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Propagule pressure and native community connectivity interact to influence invasion success in metacommunities

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Mechanistic insights from invasion biology indicate that propagule pressure of exotic species and native community structure can independently influence establishment success. The role of native community connectivity via species dispersal and its potential interaction with propagule pressure on invasion success in metacommunities, however, remains unknown. Native community connectivity may increase biotic resistance to invasion by enhancing species richness and evenness, but the effects could depend upon the level of propagule pressure. In this study, a mesocosm experiment was used to evaluate the independent and combined effects of exotic propagule pressure and native community connectivity on invasion success. The effects of three levels of exotic *Daphnia lumholtzi* propagule pressure on establishment success, community structure and ecosystem attributes were evaluated in native zooplankton communities connected by species dispersal versus unconnected communities, and relative to a control without native species. Establishment of the exotic species exhibited a propagule dose-dependent relationship with high levels of propagule pressure resulting in the greatest establishment success. Native community connectivity, however, effectively reduced establishment at the low level of propagule pressure and further augmented native species richness across propagule pressure treatments. Propagule pressure largely determined the negative impacts of the exotic species on native species richness, native biomass and edible producer biomass. The results highlight that native community connectivity can reduce invasion success at a low propagule dose and decrease extinction risk of native competitors, but high propagule pressure can overcome connectivity-mediated biotic resistance to influence establishment and impact of the exotic species. Together, the results emphasize the importance of the interaction of propagule pressure and community connectivity as a regulator of invasion success, and argue for the maintenance of metacommunity connectivity to confer invasion resistance.

Keywords: biotic resistance, dispersal, invasive species, propagule size, zooplankton

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Introduction

Although much research on biological invasions has been conducted in the last half-century, the factors contributing to invasion success are still being determined (Gallien and Carboni 2017). Many species- and site-specific traits can affect invasion success; consequently, identifying trends and interactive effects across diverse taxonomic groups and environments has proven challenging (Hayes and Barry 2008). However, propagule pressure has consistently emerged as having strong explanatory and predictive power for the successful establishment of exotic (non-native) species (Lockwood et al. 2005, Duncan et al. 2014, Blackburn et al. 2015). Propagule pressure can include both propagule size, as the number of individuals introduced in a single event, and propagule number as the total number of introduction events (Lockwood et al. 2005). Of these two components, propagule size is often the most influential factor determining establishment success (Simberloff 2009, Sinclair and Arnott 2016). Introducing a greater number of individuals at one time leads to larger population sizes which are more robust, while introducing only a few individuals results in small populations that are more susceptible to extinction from demographic and environmental stochasticity (Lockwood et al. 2005). Additionally, propagule pressure can play an important role in every stage of biological invasion (Blackburn et al. 2015), yet the initial dispersal and introduction stage is simultaneously the most understudied and crucial for identifying factors that determine establishment success (Puth and Post 2005).

Propagule pressure may aid in the successful establishment of exotic species, but community context in the non-native environment can also influence establishment and biotic resistance to invasion (Shea and Chesson 2002, Jones et al. 2017). Indeed, propagule pressure and local biotic factors have been incorporated into many proposed conceptual frameworks for biological invasion (Catford et al. 2009, Gurevitch et al. 2011). Communities with low diversity or simple structure can have higher invasibility from greater niche opportunities available to the exotic species (Stachowicz et al. 1999, Tilman 2004). Conversely, communities with complex food web structure and higher native diversity are often less invasible from greater competition and predation among species and fewer available niches (Levine et al. 2004, Kimbro et al. 2013, Alofs and Jackson 2014). Despite acknowledgment of the role of diversity in invasion, the importance of community connectivity in a landscape via species dispersal to influencing local native community composition and invasibility remains understudied. Communities connected by dispersal in a metacommunity can support higher local diversity than isolated communities in a landscape (Cadotte 2006, Damschen et al. 2006) and may therefore confer invasion resistance to native communities (Howeth 2017). Community connectivity may additionally minimize impacts of recently established exotic species on community structure and ecosystem properties. Specifically, dispersal can maintain local populations of native predators or superior competitors and can further sustain population sizes of inferior competitors and prey of the exotic species (Strecker and Arnott 2010, Sinclair et al. 2015, Loewen and Vinebrooke 2016). Thus, community connectivity may increase biotic resistance to invasion of exotic species, or minimize their impacts once established, through several mechanisms. The relative influence of native community connectivity and propagule pressure of the exotic species on invasion success, however, remains empirically untested.

Recent studies have shown that biotic resistance can be robust to propagule pressure (Barney et al. 2016), yet other work illustrates that propagule pressure can overcome biotic resistance of native communities (Hollebone and Hay 2007, Britton and Gozlan 2013). This apparent conflict in findings can be reconciled by considering the potential dose-dependent effects of propagule pressure (Houseman et al. 2014). Studies have found that lower propagule pressures correlate with establishment failure, while higher pressures often result in establishment success (Drake et al. 2005, Britton and Gozlan 2013, Brockerhoff et al. 2014). Similar to how certain species require a critical density to overcome Allee effects (Stephens et al. 1999, Simberloff 2009), exotic species may need a threshold introduction density in order to overcome local biotic resistance (Jones et al. 2017). In addition to differentially affecting establishment success, dose-dependent effects of propagule pressure could also influence native community composition and biomass partitioning within invaded ecosystems by supplying different abundances of the invader. Higher propagule pressures could initially increase exotic biomass, but native community connectivity may moderate these effects over time from dispersal-driven interspecific interactions. Though community connectivity has been shown to increase species diversity in metacommunities (reviewed in Grainger and Gilbert 2016), high propagule pressure could counter such effects if the exotic species establishes and has large ecological impacts. Thus, community connectivity and propagule pressure could have opposing effects on establishment success and the response of community structure and ecosystem attributes.

This study experimentally tested whether different levels of propagule pressure, as the number of individuals introduced (propagule size), and native community connectivity could independently or interactively affect invasion success of an exotic species. Freshwater zooplankton communities were leveraged as a model system to test these mechanisms of invasion operating at the interface of local and regional spatial scales in metacommunities (Leibold and Norberg 2004, Howeth et al. 2010). Hydrologic and overland connectivity of lake and pond communities in a landscape has been shown to facilitate dispersal of zooplankton and lead to higher species diversity and corresponding effects on ecosystem properties relative to isolated communities (Howeth and Leibold 2010a, Pedruski and Arnott 2011, Thompson and Shurin 2012). In particular, the dispersal and colonization of *Daphnia* spp. can alter community structure and ecosystem function as the species strongly interact within communities as keystone herbivores (Leibold 1996, Walsh et al. 2012). Using a mesocosm experiment, establishment success and ecological effects of the exotic *Daphnia lumholtzi* were contrasted under three different levels of propagule pressure and in native zooplankton communities that were either connected by dispersal to a metacommunity or unconnected (isolated) and relative to a control without native species. In the connected treatment, native communities in mesocosms were coupled by immigration to a natural native zooplankton metacommunity in order to yield connectivity-driven differences in community structure prior to, and after, invasion. After approximately three generations of native species immigration from the metacommunity (Gillooly 2000, Lemke and Benke 2003), mesocosm communities were invaded with different propagule pressures (propagule sizes) of the exotic species.

Establishment success of the exotic species was hypothesized to correlate positively with propagule pressure levels (Colautti et al. 2006, Simberloff 2009) and negatively with connectivity (Howeth 2017). Likewise, propagule pressure was predicted to have a positive effect on the density and biomass of the exotic species (Tanentzap and Bazely 2009) and a negative effect on the biomass of native communities from increased competition. Connectivity was predicted to have a negative influence on exotic biomass through effects on native community structure (Howeth 2017). Previous studies have found that dispersal of grazers can augment grazer biomass and thereby negatively affect primary producer biomass (France and Duffy 2006, Howeth and Leibold 2008) with consequent negative effects to ecosystem productivity (Howeth and Leibold 2010a, Howeth 2017). Thus, primary and whole-ecosystem productivity were also predicted to negatively respond to the effects of propagule pressure and native community connectivity.

Material and methods

Study system

The zooplankter *Daphnia lumholtzi* is native to lakes in eastern Australia, Africa and India (Havel and Hebert 1993). The species was first observed in North America in 1991 in a Texas reservoir (Sorensen and Sterner 1992) and has since expanded its range northward to the Great Lakes (Muzinic 2000), eastward to Florida (Havens et al. 2012), and westward to the current invasion front in California (Frisch et al. 2013). The large introduced range has been attributed to inducible anti-predator traits, including a head and tail spine (Kolar and Wahl 1998, Engel and Tollrian 2009), and ability to coexist with native congeners through temperature-based niche partitioning in late summer (Kolar et al. 1997, Lennon et al. 2003). Once established, the species can modify native zooplankton community structure and the functioning of ecosystems (Lennon et al. 2003, Dzialowski 2010). The widespread colonization of reservoirs by *D. lumholtzi* in North America facilitates hydrologic dispersal to uninvaded reservoirs via riverine connections that differ in their strength of community connectivity depending on regional climatic variation and local anthropogenic regulation (Havel and Shurin 2004, Poff et al. 2007). Therefore, the propagule pressure of *D. lumholtzi* varies greatly in the introduced range from passive aerial dispersal (low propagule pressure) and hydrologic dispersal (high propagule pressure), and may be critically important to the species' establishment success and ecological effects.

