sieve, and animals were preserved in 95% EtOH. To ensure species were not transported among pools, all sampling gear was either dedicated to individual pools or rinsed with 10% bleach (sodium hypochlorite) and then wiped and rinsed between each pool. Zooplankton were counted and identified to the lowest taxonomic identity possible according to Haney et al. (2013). Each sample was scanned for rare taxa; taxa with fewer than 300 individuals were counted completely, and those with over 300 individuals were subsampled (2-mL subsamples following whole sample dilution to 100 mL).

To obtain estimates of overland dispersal (propagule pressure) occurring in each landscape hexagon, in July 2012, four 26-L containers (57 cm \times 41 cm \times 14 cm) were placed in excavated holes so they were flush with the ground, in six out of the nine hexagons (nine-pool hexagons: 5 and 11, three-pool hexagons: 9 and 10, and one-pool hexagons: 8 and 14; Fig. 1). We attempted to place the containers equidistant from as many pools as possible, resulting in containers being located anywhere from 5 to 20 m from neighboring pools. Containers were filled with ~15 L reclaimed DI water (0.26 g/L, RO Right, Kent Marine, Franklin, Wisconsin, USA). Seven days after establishment,

containers were destructively sampled (through an 80- μ m sieve), and animals preserved in 95% EtOH. We chose 7-day trials as to not confound dispersal with reproduction following colonization. All animals and dormant eggs were counted and identified to the lowest taxonomic unit.

We used a one-way repeated measures analysis of variance (ANOVA) in R to investigate the effects of time and stocking diversity (including control pools) on cumulative species richness in our zooplankton metacommunity (R Development Core Team 2013). To avoid potential confounding interactions between treatment and dispersal differences based on number of neighboring source pools, we analyzed both the entire data set, and only those pools in the nine-pool hexagons. The dispersal data were analyzed using a multivariate analysis of variance (MANOVA) to examine differences in dispersing propagule pressure for each major taxonomic group (cladocerans or copepods) based on number of source pools (nine vs. three vs. one source pools). To determine if hexagons with more pools had more potential dispersing propagules, we also conducted a one-way ANOVA with zooplankton samples taken from experimental pools for one sampling period in July 2012.

RESULTS

The zooplankton assemblages added to the high species diversity treatments were dominated by immature cyclopoid copepods, the majority of which most likely belonged to one of the three species of cyclopoid adults recorded (Table 1). *Chydorus sphaericus* was the dominant cladoceran. The initial inoculum contained at least 13 species of crustacean zooplankton; however, seven of the inoculated species were never detected throughout the course of sampling. These nonpersisting species were added at the lowest densities (< 1% of initial inoculum), which may not have exceeded the minimum threshold of individuals needed to establish viable populations. Early successional communities were dominated by copepods in May 2011. However, by May of 2013 and 2014, we observed higher proportions of cladocerans and ostracods than were observed in 2011 and 2012, with *D. pulex* constituting 17.5% and 11.1% of sampled individuals in 2013 and 2014, respectively (Appendix S1: Fig. S1).

Despite the differing stocking treatments, all pools followed similar colonization curves with most species accumulating during the spring and summer months (Fig. 2). Even though a total of 24 taxa were recorded in the entire metacommunity by May 2014, the average cumulative taxonomic richness per pool ranged from 6.8 (in control pools) to 8.1 (in monoclonal/high species diversity pools). The highest cumulative richness observed in any one pool was 13 taxa (pool 11A: high clonal/low species diversity treatment). Colonization rates were variable among pools and ranged from 0.98 to 4.9 taxa/yr. The results of the rmANOVA revealed a significant effect of time ($F_{14,462} = 143.35$, $P < 0.001$), but no effects of stocking diversity ($F_{4,33} = 0.928$, $P = 0.45$) or a treatment \times time interaction ($F_{56,462} = 0.54$, $P = 0.99$) on cumulative species richness for all pools (Fig. 2A).

Given the clustering of pools in the landscape, the analysis of all pools potentially confounds diversity treatments with number of neighboring pools; hence, we also analyzed the data only from those hexagons with nine pools. A similar pattern emerged for the nine-pool hexagons, suggesting

that the number of neighboring pools did not confound patterns of species accumulation (Fig. 2B, statistics reported in Appendix S1: Table S1).