Experimental design

The experiment was conducted in 22 l high-density polyethylene bucket mesocosms located in the Aquatic Mesocosm Facility glasshouse at the University of Alabama, Tuscaloosa, AL, USA from September to December 2015. The mesocosm experiment evaluated independent and interactive effects of three levels of native community connectivity (control, unconnected, connected) and four levels of *D. lumholtzi* propagule pressure (uninvaded, low, medium, high), corresponding to the number of individuals added in a single introduction event (propagule size), in a full factorial design. Each treatment combination was replicated four times, for a total of 48 mesocosms in the experiment. The mesocosms were acid washed, filled with 18 l of COMBO growth medium (Kilham et al. 1998), and covered with black 1 mm window screen mesh to prevent contamination with external organisms. Mesocosms were randomly assigned to one of eight 120 l deionized water-filled pools to minimize internal temperature fluctuations, and were rotated every seven days to adjacent pools to control for any location effects within the glasshouse. Mesocosm temperature was monitored every 6 h over the course of the 10-week experiment by two temperature data loggers located within stationary deionized water-filled 22-l buckets positioned within the plastic pools located on opposite ends of the experimental array (Supplementary material Appendix 1). On 16 September 2015, 20 l of water were collected at each of five natural ponds that varied in size and productivity and that were located in the Talladega National Forest (Bibb, Hale and Tuscaloosa counties) of Alabama (Supplementary material Appendix 2). Pond water was combined in the laboratory and filtered through 35 µm Nitex mesh to remove zooplankton. The 48 mesocosms in the experiment were each inoculated with 300 ml of the resulting phytoplankton filtrate.

The three native community connectivity treatments included a 'control' treatment that supported phytoplankton only. This treatment provided a reference in which to evaluate the establishment success and resource consumption of *D. lumholtzi* in the absence of native zooplankton competitors. The 'unconnected' treatment supported native zooplankton added only once at the start of the experiment to establish standing communities, with no additional immigration (inoculations). This treatment simulated native communities closed to dispersal. The 'connected' treatment was inoculated with native zooplankton every seven days to simulate communities connected by dispersal to a metacommunity. This immigration interval corresponds to approximately half of one generation of component native species (Gillooly 2000, Lemke and Benke 2003). The unconnected and connected treatments received naïve native zooplankton from the five forest ponds that were sampled for phytoplankton. Native zooplankton were sourced from these ponds because *D. lumholtzi* is not known to be present from repeated sampling in previous studies (Howeth 2017, Sferra et al. 2017). Thus, competitive outcomes between the native and exotic species in this experiment yielded results representative of an authentic invasion scenario since the native zooplankton had no known previous interactions with *D. lumholtzi*. Additionally, previous work suggests that there is good congruence between the composition of native zooplankton maintained in mesocosms and the natural forest ponds, indicating an experimental venue reflective of natural communities (Howeth 2017, Sferra et al. 2017, Supplementary material Appendix 3). On 23 September 2015, native zooplankton were collected from 10 l of water sampled from each of the five ponds, combined in the laboratory, filtered through 80 μm Nitex mesh to isolate and concentrate zooplankton, and screened for invertebrate predators (e.g. *Buenoa*, *Chaoborus*) under a dissecting microscope with any observed predators removed. Each mesocosm in the unconnected and connected treatments received a 25 ml inoculum of the diverse zooplankton suspended in COMBO. Concurrently, the control treatment mesocosms received 25 ml of COMBO only. Every seven days of the remaining nine weeks of the experiment, 5 l of water were collected from each pond, filtered through 80 μm mesh, screened for predators, and 25 ml of the resultant zooplankton in COMBO added to the connected treatment mesocosms. The control and unconnected treatment mesocosms received 25 ml of COMBO.

The four *D. lumholtzi* propagule pressure treatments included an 'uninvaded' treatment (0 individuals), 'low' propagule pressure where 28 individuals of a mixed age structure were introduced (corresponding to 1.6 indv. l^{-1}), 'medium' propagule pressure (56 individuals, 3.1 indv. l^{-1}) and 'high' propagule pressure (112 individuals, 6.2 indv. l^{-1}). The propagule pressure values were selected by comparing *D. lumholtzi* propagule pressure and the respective establishment success from other studies (Lennon et al. 2003, Dzialowski and Smith 2008, Engel and Tollrian 2009, Fey and Herren 2014, Howeth 2017) and are within the range of densities that occur in invaded North American lakes (Soeken-Gittinger et al. 2009, Havens et al. 2012). The uninvaded treatment served as a reference in which to evaluate native zooplankton community structure and ecosystem response to native connectivity in the absence of *D. lumholtzi*. Each propagule pressure treatment received an equal proportion of four *D. lumholtzi* clones sourced from Southern California, the species' westernmost invasion front in the US (Frisch et al. 2013): CR22 (Corona Lake, Riverside County), EC10 (El Capitan Reservoir, San Diego County), LL82 (Loveland Reservoir, San Diego County) and SW9 (Sweetwater Reservoir, San Diego County). Introducing equal numbers of *D. lumholtzi* from each of the four clonal lines eliminated the possibility of differential establishment success influenced by different levels of genetic diversity (Bock et al. 2015). Invasion occurred once on week six of the experiment (11 November 2015) according to the propagule pressure treatment level. *Daphnia lumholtzi* was suspended in 200 ml of COMBO for introduction and added to mesocosms after routine weekly sampling. Concurrently, the uninvaded treatment received 200 ml of COMBO as a control for medium addition. This interval to invasion provided opportunity for native community divergence as a function of connectivity to the metacommunity (Howeth and Leibold 2010a, b).

Sampling

To evaluate community structure and ecosystem response to treatments over time, 1.02 l of media was removed from each mesocosm (approximately 5% of mesocosm volume; 0.51 l from center and side) every seven days for the 10 week experiment using a depth-integrated PVC sampler. From each mesocosm sample, zooplankton were collected from 1 l passed through an 80 μm filter, and were preserved in acid-sucrose Lugol's iodine solution for later microscopic enumeration. Zooplankton were identified to species or the lowest taxonomic group possible using standard keys (Smith 2001, Haney et al. 2013) and regional species lists (Benke et al. 1999, Lemke and Benke 2009, Sferra et al. 2017). Zooplankton dry biomass estimates were obtained from body lengths of up to 30 individuals of each species, genus or order and published body-length weight regressions (Dumont et al. 1975, McCauley 1984, Eisenbacher 1998). Total phytoplankton biomass and the biomass size fraction edible to zooplankton (<35 μm, Burns 1968) were analyzed from 20 ml of the sampled volume from each mesocosm. The edible phytoplankton fraction was obtained by passing 10 ml of sample through a 35 μm filter. In vivo fluorescence was measured for the total and edible fraction using a handheld fluorometer. The corresponding absorbance values were converted to extracted chlorophyll a (μg l^{-1}) using a linear regression equation generated from the forest pond study system from which biota were sourced (Howeth 2017). To measure ecosystem productivity, dissolved oxygen of each mesocosm was obtained with a handheld O_2-meter at dawn and dusk of each sampling day (following Howeth and Leibold 2010a). After sampling, COMBO was added to each mesocosm to replace the sampled volume. Weekly immigration in the connected communities occurred the day following mesocosm sampling.

Nitrogen and phosphorus can be limiting nutrients in aquatic systems (Elser et al. 2007) and can thus serve as an informative measure of ecosystem response to treatments. At the completion of the experiment, 250 ml of media were removed from each mesocosm and frozen at −20°C for later analysis of total phosphorus (TP) and total nitrogen (TN). An additional 250 ml of media were removed from each mesocosm, vacuum-filtered through glass fiber filters and frozen for subsequent analyses of total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN). Nutrients were analyzed from thawed samples using persulfate digestion (Crumpton et al. 1992, Bachmann and Canfield 1996) and spectrophotometric methods.

Statistical analyses

Establishment success of the invader was defined as the presence of sampled individuals on the final week of the experiment (week 10) as this reflects a reproducing population, corresponding to approximately four generations of the exotic species after invasion (Whittington and Walsh 2015). Establishment success was calculated as the proportion of replicates in each propagule pressure treatment that supported *D. lumholtzi*. Population growth rate of *D. lumholtzi* over the four weeks after invasion was evaluated by calculating the difference in density between weekly sampling periods, starting with the known initial introduction density. The density changes by week were averaged for each replicate and the mean growth rate values contrasted by connectivity and propagule pressure treatments with a two-way ANOVA. Additionally, *D. lumholtzi* density, biomass and proportion of total zooplankton biomass were analyzed using repeated measures ANOVA (RM-ANOVA) for weeks 7–10. The proportion of *D. lumholtzi* biomass was arcsine-square root transformed prior to analysis. *D. lumholtzi* density and biomass analyses excluded the uninvaded propagule pressure treatment, where no *D. lumholtzi* were introduced or observed.

To assess the community and ecosystem structure into which the exotic species was introduced, native zooplankton species richness, native zooplankton species evenness (Shannon's J), native zooplankton biomass, phytoplankton (total, edible and inedible) biomass, and ecosystem productivity were analyzed using one-way ANOVA on week six data. Inedible phytoplankton biomass was calculated by subtracting the edible phytoplankton biomass fraction from total phytoplankton biomass. After invasion, these variables were assessed using RM-ANOVA for weeks 7–10 to test for effects of community connectivity and propagule pressure over time. Native species richness, evenness and biomass analyses excluded the connectivity control treatment since no zooplankton were present (introduced or observed). Phytoplankton biomass and ecosystem productivity analyses included all treatments. Nutrients (TP/TDP, TN/TDN) were analyzed for all treatments using two-way ANOVA.