Dispersal occurred frequently across the experimental pool landscape; we recorded a total of 445 zooplankton propagules from eight taxa in the dispersal traps (Copepods: *Eucyclops agilis*, *Acanthocyclops* spp., *Tropocyclops prasinus mexicanus*, harpacticoid copepods; Cladocerans: *Chydorus sphaericus*, *Eurycerus* spp., *Ceriodaphnia ephippia*, and *D. pulex* individuals and ephippia), all of which colonized within 7 days. Number of cladocerans found in the traps ranged from 0 to 46, whereas copepods ranged from 6 to 225. Some of the species found in our dispersal traps were not detected in the source pools during the time of this study (*Eurycerus* spp. and *Ceriodaphnia* spp.). Samples from the source pools during this study revealed that, as expected, locations (hexagons) with nine neighboring source pools had more animals (summed across all pools in the hexagon) than locations with three or one neighboring pools (ANOVA, $F_{2,6} = 6.94$, $P = 0.02$). This suggests that hexagons with nine source pools had more potential propagules than

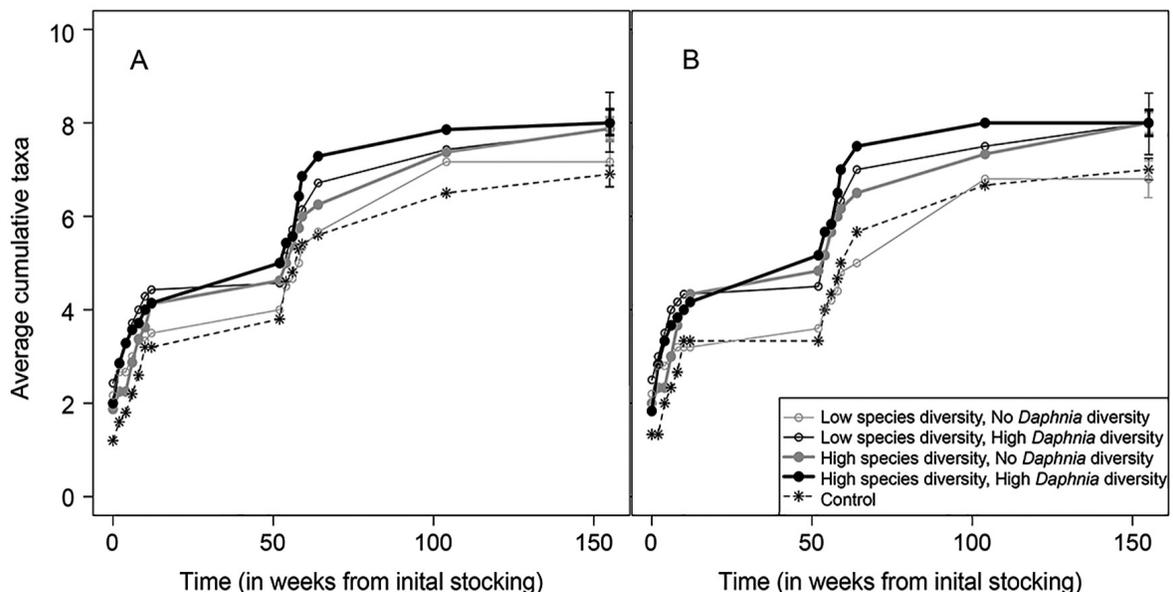


Fig. 2. Cumulative colonization curves for each stocking treatment and control (\pm SE for final sampling date in May 2014). For each time period, the cumulative number of taxa was averaged either (A) across all ponds for each treatment or control in the experimental pond infrastructure or (B) only across pools in the nine-pool hexagons (hexagons 5, 11, 20) for each treatment or control. For clarity, error bars (\pm SE) are only provided on the final point. Gaps between weeks 12 to 52, 64 to 104, and 104 to 155 represent winter months when pools were not sampled.

three- or one-pool hexagons. However, we found in our propagule pressure study that the number of dispersing propagules (for both copepods and cladocerans) was not influenced by number of neighboring source pools (Fig. 3, MANOVA, $F_{4,4} = 0.28$, $P = 0.87$), which is likely explained by high variance between samples for both copepods and cladocerans.