The response of native community composition to community connectivity prior to invasion (week 6) and propagule pressure and connectivity after invasion (weeks 7–10 average) was analyzed using PERMANOVA with Bray–Curtis distance on log(x + 1) transformed density data and 10 000 permutations of the distances. To evaluate the response of individual taxa to connectivity and propagule pressure, an indicator species analysis (Dufrene and Legendre 1997) was performed on pre- (week six) and post-invasion (weeks 7–10 average) zooplankton log(x + 1) transformed density data. This approach takes into consideration both the relative abundance and the relative frequency of a species across treatments in order to determine treatment specificity which is represented by an indicator value (IV). This IV score is higher when a species is found primarily in a particular treatment, and a score of 100 means that a species is a perfect predictor or 'indicator' of that treatment. The score is based upon within-species density comparisons and is thus independent of other species responses. Statistical

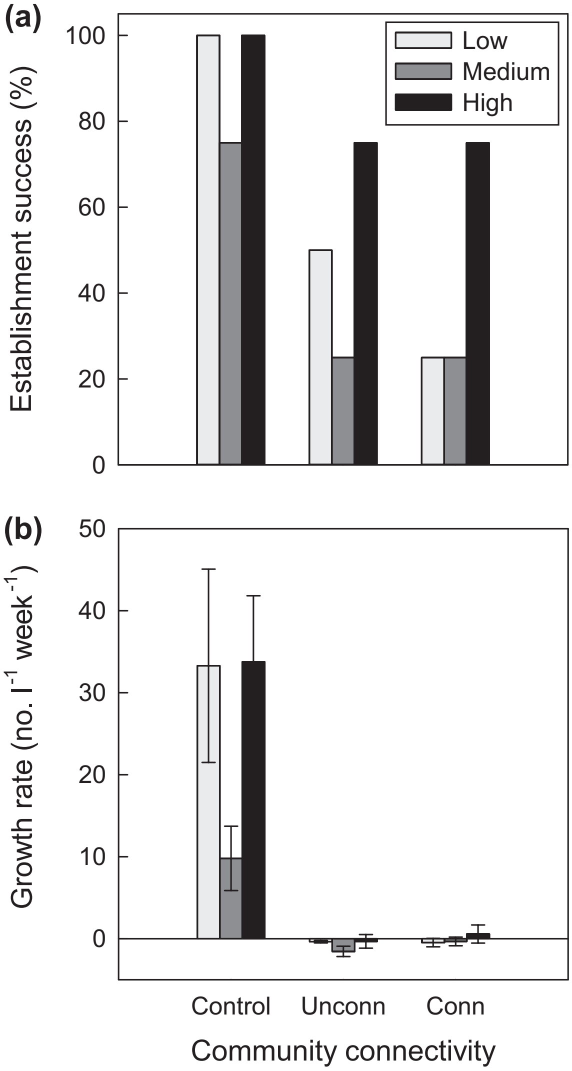

Figure 1. Establishment success and population growth of the exotic *Daphnia lumholtzi* across propagule pressure and native community connectivity treatments. (a) Establishment success is measured as the proportion of replicates within each treatment (n = 4 mesocosms) supporting the exotic species at the end of the experiment. (b) Population growth rate reported as the mean density difference (no. l^{-1} week^{-1}) over the four weeks after invasion (weeks 7–10). Rate of growth values are mean ± SE; n = 4 mesocosms. For propagule pressure treatments, 'low' = 1.6 *D. lumholtzi*/l, 'medium' = 3.1 *D. lumholtzi*/l and 'high' = 6.2 *D. lumholtzi*/l.

significance was determined by a Monte Carlo test with 10 000 permutations.

The population, community and ecosystem response variables were assessed for normality with a Shapiro–Wilks test and log transformed if required prior to ANOVA and PERMANOVA. For RM-ANOVA analyses, the assumption of sphericity was evaluated with Mauchley's test and reported probability values were Greenhouse–Geisser corrected if the assumption was not met. STATISTICA was used to conduct all ANOVA analyses. PERMANOVA and indicator species analyses were conducted using PC-ORD ver. 6 (McCune and Mefford 2011; MjM Software Design, Gleneden Beach, OR, USA).

Data deposition

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.j6h2852> (King and Howeth 2019).

Results

Establishment success of the exotic

The exotic *Daphnia lumholtzi* established populations in all treatment conditions, but not in all mesocosm replicates (Fig. 1a). Establishment was most successful at high propagule pressure (75–100%), with little effect from changing community connectivity (Fig. 1a). In contrast, when propagule pressure was at low or medium levels, native community connectivity resulted in a reduction of establishment success. Exotic population growth rate responded positively to propagule pressure but negatively to connectivity (Fig. 1b; two-way ANOVA, connectivity: $F_{2,27} = 44.59$, $p < 0.001$, propagule pressure: $F_{2,27} = 3.27$, $p = 0.053$, connectivity × propagule pressure: $F_{4,27} = 1.23$, $p = 0.323$, Tukey's post hoc: control versus unconnected, $p < 0.001$; control versus connected, $p < 0.001$; unconnected versus connected, $p = 0.745$; low versus medium, $p = 0.158$; low versus high, $p = 0.856$; medium versus high, $p = 0.055$). Likewise, densities of the exotic species responded positively to propagule pressure and negatively to community connectivity (Fig. 2a–c, Table 1). Across propagule pressure treatments, densities at high propagule pressure were significantly greater than at low or medium propagule pressure. The connectivity control had significantly higher *D. lumholtzi* densities but unconnected and connected communities did not differ from each other.

Exotic biomass reflected density responses to propagule pressure and community connectivity (Table 1). The proportion of total zooplankton biomass comprised of *D. lumholtzi* responded to propagule pressure but not connectivity (Fig. 2d–e, Table 1). The proportion was

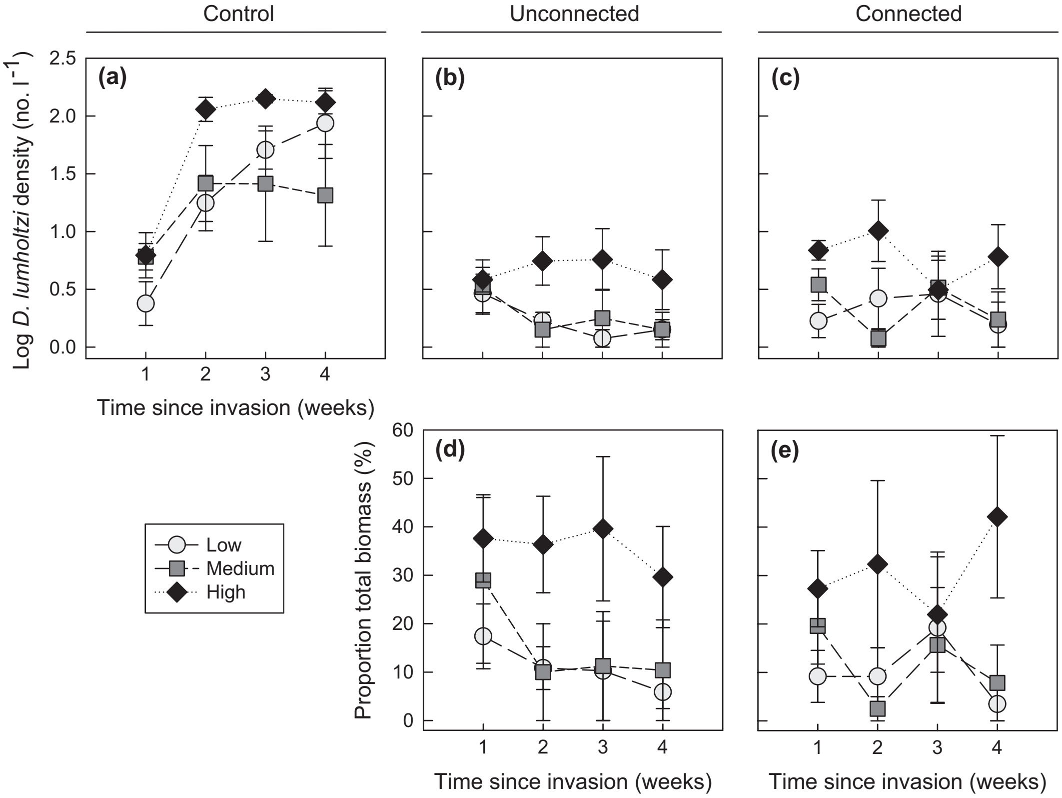

Figure 2. Exotic *Daphnia lumholtzi* (a–c) density ($\log_{10}(x+1)$) and (d–e) proportion of biomass comprising total zooplankton biomass over the four weeks after invasion (weeks 7–10) as a function of propagule pressure and native community connectivity. Values are mean ± SE, n = 4 mesocosms. For propagule pressure treatments, 'low' = 1.6 *D. lumholtzi*/l, 'medium' = 3.1 *D. lumholtzi*/l and 'high' = 6.2 *D. lumholtzi*/l.

significantly greater at high propagule pressure than at low or medium pressures.

Community structure pre- and post-invasion

Prior to invasion, native species richness in unconnected and connected communities did not differ (Fig. 3a; one-way ANOVA, $F_{1,30} = 0.02$, $p = 0.899$), but native species evenness was marginally higher in connected communities (Fig. 3d; one-way ANOVA, $F_{1,30} = 3.34$, $p = 0.077$). There was no difference in community composition between connected and unconnected communities (PERMANOVA, $F_{1,30} = 1.65$, $p = 0.145$). However, *Bosmina* was an indicator of the connected treatment (Fig. 4a, Table 2).

After invasion, native species richness responded positively to community connectivity and negatively to propagule pressure (Fig. 3b–c, Table 3). Native species richness was higher in connected communities compared to unconnected communities and in the absence of the exotic species compared to the low and medium propagule pressure treatments. Connectivity and propagule pressure had a significant interactive effect on native species evenness, but not main effects (Fig. 3e–f, Table 3). Native community composition was significantly different between connected and unconnected communities but did not differ among propagule pressure treatments (PERMANOVA, connectivity: $F_{1,24} = 2.85$, $p = 0.029$, propagule pressure: $F_{3,24} = 1.18$, $p = 0.309$, connectivity × propagule pressure: $F_{3,24} = 0.79$, $p = 0.661$). *Bosmina* remained an indicator for connected communities after invasion, in addition to cyclopoid copepods and two native daphnid species (*D. ambigua*, *D. pulex*) becoming indicators for the connected treatment (Fig. 4a–d, Table 2). Native *D. pulex* was also an indicator for the uninvaded treatment (Fig. 4e).

Ecosystem properties pre- and post-invasion

There was no effect of community connectivity on native zooplankton biomass prior to invasion (one-way ANOVA, $F_{1,30} = 0.28$, $p = 0.600$). After invasion, native zooplankton biomass responded to propagule pressure with uninvaded communities supporting greater biomass than all three treatments where the exotic species was introduced (Fig. 5a–b, Table 3). There was no effect of connectivity on native zooplankton biomass after invasion.

Table 1. Effects of native community connectivity (C) and propagule pressure (P) over time (T) after invasion (week 7–10) on exotic *Daphnia lumholtzi* density, biomass and proportion of total zooplankton biomass, as analyzed with repeated-measures ANOVA.

Response variable	df	SS	F	p-value	Contrasts
Density[†]					
C	2,27	32.69	33.30	<0.001***	[CTRL↑, UN***]; [CTRL↑, CN***]
P	2,27	6.70	6.83	0.004**	[LW, HI↑*]; [MD, HI↑**]
C×P	4,27	0.11	0.06	0.994	
T[‡]	2.2,58.9	2.01	5.85	0.004**	
T×C[‡]	4.4,58.9	8.78	12.78	<0.001***	
T×P[‡]	4.4,58.9	1.44	2.09	0.088	
T×C×P[‡]	8.7,58.9	1.95	1.42	0.202	
Biomass[†]					
C	2,27	66.66	21.11	<0.001***	[CTRL↑, UN***]; [CTRL↑, CN***]
P	2,27	20.99	6.64	0.005**	[LW, HI↑*]; [MD, HI↑**]
C×P	4,27	0.85	0.13	0.968	
T[‡]	2.1,56.6	0.59	0.48	0.632	
T×C[‡]	4.2,56.6	16.92	6.83	<0.001***	
T×P[‡]	4.2,56.6	4.92	1.99	0.106	
T×C×P[‡]	8.4,56.6	5.65	1.14	0.351	
Proportion Biomass[§]					
C	1,18	0.03	0.10	0.755	
P	2,18	2.34	4.23	0.031*	[LW, HI↑*]; [MD, HI↑[+]]
C×P	2,18	0.01	0.03	0.973	
T	3,54	0.32	2.38	0.079	
T×C	3,54	0.07	0.53	0.667	
T×P	6,54	0.32	1.20	0.320	
T×C×P	6,54	0.20	0.77	0.600	

Notes: Tukey's post hoc pairwise comparisons are reported for significant ($p < 0.05$) and marginally significant ($p < 0.06$) main effects. Abbreviations for community connectivity contrasts are CTRL = control, UN = unconnected and CN = connected, and for propagule pressure are UI = uninvaded, LW = low, MD = medium and HI = high; an upward-pointing arrow (↑) indicates the higher mean response variable value in significant comparisons.

[+] $p < 0.06$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

[†] Log transformed.

[§] Arcsine square root transformed.

[‡] Greenhouse–Geisser modified probability values.

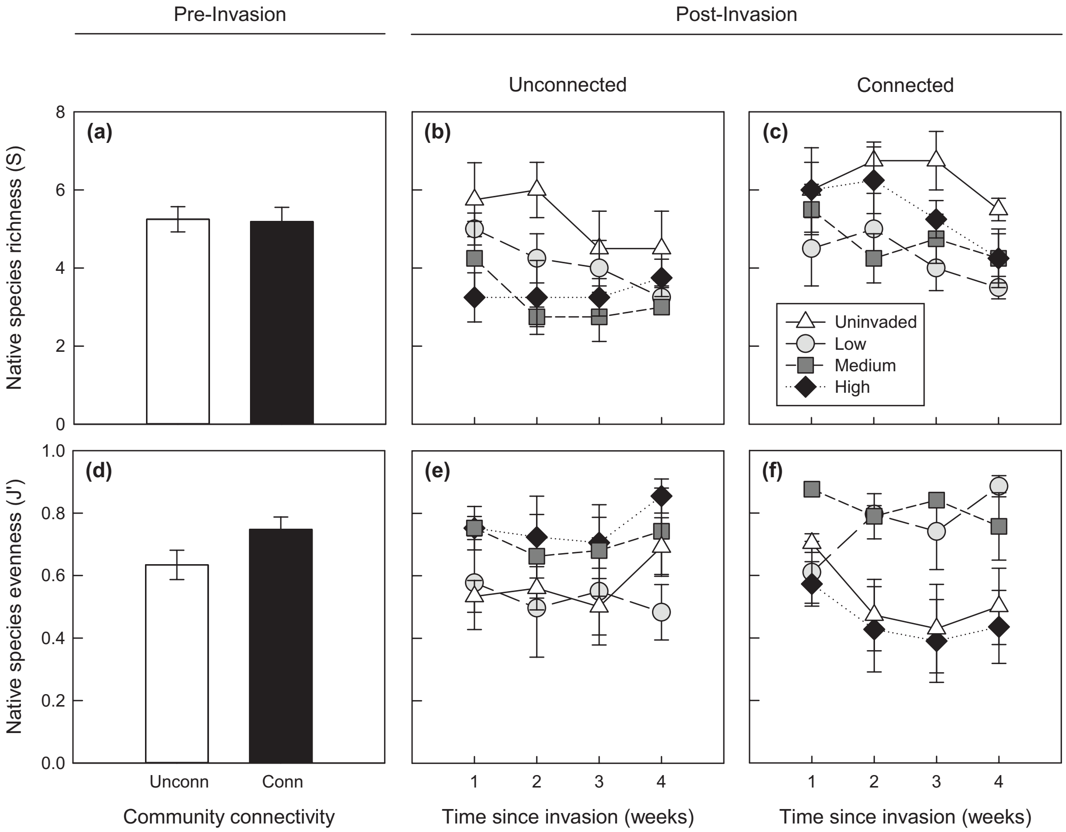

Figure 3. Community response to connectivity and propagule pressure of exotic *Daphnia lumholtzi*: native zooplankton species (a–c) richness and (d–f) evenness (Shannon's J). Richness and evenness shown prior to invasion (pre-invasion, week six, n = 16 mesocosms) and over the four weeks after invasion of the exotic species (post-invasion, weeks 7–10, n = 4 mesocosms). Values are mean ± SE. For propagule pressure treatments, 'uninvaded' = 0 *D. lumholtzi*/l, 'low' = 1.6 *D. lumholtzi*/l, 'medium' = 3.1 *D. lumholtzi*/l and 'high' = 6.2 *D. lumholtzi*/l.

Before invasion, total phytoplankton biomass responded to community connectivity (one-way ANOVA, $F_{2,45} = 53.14$, $p < 0.001$). The control without native zooplankton supported significantly greater total phytoplankton biomass than unconnected and connected treatments, but connectivity treatments were not different from each other (Tukey's post hoc: control versus unconnected, $p < 0.001$; control versus connected, $p < 0.001$; unconnected versus connected, $p = 0.899$). Edible and inedible phytoplankton biomass exhibited the same significant response pattern to community connectivity as total phytoplankton biomass (one-way ANOVA, edible: $F_{2,45} = 65.60$, $p < 0.001$, Tukey's post hoc: control versus unconnected, $p < 0.001$; control versus connected, $p < 0.001$; unconnected versus connected, $p = 0.911$, inedible: $F_{2,45} = 32.14$, $p < 0.001$, Tukey's post hoc: control versus unconnected, $p < 0.001$; control versus connected, $p < 0.001$; unconnected versus connected, $p = 0.288$). The significant effects of community connectivity on ecosystem productivity (dissolved oxygen) followed the phytoplankton response (one-way ANOVA, $F_{2,45} = 22.57$, $p < 0.001$, Tukey's post hoc: control versus unconnected, $p < 0.001$; control versus connected, $p < 0.001$; unconnected versus connected, $p = 0.990$).

Following invasion, the control treatment without native zooplankton supported higher total, edible and inedible phytoplankton biomass than unconnected and connected treatments, but the unconnected and connected treatments did not differ from each other (Fig. 5c–h, Table 3). Edible phytoplankton biomass additionally responded to propagule pressure, where uninvaded ecosystems supported greater edible phytoplankton biomass compared to high propagule pressure ecosystems (Table 3). There was a significant interactive effect of connectivity and propagule pressure on inedible phytoplankton biomass and a marginally significant interactive effect on total phytoplankton biomass. Ecosystem productivity was greatest in the control but did not differ between unconnected and connected mesocosms (Table 3).

Total and dissolved phosphorus responded to community connectivity but not propagule pressure where the control treatment supported lower levels of phosphorus compared to unconnected and connected treatments (Table 4, Supplementary material Appendix 4). The unconnected and connected treatments did not differ from each other in phosphorus. Total nitrogen did not respond to community connectivity, propagule pressure or their interaction (Table 4, Supplementary material Appendix 4).