DISCUSSION

We hypothesized that manipulations of initial clonal and species diversity would affect the number of species accumulated in the pools. Specifically, we predicted that introducing species-rich communities into newly created pools would relax dispersal limitation, allowing these pools to attain higher overall species richness and reach species saturation more rapidly

compared to pools that were not stocked with the regional species. Additionally, we predicted that priority effects would be enhanced in populations stocked with high clonal diversity of a focal grazer population, *D. pulex*, thereby decreasing species richness and diversity. However, by May 2014, we observed no significant differences in colonization dynamics between treatment and control pools, suggesting limited observed effects of our initial stocking.

Even though species richness increased rapidly within the first 2 yr of study, our system was less species-rich (24 recorded zooplankton species) than other temporary pond systems (51 species: Mahoney et al. 1990, 53 species: Dodson and Silva-Briano 1996). The number of species in the regional pool can have a substantial effect on the predicted outcomes of community assembly (Chase 2003). Chase (2003) summarized the

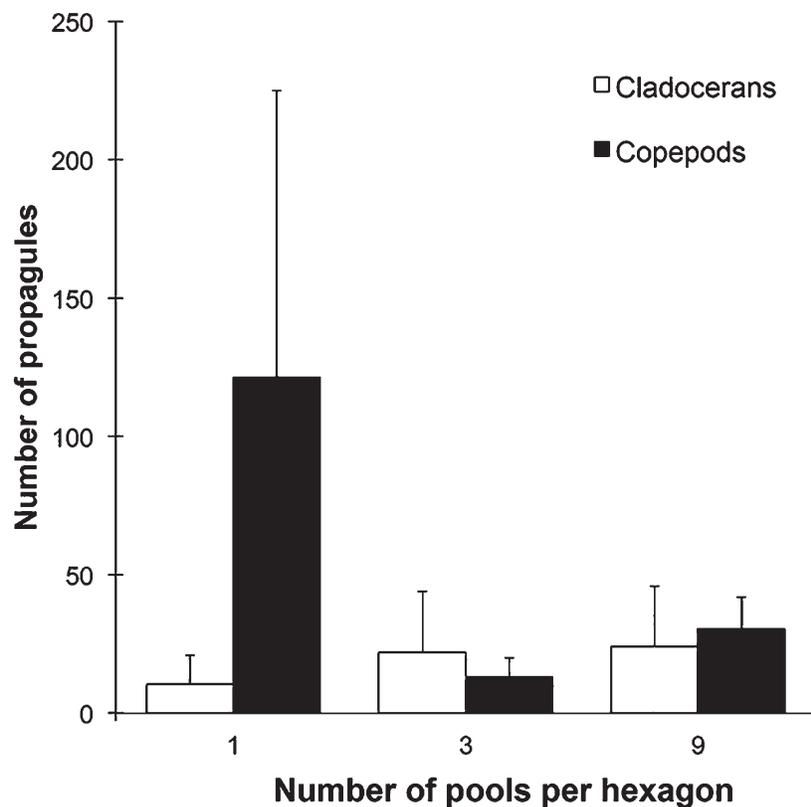


Fig. 3. Dispersal traps sampled after 7 d found a total of 445 propagules, but there was no difference in propagule abundance between major taxonomic groups (cladocera or copepods) or across treatments (no. of pools/hexagon). Bars represent number of zooplankton propagules (cladocera [white bars] and copepods [black bars]) averaged among replicate hexagons (\pm SE among replicates).

evidence for multiple stable equilibria and provided a set of explicit predictions for when a single vs. multiple community state should be observed. He predicted that local sites in less species-rich areas should converge on a single stable state. However, in our system, equilibrium may not yet be reached. Other studies have demonstrated that community saturation in zooplankton can be achieved rapidly within 6 months to 2 yr (Jenkins and Buikema 1998, Cáceres and Soluk 2002); Chase (2003) found in his zooplankton system that community composition was stable after 3 yr of study. Additional temporal sampling would reveal whether our treatments promote multiple stable equilibria or convergence on a single stable state.