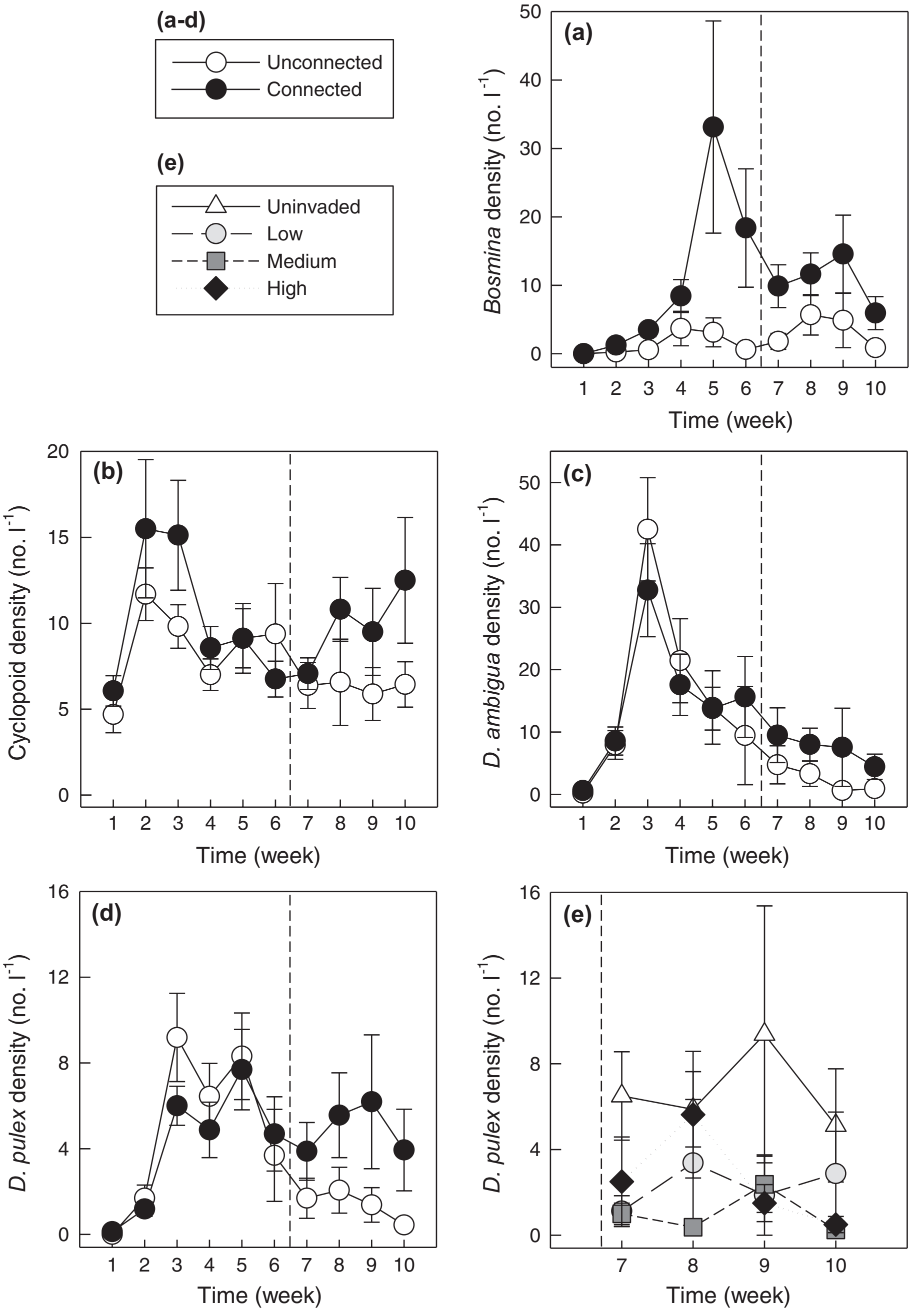

Figure 4. Densities of native indicator species through time as a function of (a–d) native community connectivity (n = 16 mesocosms per treatment, aggregated across propagule pressure treatments) and (e) propagule pressure of exotic *Daphnia lumholtzi* (n = 8 mesocosms per treatment, aggregated across community connectivity treatments). Values are mean ± SE. Vertical dashed line represents addition of the exotic *D. lumholtzi* to the experiment (week six). For propagule pressure treatments, 'uninvaded' = 0 *D. lumholtzi*/l, 'low' = 1.6 *D. lumholtzi*/l, 'medium' = 3.1 *D. lumholtzi*/l and 'high' = 6.2 *D. lumholtzi*/l.

Total dissolved nitrogen, however, responded positively to propagule pressure where the uninvaded treatment supported greater concentrations of dissolved nitrogen compared to the other three invaded treatments (Table 4, Supplementary material Appendix 4).

Discussion

Propagule pressure exerted the greatest influence on establishment success and impact of the exotic overall, while native species immigration from the metacommunity served

Table 2. Results of the indicator species analysis assessing the strength of native zooplankton taxa association with community connectivity (C: UN = unconnected, CN = connected) and exotic *Daphnia lumholtzi* propagule pressure (P: UI = uninvaded, LW = low, MD = medium, HI = high) prior to invasion (week six density) and after invasion (mean densities week 7–10). Species absence denoted by (–).

	Pre-invasion				Post-invasion							
Species	C	I.V.	I.V.rand	p	C	I.V.	I.V.rand	p	P	I.V.	I.V.rand	p
Bosmina longirostris	CN	58.6	33.5	0.005**	CN	60.5	37.9	0.005**	HI	23.4	26.3	0.632
Camptocercus macrurus	–	–	–	–	CN	12.5	8.5	0.483	UI	9.6	13.0	1.000
Ceriodaphnia dubia	UN	12.5	8.5	0.486	UN	6.2	6.2	1.000	UI	12.5	12.5	1.000
Chydorus sphaericus	UN	44.1	48.0	0.693	CN	49.3	52.2	0.644	UI	31.9	31.8	0.460
Cyclopoid copepods	CN	50.0	52.7	0.997	CN	55.8	52.1	0.028*	UI	25.7	27.7	0.980
Daphnia ambigua	CN	30.4	33.7	0.603	CN	56.6	42.8	0.046*	UI	37.2	28.8	0.099
Daphnia pulex	CN	34.9	39.5	0.707	CN	57.9	39.8	0.019*	UI	40.4	27.5	0.041*
Ilyocryptus spinifer	UN	22.5	27.3	0.695	CN	24.8	30.9	0.773	UI	30.9	24.4	0.182
Pleuroxus denticulatus	CN	8.2	10.7	0.734	CN	11.4	18.0	0.836	UI	26.4	20.0	0.312
Scapholeberis mucronata	UN	26.1	33.2	0.897	UN	50.6	47.6	0.256	MD	25.2	29.5	0.826
Simocephalus serrulatus	UN	47.2	44.4	0.263	UN	40.7	47.7	0.978	MD	32.9	29.7	0.231

Significance levels indicated as: * $p < 0.05$; ** $p < 0.01$.

to enhance local invasion resistance at the lower propagule size and increase native species richness after invasion. The connectivity of native communities to the regional species pool augmented native species densities which contributed to biotic resistance through increased interspecific interactions and further prevented extinction of strongly interacting competitors of the exotic species. Propagule dose-dependent effects of establishment were observed on native species richness, the proportion of the exotic represented in total zooplankton biomass, and edible producer biomass. Taken together, the results highlight that community connectivity can buffer against invasion at lower propagule sizes and reduce extinction risk of native competitors, but larger numbers of introduced individuals can overcome connectivity-conferred biotic resistance to influence establishment and impact of the exotic species. These results emphasize the importance of considering the interactive effects of propagule pressure of the exotic species and native community connectivity as regulators of invasion success, and argue for the maintenance of landscape connectivity to increase resistance and resilience to biological invasion.

Propagule pressure and community connectivity had contrasting influences on the establishment success of the exotic species only at lower propagule sizes. High propagule pressure resulted in the greatest establishment overall in addition to significantly higher densities, biomass and proportion biomass of the exotic species as compared to low and medium propagule pressure regardless of connectivity. These results are congruent with other studies that identify propagule pressure as a key factor contributing to the establishment success of exotic species (Lockwood et al. 2005, Simberloff 2009). Some of the previous work evaluating effects of propagule pressure over a propagule size gradient (i.e. number of individuals introduced) has found that the positive relationship between propagule dose and establishment success is non-linear and asymptotic (Drake et al. 2005, Clark and Johnston 2009, Sinclair and Arnott 2016). Consistent with these findings, in this study a dose-dependent threshold response of establishment success was observed at high propagule pressure which consistently yielded 75% establishment in the presence of native species. The low and medium propagule pressure treatments experienced only 25–50% and 25% establishment success, respectively. The range in establishment success at low propagule pressure is driven by the positive influence of community connectivity on biotic resistance, dropping success by 25%. Thus, while lower propagule pressure could not overcome connectivity-conferred biotic resistance, high propagule pressure and associated resource competition with the invader could overwhelm it. The ability for propagule pressure to overcome biotic resistance has been reported in other studies that have directly manipulated local richness, but not community connectivity (Von Holle and Simberloff 2005, Hollebone and Hay 2007). The results reported here are among the first to highlight that species dispersal in the landscape has the potential to increase resistance to invasion and provide biotic insurance to native communities, but that the effects depend upon propagule dose (size).

Connectivity-conferred invasion resistance was contributed by a dispersal-mediated increase in species abundance. Consistent augmentation of species densities by recurrent immigration from the regional pool throughout the experiment (i.e. *Bosmina*), and invasion-mediated shifts in population density response to immigration (i.e. Cyclopoid, native *Daphnia*), likely increased competition among the native species and the exotic. Prior studies of the natural source pond metacommunity over the same timeframe as the experiment identify Cyclopoid copepods as the dominant taxa while *Bosmina* and native *Daphnia* are common but relatively less abundant (Howeth 2017, Sferra et al. 2017; Supplementary material Appendix 3). Thus, while the greater density of zooplankton in connected communities reflects immigrant composition and is maintained at least partly by immigrant pressure, more complex dispersal- and invasion-mediated interspecific interactions could also be occurring. For example, two native *Daphnia* species supported higher densities in the connected treatment only after invasion which suggests that repeated immigration of these species served to maintain larger populations that were probably depressed by strong

Table 3. Effects of native community connectivity (C) and propagule pressure (P) over time (T) after invasion (week 7–10) by exotic *Daphnia lumholtzi* on native zooplankton community structure, native zooplankton biomass, phytoplankton biomass and ecosystem productivity, as analyzed with repeated-measures ANOVA.

Response variable	df	SS	F	p-value	Contrasts
Native richness (S)					
C	1,24	45.13	8.97	0.006**	[UN, CN↑**]
P	3,24	60.56	4.01	0.019*	[UI↑, LW^{+}], [UI↑, MD*]
C×P	3,24	16.06	1.06	0.383	
T	3,72	19.94	7.63	<0.001***	
T×C	3,72	3.94	1.51	0.220	
T×P	9,72	10.00	1.27	0.265	
T×C×P	9,72	10.38	1.32	0.241	
Native evenness (J′)					
C	1,24	0.0002	0.002	0.967	
P	3,24	0.61	1.96	0.146	
C×P	3,24	1.44	4.63	0.011*	
T	3,72	0.12	1.68	0.179	
T×C	3,72	0.03	0.44	0.726	
T×P	9,72	0.21	1.00	0.452	
T×C×P	9,72	0.27	1.30	0.254	
Native zooplankton biomass†					
C	1,24	0.60	1.57	0.222	
P	3,24	6.67	5.84	0.004**	[UI↑, LW**]; [UI↑, MD*]; [UI↑, HI*]
C×P	3,24	0.72	0.63	0.601	
T	3,72	0.75	2.75	0.049*	
T×C	3,72	0.31	1.14	0.340	
T×P	9,72	2.58	3.16	0.003**	
T×C×P	9,72	0.67	0.82	0.598	
Total phytoplankton biomass†					
C	2,36	26.39	33.35	<0.001***	[CTRL↑, UN***]; [CTRL↑, CN***]
P	3,36	3.12	2.63	0.065	
C×P	6,36	5.47	2.30	0.055^{+}	
T‡	2.5,89.5	0.10	0.44	0.691	
T×C‡	5.0,89.5	1.26	2.66	0.028*	
T×P‡	7.5,89.5	1.30	1.83	0.086	
T×C×P‡	14.9,89.5	1.36	0.96	0.507	
Edible phytoplankton biomass†					
C	2,36	24.93	33.00	<0.001***	[CTRL↑, UN***]; [CTRL↑, CN***]
P	3,36	3.90	3.44	0.027*	[UI↑, HI*]
C×P	6,36	2.66	1.17	0.343	
T‡	2.5,91.4	0.09	0.62	0.580	
T×C‡	5.1,91.4	1.17	3.90	0.003**	
T×P‡	7.6,91.4	0.60	1.34	0.235	
T×C×P‡	15.2,91.4	1.30	1.45	0.139	
Inedible phytoplankton biomass†					
C	2,36	18.08	22.03	<0.001***	[CTRL↑, UN***]; [CTRL↑, CN***]
P	3,36	1.48	1.20	0.323	
C×P	6,36	8.71	3.54	0.007**	
T‡	2.4,87.4	0.64	1.53	0.218	
T×C‡	4.9,87.4	1.35	1.62	0.165	
T×P‡	7.3,87.4	2.00	1.60	0.144	
T×C×P‡	14.6,87.4	1.79	0.71	0.759	
Ecosystem productivity					
C	2,36	2.84	6.71	0.003**	[CTRL↑, UN*]; [CTRL↑, CN**]
P	3,36	0.44	0.70	0.559	
C×P	6,36	0.34	0.27	0.949	
T‡	1.9,68.3	100.47	141.92	<0.001***	
T×C‡	3.8,68.3	3.02	2.13	0.089	
T×P‡	5.7,68.3	0.64	0.30	0.927	
T×C×P‡	11.4,68.3	1.80	0.42	0.944	

Notes: Tukey's post hoc pairwise comparisons are reported for significant ($p < 0.05$) and marginally significant ($p < 0.06$) main effects. Abbreviations for contrasts are CTRL = control, UN = unconnected and CN = connected for community connectivity and UI = uninvaded, LW = low, MD = medium and HI = high for propagule pressure; an upward-pointing arrow (↑) indicates the higher value.

$^{+}$ $p < 0.06$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

† Log-transformed.

‡ Greenhouse–Geisser modified probability values.

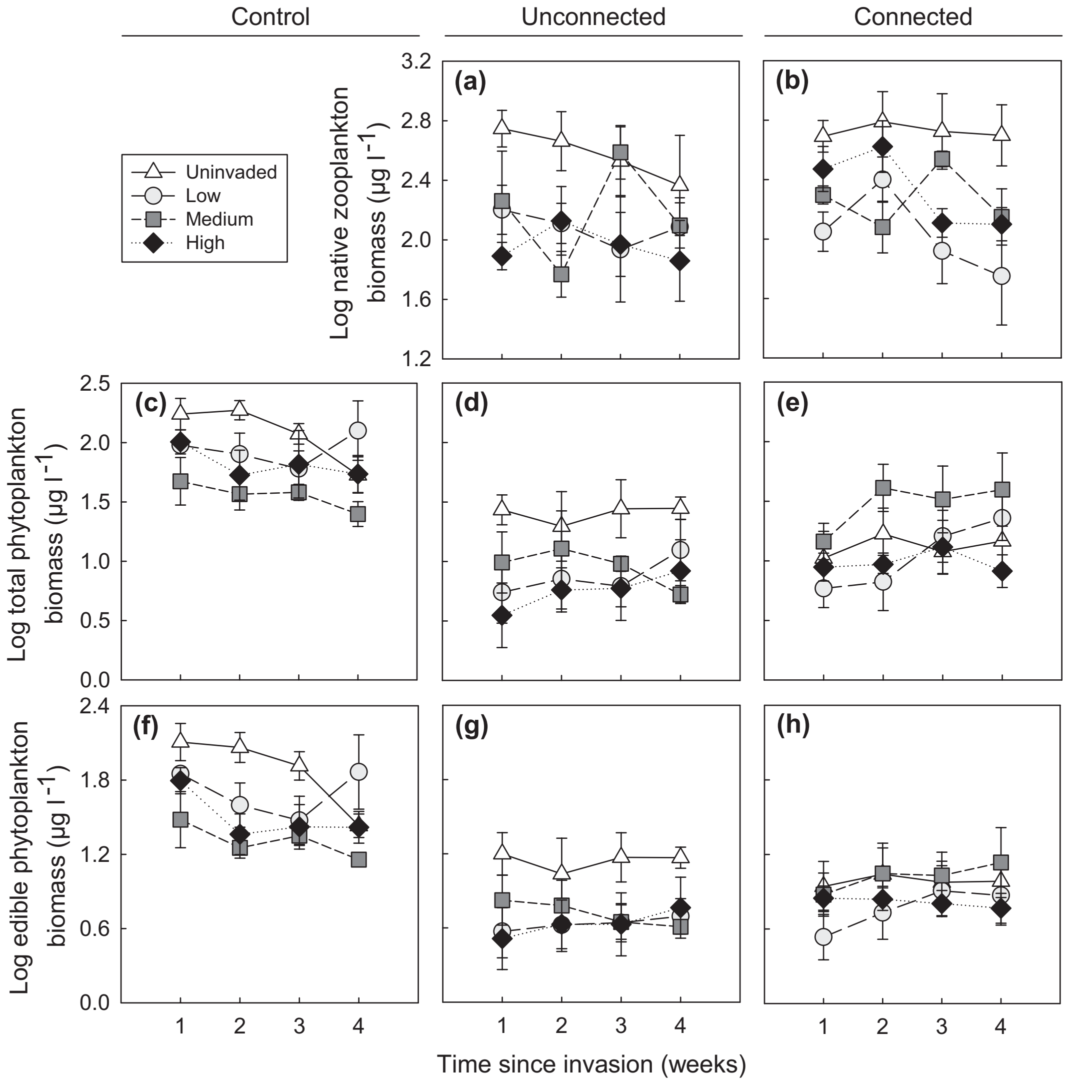

Figure 5. Ecosystem response to community connectivity and propagule pressure of the exotic *Daphnia lumholtzi* over the four weeks after invasion (weeks 7–10): (a–b) native zooplankton biomass ($\log_{10}(x + 1)$), (c–e) total and (f–h) edible phytoplankton biomass. (c–h) Biomass data are $\log_{10}$ transformed. Values are mean ± SE, n = 4 mesocosms. For propagule pressure treatments, 'uninvaded' = 0 *D. lumholtzi*/l, 'low' = 1.6 *D. lumholtzi*/l, 'medium' = 3.1 *D. lumholtzi*/l and 'high' = 6.2 *D. lumholtzi*/l.

competition for shared algal resources with *D. lumholtzi* in unconnected communities. *Daphnia pulex* was also an indicator for uninvaded communities which is likely due to the absence of exploitative competition with the exotic congener. These results are in agreement with previous experimental and theoretical studies that find immigration from the regional species pool can sustain local populations of consumers in competitive metacommunities (Mouquet and Loreau 2003, Grainger and Gilbert 2016). In natural ecosystems, however, the strength of local interspecific competition between the exotic and native species can be reduced by partitioning temporal niches as has been shown to occur previously between *D. lumholtzi* and native *Daphnia* in lakes (East et al. 1999, Havel and Graham 2006). While the importance of interspecific competition in contributing to invasion resistance is well documented in terrestrial ecosystems (Gurevitch et al. 1992), studies have shown that biotic resistance in aquatic systems is often due to consumption (Alofs and Jackson 2014). Results of this experiment demonstrate that competition can also be a key mechanism conferring biotic resistance in aquatic ecosystems and therefore increases the generality of reported findings and invasion prediction at large.

Native community connectivity and propagule pressure had opposing effects on exotic species richness over the course of the experiment. After the introduction of the exotic species, immigration of native species yielded higher richness in connected communities relative to unconnected communities in part by maintaining native *Daphnia* that would otherwise likely be driven extinct from resource competition with the exotic. Propagule pressure generally had a negative effect on native species richness with the largest impacts at low and medium pressures while at high pressure

Table 4. Effects of native community connectivity (C) and propagule pressure (P) after invasion (week 10) on total phosphorus (TP), total dissolved phosphorus (TDP), total nitrogen (TN) and total dissolved nitrogen (TDN) as analyzed with a two-way ANOVA.

Response variable	df	SS	F	p-value	Contrasts
TP					
C	2,36	0.75	11.40	<0.001***	[CTRL, UN↑**]; [CTRL, CN↑***]
P	3,36	0.15	1.52	0.225	
C×P	6,36	0.23	1.18	0.341	
TDP					
C	2,36	0.91	12.96	<0.001***	[CTRL, UN↑**]; [CTRL, CN↑***]
P	3,36	0.21	1.97	0.135	
C×P	6,36	0.30	1.41	0.239	
TN					
C	2,36	3.47	0.42	0.663	
P	3,36	25.68	2.05	0.124	
C×P	6,36	18.00	0.72	0.637	
TDN					
C	2,36	33.73	1.02	0.371	
P	3,36	205.47	4.14	0.013*	[UI↑, LW^{+}]; [UI↑, MD^{+}]; [UI↑, HI*]
C×P	6,36	53.81	0.54	0.772	

Notes: Tukey's post hoc pairwise comparisons are reported for significant ($p < 0.05$) and marginally significant ($p < 0.06$) main effects. Abbreviations for community connectivity contrasts are CTRL = control, UN = unconnected and CN = connected, and for propagule pressure are UI = uninvaded, LW = low, MD = medium and HI = high; an upward-pointing arrow (↑) indicates the higher mean response variable value in significant comparisons.