Manipulations of species stocking diversity were intended to relax dispersal limitation; however, we did not see an effect of this manipulation on cumulative species richness in our study. Dispersal limitation has been shown on multiple occasions to reduce community richness and diversity (Cornell and Lawton 1992, Cornell and Karlson 1997, Shurin 2000). We inoculated pools with species at their observed natural densities in regional ponds, and did not make an attempt to control for evenness during initial stocking. All but six species stocked in the high diversity treatments failed to establish detectable populations throughout the entire course of this study. This failure of many species to establish may be explained by stochastic extinction resulting from many species in our inoculum being present at very low numbers. Previous studies have demonstrated that environmental factors can determine establishment success of many taxa and play a large role in shaping communities (Gliwicz and Pijanowska 1989, King et al. 1996, Shurin 2000, Cottenie and De Meester 2004, Vanormelingen et al. 2009, Algar et al. 2011). The experimental pools varied in several structural and water chemistry parameters both over time and among pools (Appendix S1: Table S2). This may explain why some species collected from these ponds for use in the stocking inoculum failed to establish (Appendix S1: Tables S2 and S3). Nevertheless, the failure of these species to successfully colonize (e.g., “ghost species”) may have had immeasurable effects on community assembly and thus the final community structure (Miller et al. 2009).

We predicted that in the “high” clonal diversity treatments, there would be an increased

likelihood that one or more introduced genotypes would exhibit high fitness in the pool in which it was stocked, resulting in rapid population establishment and reduced invasion by competing species (De Meester et al. 2002, Leibold et al. 2004, Urban et al. 2008, 2012, Urban and De Meester 2009). Multiple studies have shown that genotypic diversity can impact population-, community-, and ecosystem-level processes (Hughes et al. 2008, Ellers et al. 2011, Crawford and Rudgers 2012, 2013, Forsman et al. 2012, Gibson et al. 2014). In addition, several studies suggest that genetic identity, and not richness per se, is responsible for explaining both intra- and interspecific dynamics (Birch 1960, Pimentel 1968, Vellend et al. 2010, Gibson et al. 2014; Holmes et al. 2016). For example, Fridley et al. (2007) demonstrated that genetic identity of interspecific neighbors influenced patterns of plant growth and fertility in populations of tussock grass (*Koeleria macrantha*) and sedge (*Carex caryophyllea*). In a parallel study in this experimental pool infrastructure, we found that, while initial genotypic diversity enhanced *D. pulex* population establishment and persistence, clonal identity played a larger role in determining landscape population genetic structure (Holmes et al. 2016). However, we found no evidence that initial genetic diversity influenced patterns of community assembly.

Given the importance of dispersal on metacommunity dynamics, we attempted to quantify dispersal occurring in our experimental infrastructure. While actual dispersal rates are difficult to quantify in passive and cryptic dispersers, many studies conducted on freshwater zooplankton have concluded through quantification of dispersal mode, distance, and rate that several taxa of zooplankton can colonize new habitats from within days to a few weeks (Pajunen 1986, Holland and Jenkins 1998, Jenkins and Buikema 1998, Shurin 2000, Bilton et al. 2001, Cáceres and Soluk 2002, Cohen and Shurin 2003, Havel and Shurin 2004, Allen 2007). We provide additional evidence that zooplankton can exhibit high dispersal capacity as evinced by the rapid increase in cumulative colonization in the control ponds over the first 2 yr of the study and large numbers of propagules found in the dispersal traps (Figs. 2 and 3). Of the eight taxa observed in our traps, two taxa (*Eurycercus* spp. and *Ceriodaphnia*) went undetected in all sampled pools throughout the course of

study. This suggests these taxa were present in one or more experimental pools at abundances too low to be detected during sampling (below 0.3 individuals/L), or were introduced via long-distance dispersal events from ponds outside of our experimental pool landscape. Zooplankton are capable of regular long-distance dispersal events (20–100 km; Shurin 2000). However, we cannot conclude that dispersal was not limiting in our communities, as only a small portion of the regional taxa were caught in our dispersal traps.

Ecological theory has highlighted the importance of both intra- and interspecific diversity for community assembly (Elton 1958, Tilman 1997, Shurin 2000, Loreau and Hector 2001, Fukami et al. 2005, Crutsinger et al. 2006, Bolnick et al. 2011, Violle et al. 2012). Previous studies have provided mixed results regarding the role of history on community assembly (Diamond 1975, Neill 1975, Tilman et al. 1986, Sommer 1991, Luh and Pimm 1993, Law and Morton 1996, Samuels and Drake 1997, Law 1999, Chase 2003). Some have shown that history primarily influences patterns of community assembly (Drake 1991, Inouye and Tilman 1995). However, the importance of local factors in shaping communities has been documented in multiple systems (Gliwicz and Pijanowska 1989, King et al. 1996, Vanormelingen et al. 2009). We simultaneously tested the consequences of both species and genotypic diversity of a focal population on the outcomes of community assembly in a multiyear field manipulation of experimental woodland ponds. Despite theoretical predictions regarding diversity and community assembly, in this system, initial diversity appeared to have no effect on early successional community species richness.

ACKNOWLEDGMENTS

We thank our undergraduate research assistants, Ilona Menel, Kelly Hogan, Glynn Davis, Ping Lee, Hannah Wright, Rachel Abbott, Chad Walz, Rachael Weiter, and Ryan Smith for their field and laboratory assistance on this project. Jessica Kirkpatrick was an invaluable asset for assisting with field collections. We also thank Jim Dalling for reviewing an earlier draft of the manuscript and Jelena Pantel for her input during the inception of this project. Feedback from Jessica Kirkpatrick and two anonymous reviewers substantially improved the manuscript. This research was supported by United States National Science Foundation grants

DEB-0947314, DEB-0947245, and DEB-1120804, a Sigma XI GIAR, and University of Illinois at Urbana-Champaign School of Integrative Biology and Department of Animal Biology grants to CJH. We also thank James Gibbs for allowing us to use the experimental pools.

LITERATURE CITED

- Algar, A. C., J. T. Kerr, and D. J. Currie. 2011. Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. *Ecology* 92:903–914.
- Allen, M. R. 2007. Measuring and modeling dispersal of adult zooplankton. *Oecologia* 153:135–143.
- Allen, M. R., J. N. VanDyke, and C. E. Cáceres. 2011. Metacommunity assembly and sorting in newly formed lake communities. *Ecology* 92:269–275.
- Altermatt, F., J. Hottinger, and D. Ebert. 2007. Parasites promote host gene flow in a metapopulation. *Evolutionary Ecology* 21:561–575.
- Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in freshwater invertebrates. *Annual Review of Ecology and Systematics* 32:159–181.
- Birch, L. C. 1960. The genetic factor in population ecology. *American Naturalist* 94:5–24.
- Boileau, M. G., P. D. N. Hebert, and S. S. Schwartz. 1992. Non-equilibrium gene frequency divergence: persistent founder effects in natural populations. *Journal of Evolutionary Biology* 5:25–39.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* 26:183–192.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Cáceres, C. E., and D. A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* 131:402–408.
- Case, T. J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* 42:239–266.
- Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136:489–498.
- Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328:1388–1391.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.