$^{+}$ $p < 0.06$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

the interactive positive effect of connectivity appears to mitigate the richness response. The negative effect of propagule pressure on richness may be a result of strong interspecific competition with native congeners, as highlighted by the observed propagule dose-dependent impacts on the abundance of native *D. pulex*. Thus, immigration from the regional pool not only served to increase local biotic resistance due to the augmentation of abundance of native species, but also enhanced native species richness by rescuing native competitors from invasion-driven extinction. Metacommunity dynamics therefore reduced extinction risk of strongly interacting native species. This result concurs with previous work that has found dispersal can increase species diversity, richness and evenness in metacommunities (Kneitel and Miller 2003, Howeth and Leibold 2010a, Pedruski and Arnott 2011), but is among the first to illustrate the associated reduction in extinction risk of native species from biological invasion. If the rate of immigration had been higher or lower in connected communities, local native species richness may have been greater than or less than what was observed in this experiment based upon predictions of unimodal dispersal–diversity relationships in competitive metacommunities (Mouquet and Loreau 2003, Grainger and Gilbert 2016). As a consequence, the degree of connectivity-conferred biotic resistance and the reduction in invasion-mediated extinction risk of native species should depend upon dispersal rate in the metacommunity (Howeth 2017) and also be a function of propagule dose. Maximizing biotic resistance of native communities and minimizing extinction risk of native species should occur at the dispersal rate where local native species richness is greatest in metacommunities, or as predicted by theory, an intermediate dispersal rate (Mouquet and Loreau 2003).

Invasion of the exotic species had larger impacts than connectivity on ecosystem attributes. The proportion of total zooplankton biomass represented by the invader was positively propagule dose-dependent. Over all propagule sizes, invaded communities supported lower native zooplankton biomass compared to uninvaded communities because of resource competition with the exotic species. Invaded communities under high propagule pressure had lower edible phytoplankton biomass compared to uninvaded communities due to the large grazing impacts from the greatest *D. lumholtzi* densities. Interactive effects of propagule pressure and connectivity were detected in inedible phytoplankton biomass, possibly due to treatment-specific competitive release from edible algal species suppressed by strong grazing pressure. Together, these results indicate that the impact of invasion on planktonic biomass partitioning largely overrode any influences of connectivity that can occur in metacommunities from effects of dispersal on diversity and population growth rates (France and Duffy 2006, Matthiessen and Hillebrand 2006, Howeth and Leibold 2008). The availability of nutrients was additionally influenced by invasion, where total dissolved nitrogen was lowest in invaded ecosystems. Selective grazing pressure from the exotic species may have shifted the algal community composition toward species that have higher nitrogen requirements, indicating potential for invasion-driven metaecosystem dynamics across natural landscapes (Gounand et al. 2018).

Ecologists have previously recognized the importance of acknowledging both propagule pressure and biotic factors such as species diversity in conceptual frameworks of biological invasions (Shea and Chesson 2002, Catford et al. 2009, Gurevitch et al. 2011). However, biotic resistance in many empirical invasion studies has been implemented by manipulating species richness and evenness directly rather than through species dispersal mechanisms as in this study. By simulating native species immigration, the connected treatment reflected a more realistic landscape scenario of local communities in a metacommunity connected by asymmetric pairwise dispersal rates and elucidated unique interactions between dispersal and propagule pressure. While this experiment is novel in its approach to elucidate mechanisms of invasion success, it does have some limitations relative to studying invasion in natural systems. Only propagule size was investigated which has been shown to more strongly influence establishment success compared to propagule number (i.e. number of introductions; Sinclair and Arnott 2016); however, propagule number can still play an important role in establishment success (Britton and Gozlan 2013, Koontz et al. 2018). This study controlled for genetic diversity within introduced populations, but larger propagule sizes and multiple introduction events could lead to higher genetic diversity and thus greater establishment success in exotic populations (Blackburn et al. 2015, Vahsen et al. 2018). The interaction of propagule size, propagule number and genetic diversity on invasion success in metacommunities remains unknown but becomes increasingly relevant as contemporary biotic homogenization ensues (Baiser et al. 2012, Briski et al. 2018). Opportunities to experimentally address these questions in more complex metacommunities include accounting for different native species dispersal rates, incorporating heterogeneous starting communities, and utilizing three trophic levels (Howeth and Leibold 2010b, Grainger and Gilbert 2016).

Invasive species are one of the top threats to biodiversity worldwide; thus, it is vital to understand the mechanisms behind biological invasions in order to implement better prevention and management strategies (Wilcove et al. 1998, Lodge et al. 2016). The recognition of propagule pressure in the last decade (Lockwood et al. 2005, Simberloff 2009) has greatly improved the way ecologists understand biological invasions, but the role of native community connectivity in altering invasion success and impacts of exotic species has remained largely unaddressed (Schiesari et al. 2018). The primary goal of this study was to determine the effects of propagule pressure of an exotic species over a propagule size gradient in unconnected and connected native communities. The results reported highlight the importance of interactive effects of propagule pressure and native community connectivity on the establishment success and influence of an introduced species. While propagule pressure can yield dose-dependent effects on exotic establishment, native species richness and native species biomass, connectivity can confer biotic resistance to invasion at smaller propagule sizes and further maintain greater native species richness within invaded communities. Therefore, ensuring that local communities within landscapes are connected by native species dispersal can provide ecological insurance by minimizing risk and impacts of invasion.

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References

Alofs, K. M. and Jackson, D. A. 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. – Ecology 95: 3259–3270.

Bachmann, R. W. and Canfield, D. E. 1996. Use of an alternative method for monitoring total nitrogen concentrations in Florida lakes. – Hydrobiologia 323: 1–8.

Baiser, B. et al. 2012. Pattern and process of biotic homogenization in the new Pangaea. – Proc. R. Soc. B 279: 4772–4777.

Barney, J. N. et al. 2016. Propagule pressure cannot always overcome biotic resistance: the role of density-dependent establishment in four invasive species. – Weed Res. 56: 208–218.

Benke, A. C. et al. 1999. Beaver-impounded wetlands of the Southeastern Coastal Plain: habitat-specific composition and dynamics of invertebrates. – In: Batzer, D. P. et al. (eds), Invertebrates of freshwater wetlands of North America. Wiley, pp. 214–245.

Blackburn, T. M. et al. 2015. The influence of numbers on invasion success. – Mol. Ecol. 24: 1942–1953.

Bock, D. G. et al. 2015. What we still don't know about invasion genetics. – Mol. Ecol. 24: 2277–2297.

Briski, E. et al. 2018. Beyond propagule pressure: importance of selection during the transport stage of biological invasions. – Front. Ecol. Environ. 16: 345–353.

Britton, J. R. and Gozlan, R. E. 2013. How many founders for a biological invasion? Predicting introduction outcomes from propagule pressure. – Ecology 94: 2558–2566.

Brockerhoff, E. G. et al. 2014. Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. – Ecology 95: 594–601.

Burns, C. W. 1968. Relationship between body size of filter-feeding Cladocera and maximum size of particle ingested. – Limnol. Oceanogr. 13: 675–678.

Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. – Am. Nat. 167: 913–924.

Catford, J. A. et al. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. – Divers. Distrib. 15: 22–40.

Clark, G. F. and Johnston, E. L. 2009. Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. – Oikos 118: 1679–1686.

Colautti, R. I. et al. 2006. Propagule pressure: a null model for biological invasions. – Biol. Invas. 8: 1023–1037.

Crumpton, W. G. et al. 1992. Nitrate and organic N analyses with 2nd-derivative spectroscopy. – Limnol. Oceanogr. 37: 907–913.

Damschen, E. I. et al. 2006. Corridors increase plant species richness at large scales. – Science 313: 1284–1286.

Drake, J. M. et al. 2005. Propagule pressure and persistence in experimental populations. – Biol. Lett. 1: 480–483.

Dufrene, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.

Dumont, H. J. et al. 1975. Dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from plankton, periphyton and benthos of continental waters. – Oecologia 19: 75–97.

Duncan, R. P. et al. 2014. Quantifying invasion risk: the relationship between establishment probability and founding population size. – Methods Ecol. Evol. 5: 1255–1263.

Dzialowski, A. R. 2010. Experimental effect of consumer identity on the invasion success of a exotic cladoceran. – Hydrobiologia 652: 139–148.

Dzialowski, A. R. and Smith, V. H. 2008. Nutrient dependent effects of consumer identity and diversity on freshwater ecosystem function. – Freshwater Biol. 53: 148–158.

East, T. L. et al. 1999. *Daphnia lumholtzi* and *Daphnia ambigua*: population comparisons of an exotic and a native cladoceran in Lake Okeechobee, Florida. – J. Plankton Res. 21: 1537–1551.

Eisenbacher, M. 1998. Effects of the exotic cladoceran *Daphnia lumholtzi* (Sars) on the growth rate and prey selection of bluegill sunfish (*Lepomis macrochirus* Rafinesque). – MS thesis, Southwest Missouri State Univ.

Elser, J. J. et al. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. – Ecol. Lett. 10: 1135–1142.

Engel, K. and Tollrian, R. 2009. Inducible defences as key adaptations for the successful invasion of *Daphnia lumholtzi* in North America? – Proc. R. Soc. B 276: 1865–1873.

Fey, S. B. and Herren, C. M. 2014. Temperature-mediated biotic interactions influence enemy release of nonnative species in warming environments. – Ecology 95: 2246–2256.

France, K. E. and Duffy, J. E. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. – Nature 441: 1139–1143.

Frisch, D. et al. 2013. The invasion history of the exotic freshwater zooplankter *Daphnia lumholtzi* (Cladocera, Crustacea) in North America: a genetic analysis. – Biol. Invas. 15: 817–828.

Gallien, L. and Carboni, M. 2017. The community ecology of invasive species: where are we and what's next? – Ecography 40: 335–352.

Gillooly, J. F. 2000. Effect of body size and temperature on generation time in zooplankton. – J. Plankton Res. 22: 241–251.

Gounand, I. et al. 2018. Meta-ecosystems 2.0: rooting the theory into the field. – Trends Ecol. Evol. 33: 36–46.

Grainger, T. N. and Gilbert, B. 2016. Dispersal and diversity in experimental metacommunities: linking theory and practice. – Oikos 125: 1213–1223.

Gurevitch, J. et al. 1992. A meta-analysis of competition in field experiments. – Am. Nat. 140: 539–572.

Gurevitch, J. et al. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. – Ecol. Lett. 14: 407–418.

Haney, J. F. et al. 2013. 'An-image-based key to the zooplankton of North America' ver. 5.0. – Univ. of New Hampshire Center for Freshwater Biology <cfb.unh.edu> 28 March 2017

Havel, J. E. and Graham, J. 2006. Complementary population dynamics of exotic and native *Daphnia* in North American reservoir communities. – Arch. Hydrobiol. 167: 245–264.

Havel, J. E. and Hebert, P. D. N. 1993. *Daphnia lumholtzi* in North America: another exotic zooplankter. – Limnol. Oceanogr. 38: 1823–1827.

Havel, J. E. and Shurin, J. B. 2004. Mechanisms, effects and scales of dispersal in freshwater zooplankton. – Limnol. Oceanogr. 49: 1229–1238.

Havens, K. E. et al. 2012. The outcome of the invasion of Florida lakes by *Daphnia lumholtzi*. – Freshwater Biol. 57: 552–562.

Hayes, K. R. and Barry, S. C. 2008. Are there any consistent predictors of invasion success? – Biol. Invas. 10: 483–506.

Hollebone, A. L. and Hay, M. E. 2007. Propagule pressure of an invasive crab overwhelms native biotic resistance. – Mar. Ecol.-Prog. Ser. 342: 191–196.

Houseman, G. R. et al. 2014. Propagule pressure–invasibility relationships: testing the influence of soil fertility and disturbance with *Lespedeza cuneata*. – Oecologia 174: 511–520.

Howeth, J. G. 2017. Native species dispersal reduces community invasibility by increasing species richness and biotic resistance. – J. Anim. Ecol. 86: 1380–1393.

Howeth, J. G. and Leibold, M. A. 2008. Planktonic dispersal dampens temporal trophic cascades in pond metacommunities. – Ecol. Lett. 11: 245–257.

Howeth, J. G. and Leibold, M. A. 2010a. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. – Ecology 91: 2727–2741.

Howeth, J. G. and Leibold, M. A. 2010b. Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. – J. Anim. Ecol. 79: 1000–1011.

Howeth, J. G. et al. 2010. Metacommunity biology as an eco-evolutionary framework for understanding exotic invasion in aquatic ecosystems. – In: Kemp, P. F. (ed.), Eco-DAS VIII symposium proceedings. Am. Soc. Limnol. Oceanogr., Waco, TX, pp. 93–109.

Jones, M. L. et al. 2017. Biotic resistance shapes the influence of propagule pressure on invasion success in bacterial communities. – Ecology 98: 1743–1749.

Kilham, S. S. et al. 1998. COMBO: a defined freshwater culture medium for algae and zooplankton. – Hydrobiologia 377: 147–159.

Kimbro, D. L. et al. 2013. Biotic resistance in marine environments. – Ecol. Lett. 16: 821–833.

King, G. E. and Howeth, J. G. 2019. Data from: propagule pressure and native community connectivity interact to influence invasion success in metacommunities. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.xxxxx>.

Kneitel, J. M. and Miller, T. E. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. – Am. Nat. 162: 165–171.

Kolar, C. S. and Wahl, D. H. 1998. Daphnid morphology deters fish predators. – Oecologia 116: 556–564.

Kolar, C. S. et al. 1997. Potential effect of invasion by an exotic zooplankter, *Daphnia lumholtzi*. – J. Freshwater Ecol. 12: 521–530.

Koontz, M. J. et al. 2018. Parsing propagule pressure: number, not size, of introductions drives colonization success in a novel environment. – Ecol. Evol. 8: 8043–8054.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence and diversity patterns in communities. – Am. Nat. 147: 784–812.

Leibold, M. A. and Norberg, J. 2004. Biodiversity in metacommunities: plankton as complex adaptive systems? – Limnol. Oceanogr. 49: 1278–1289.

Lemke, A. M. and Benke, A. C. 2003. Growth and reproduction of three cladoceran species from a small wetland in the southeastern USA. – Freshwater Biol. 48: 589–603.

Lemke, A. M. and Benke, A. C. 2009. Spatial and temporal patterns of microcrustacean assemblage structure and secondary production in a wetland ecosystem. – Freshwater Biol. 54: 1406–1426.

Lennon, J. T. et al. 2003. Invasibility of plankton food webs along a trophic state gradient. – Oikos 103: 191–203.

Levine, J. M. et al. 2004. A meta-analysis of biotic resistance to exotic plant invasions. – Ecol. Lett. 7: 975–989.

Lockwood, J. L. et al. 2005. The role of propagule pressure in explaining species invasions. – Trends Ecol. Evol. 20: 223–228.

Lodge, D. M. et al. 2016. Risk analysis and bioeconomics of invasive species to inform policy and management. – Annu. Rev. Environ. Resour. 41: 453–488.

Loewen, C. J. G. and Vinebrooke, R. D. 2016. Regional diversity reverses the negative impacts of an alien predator on local species-poor communities. – Ecology 97: 2740–2749.

Matthiessen, B. and Hillebrand, H. 2006. Dispersal frequency affects local biomass production by controlling local diversity. – Ecol. Lett. 9: 652–662.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. – In: Downing, J. A. and Rigler, F. H. (eds), A manual on methods for the assessment of secondary productivity in freshwaters. Blackwell Scientific Publications.

McCune, B. and M. J. Mefford. 2011. PC-ORD. multivariate analysis of ecological data. Ver. 6. – MjM Software, Gleneden Beach, OR, USA.

Mouquet, N. and Loreau, M. 2003. Community patterns in source-sink metacommunities. – Am. Nat. 162: 544–557.

Muzinic, C. J. 2000. First record of *Daphnia lumholtzi* Sars in the Great Lakes. – J. Great Lakes Res. 26: 352–354.

Pedruski, M. T. and Arnott, S. E. 2011. The effects of habitat connectivity and regional heterogeneity on artificial pond metacommunities. – Oecologia 166: 221–228.

Poff, N. L. et al. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. – Proc. Natl Acad. Sci. USA 104: 5732–5737.

Puth, L. M. and Post, D. M. 2005. Studying invasion: have we missed the boat? – Ecol. Lett. 8: 715–721.

Schiesari, L. et al. 2018. Towards an applied metaecology. – BioRχiv. doi: <https://doi.org/10.1101/422501>.

Sferra, C. O. et al. 2017. Habitat age influences metacommunity assembly and species richness in successional pond ecosystems. – Ecosphere 8: e01871.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – Trends Ecol. Evol. 17: 170–176.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. – Annu. Rev. Ecol. Evol. Syst. 40: 81–102.

Sinclair, J. S. and Arnott, S. E. 2016. Strength in size not numbers: propagule size more important than number in sexually reproducing populations. – Biol. Invas. 18: 497–505.

Sinclair, J. S. et al. 2015. Dispersal acts as both bane and balm for invaded zooplankton communities. – J. Plankton Res. 37: 462–471.

Smith, D. G. 2001. Pennak's freshwater invertebrates of the United States: Porifera to Crustacea. 4th edn. – Wiley.

Soeken-Gittinger, L. A. et al. 2009. Differing effects of suspended sediments on the performance of native and exotic *Daphnia*. – Freshwater Biol. 54: 495–504.

Sorensen, K. H. and Sterner, R. W. 1992. Extreme cyclomorphosis in *Daphnia lumholtzi*. – Freshwater Biol. 28: 257–262.

Stachowicz, J. J. et al. 1999. Species diversity and invasion resistance in a marine ecosystem. – Science 286: 1577–1579.

Stephens, P. A. et al. 1999. What is the Allee effect? – Oikos 87: 185–190.

Strecker, A. L. and Arnott, S. E. 2010. Complex interactions between regional dispersal of native taxa and an invasive species. – Ecology 91: 1035–1047.

Tanentzap, A. J. and Bazely, D. R. 2009. Propagule pressure and resource availability determine plant community invasibility in a temperate forest understorey. – Oikos 118: 300–308.

Thompson, P. L. and Shurin, J. B. 2012. Regional zooplankton biodiversity provides limited buffering of pond ecosystems against climate change. – J. Anim. Ecol. 81: 251–259.

Tilman, D. 2004. Niche tradeoffs, neutrality and community structure: a stochastic theory of resource competition, invasion and community assembly. – Proc. Natl Acad. Sci. USA 101: 10854–10861.

Vahsen, M. L. et al. 2018. Prior adaptation, diversity and introduction frequency mediate the positive relationship between propagule pressure and the initial success of founding populations. – Biol. Invas. 20: 2451–2459.

Von Holle, B. and Simberloff, D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. – Ecology 86: 3212–3218.

Walsh, M. R. et al. 2012. A cascade of evolutionary change alters consumer–resource dynamics and ecosystem function. – Proc. R. Soc. B 279: 3184–3192.

Whittington, D. and Walsh, M. R. 2015. Divergent phenotypic responses to predators and cyanobacteria in *Daphnia lumholtzi*. – Freshwater Biol. 60: 1880–1889.

Wilcove, D. S. et al. 1998. Quantifying threats to imperiled species in the United States. – Bioscience 48: 607–615.

Supplementary material (available online as Appendix oik-06354 at <www.oikosjournal.org/appendix/oik-06354>). Appendix 1–4.