- Cohen, G. M., and J. B. Shurin. 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. *Oikos* 103:603–617.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- Cornell, H. V., and R. H. Karlson. 1997. Local and regional processes as controls of species richness. Pages 250–268 in D. Tilman and P. Kareiva, editors. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61:1–12.
- Cottenie, K., and L. De Meester. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology* 85:114–119.
- Cottenie, K., E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology* 84:991–1000.
- Crawford, K. M., and J. A. Rudgers. 2012. Plant species diversity and genetic diversity within a dominant species interactively affect plant community biomass. *Journal of Ecology* 100:1512–1521.
- Crawford, K. M., and J. A. Rudgers. 2013. Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community. *Ecology* 94:1025–1035.
- Crawford, K. M., and K. D. Whitney. 2010. Population genetic diversity influences colonization success. *Molecular Ecology* 19:1253–1263.
- Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313:966–968.
- De Meester, L., A. Gómez, B. Okamura, and K. Schwenk. 2002. The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecologica* 23:121–135.
- De Meester, L., S. Declerck, R. Stoks, G. Louette, F. Van De Meutter, T. De Bie, E. Michels, and L. Brendonck. 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15:715–725.
- De Meester, L., G. Louette, C. Duvivier, C. Van Damme, and E. Michels. 2007. Genetic composition of resident populations influences establishment success of immigrant species. *Oecologia* 153:431–440.
- Diamond, J. M. 1975. Assembly of species communities. Pages 342–444 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- Dickie, I. A., T. Fukami, J. P. Wilkie, R. B. Allen, and P. K. Buchanan. 2012. Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecology Letters* 15:133–141.
- Dodson, S. I., and M. Silva-Briano. 1996. Crustacean zooplankton species richness and associations in reservoirs and ponds of Aguascalientes State, Mexico. *Hydrobiologia* 325:163–172.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *American Naturalist* 137:1–26.
- Ellers, J., S. Rog, C. Braam, and M. P. Berg. 2011. Genotypic richness and phenotypic dissimilarity enhance population performance. *Ecology* 92:1605–1615.
- Elton, C. S. 1958. *The ecology of invasions by plants and animals*. Methuen, London, UK.
- Forsman, A., L. Wennersten, M. Karlsson, and S. Caesar. 2012. Variation in founder groups promotes establishment success in the wild. *Proceedings of the Royal Society B: Biological Sciences* 279:2800–2806.
- Freeland, W. J. 1983. Parasites and the coexistence of animal host species. *American Naturalist* 121:223–236.
- Fridley, J. D., J. P. Grime, and M. Bilton. 2007. Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *Journal of Ecology* 95:908–915.
- Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8:1283–1290.
- Gadgil, M. 1971. Dispersal: population consequences and evolution. *Ecology* 52:253–261.
- Gibson, D. J., J. Dewey, H. Goossens, and M. M. Dodd. 2014. Intraspecific variation among clones of a naïve rare grass affects competition with a nonnative, invasive forb. *Ecology and Evolution* 4:186–199.
- Gliwicz, Z. M., and J. Pijanowska. 1989. The role of predation in zooplankton succession. Pages 253–296 in U. Sommer, editor. *Plankton ecology*. Springer, Berlin, Heidelberg.
- Haney, J. F., et al. 2013. An-image-based key to the zooplankton of North America. Version 5.0. University of New Hampshire Center for Freshwater Biology. cfb.unh.edu.
- Havel, J. E., and J. B. Shurin. 2004. Mechanisms, effects, and scales of dispersal in freshwater zooplankton. *Limnology and Oceanography* 49:1229–1238.

- Holland, T. A., and D. G. Jenkins. 1998. Comparison of processes regulating zooplankton assemblages in new freshwater pools. *Hydrobiologia* 387–388:207–214.
- Holmes, C. J., J. H. Pantel, K. L. Schulz, and C. E. Cáceres. 2016. Initial genetic diversity increases founder effects and alters genetic structuring of a newly established *Daphnia* metapopulation. *Molecular Ecology* <http://dx.doi.org/10.1111/mec.13672>
- Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25:495–520.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. *In* *Monographs in population biology*. Princeton University Press, Princeton, New Jersey, USA.
- Hughes, A. R., B. D. Inouye, M. T. J. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11:609–623.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* 93:145–159.
- Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95:137–145.
- Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* 76:1872–1887.
- Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:157–170.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Jenkins, D. G., and A. L. Buikema Jr. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs* 68:421–443.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.
- King, J. L., M. A. Simovich, and R. C. Brusca. 1996. Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools. *Hydrobiologia* 328:85–116.
- Law, R. 1999. Theoretical aspects of community assembly. Pages 141–171 *in* J. McGlade, editor. *Advances in ecological theory: principles and applications*. Blackwell, Oxford, UK.
- Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762–775.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- Louette, G., J. Vanoverbeke, R. Ortells, and L. De Meester. 2007. The founding mothers: the genetic structure of newly established *Daphnia* populations. *Oikos* 116:728–741.
- Louette, G., L. De Meester, and S. Declerck. 2008. Assembly of zooplankton communities in newly created ponds. *Freshwater Biology* 53:2309–2320.
- Luh, H.-K., and S. L. Pimm. 1993. The assembly of ecological communities: a minimalist approach. *Journal of Animal Ecology* 62:749–765.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Mahoney, D. L., M. A. Mort, and B. E. Taylor. 1990. Species richness of calanoid copepods, cladocerans and other branchiopods in Carolina Bay temporary ponds. *American Midland Naturalist* 123:244–258.
- Miller, T. E., C. P. TerHorst, and J. H. Burns. 2009. The ghost of competition present. *American Naturalist* 173:347–353.
- Morris, D. W., and T. W. Knight. 1996. Can consumer-resource dynamics explain patterns of guild assembly? *American Naturalist* 147:558–575.
- Mwangi, P. N., M. Schmitz, C. Scherber, C. Roscher, J. Schumacher, M. Scherer-Lorenzen, W. W. Weisser, and B. Schmid. 2007. Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology* 95:65–78.
- Neill, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology* 56:809–826.
- Ortells, R., J. Vanoverbeke, G. Louette, and L. De Meester. 2014. Colonization of *Daphnia magna* in a newly created pond: founder effects and secondary immigrants. *Hydrobiologia* 723:167–179.
- Pacala, S. W., and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *American Naturalist* 143:222–257.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pajunen, V. I. 1986. Distributional dynamics of *Daphnia* species in a rock-pool environment. *Annales Zoologici Fennici* 23:131–140.
- Persson, J., M. T. Brett, T. Vrede, and J. L. Ravet. 2007. Food quantity and quality regulation of trophic transfer between primary producers and a

- keystone grazer (*Daphnia*) in pelagic freshwater food webs. *Oikos* 116:1152–1163.
- Pimentel, D. 1968. Population regulation and genetic feedback. *Science* 159:1432–1437.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rajaniemi, T. K., D. E. Goldberg, R. Turkington, and A. R. Dyer. 2012. Local filters limit species diversity, but species pools determine composition. *Perspectives in Plant Ecology, Evolution and Systematics* 14:373–380.
- Robinson, J. F., and J. E. Dickerson. 1987. Does invasion sequence affect community structure? *Ecology* 68:587–595.
- Samuels, C. L., and J. A. Drake. 1997. Divergent perspectives on community convergence. *Trends in Ecology & Evolution* 12:427–432.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85–96 in P. L. Brezonik, and J. L. Fox, editors. *Proceedings of a symposium on water quality management through biological control*. Proc. Symp. Univ. Florida, Gainesville, Florida, USA.
- Shurin, J. B. 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. *Ecology* 81:3074–3086.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16: 269–311.
- Sommer, U. 1991. Convergent succession of phytoplankton in microcosms with different inoculum species composition. *Oecologia* 87:171–179.
- 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.
- Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82:319–327.
- Tansley, A. G. 1917. On competition between *Galium saxatile* L. (*G. hercynicum* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. *Journal of Ecology* 5:173–179.
- Thielsch, A., N. Brede, A. Petrušek, L. De Meester, and K. Schwenk. 2009. Contribution of cyclic parthenogenesis and colonization history to population structure in *Daphnia*. *Molecular Ecology* 18:1616–1628.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92.
- Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham, and F. A. Johnson. 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon, and nitrogen. *Archiv für Hydrobiologie* 106:473–485.
- Titman, D. 1976. Ecological competition between algae: experimental confirmation of resource-based competition theory. *Science* 192:463–465.
- Urban, M. C., and L. De Meester. 2009. Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proceedings of the Royal Society B: Biological Sciences* 276:4129–4138.
- Urban, M. C., et al. 2008. The evolutionary ecology of metacommunities. *Trends in Ecology & Evolution* 23:311–317.
- Urban, M. C., L. De Meester, M. Vellend, R. Stoks, and J. Vanoverbeke. 2012. A crucial step toward realism: responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications* 5:154–167.
- Vanormelingen, P., W. Vyverman, D. De Bock, K. Van der Gucht, and L. De Meester. 2009. Local genetic adaptation to grazing pressure of the green alga *Desmodesmus armatus* in a strongly connected pond system. *Limnology and Oceanography* 54:503–511.
- Vellend, M., E. B. M. Drummond, and H. Tomimatsu. 2010. Effects of genotype identity and diversity on the invasiveness and invasibility of plant populations. *Oecologia* 162:371–381.
- Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27:244–252.
- Weltzin, J. F., N. Z. Muth, B. Von Holle, and P. G. Cole. 2003. Genetic diversity and invasibility: a test using a model system with a novel experimental design. *Oikos* 103:505–518.
- Whitham, T. G., et al. 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84:559–573.
- Young, T. P., J. M. Chase, and R. T. Huddleston. 2001. Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecological Restoration* 19:5–18.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1377/supinfo>