



# High resources and infectious disease facilitate invasion by a freshwater crustacean

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## Abstract

It is well-established that both resources and infectious disease can influence species invasions, but little is known regarding interactive effects of these two factors. We performed a series of experiments to understand how resources and parasites can jointly affect the ability of a freshwater invasive zooplankton to establish in a population of a native zooplankton. In a life history trial, we found that both species increased offspring production to the same degree as algal resources increased, suggesting that changes in resources would have similar effects on both species. In a microcosm experiment simulating an invasion, we found that the invasive species reached its highest densities when there was a combination of both high resources and the presence of a shared parasite, but not for each of these conditions alone (i.e., a significant resource  $\times$  parasite interaction). This result can be explained by changes in native host population density; high resource levels initially led to an increase in the density of the native host, which caused larger epidemics when the parasite was present. This high infection prevalence caused a subsequent reduction in native host density, increasing available resources and allowing the invasive species to establish relatively dense populations. Thus, in this system, native communities with a combination of high resource levels and parasitism may be the most vulnerable to invasions. More generally, our results suggest that parasitism and resource availability can have interactive, non-additive effects on the outcome of invasions.

**Keywords** *Daphnia dentifera* · *Daphnia lumholtzi* · Eutrophication · Invasive species · Pathogen

## Introduction

Invasive species are a major ecological concern due to their ability to reduce the abundance of native species and alter community structure (Clavero and Garcia-Berthou 2005; Pimentel et al. 2005). However, not all communities are equally susceptible to species invasions. Various biotic and abiotic characteristics including resources, propagule pressure, abiotic conditions, native species richness, and the presence of predators or parasites can influence the susceptibility of a community to colonization (i.e., the invasibility

of the community) and the degree to which the community becomes invaded (i.e., the degree of invasion; Moyle and Light 1996; Kneitel and Chase 2004; Lockwood et al. 2005; Stachowicz and Byrnes 2006; Blumenthal 2006; Guo et al. 2015).

Resources are a key factor in determining the invasibility of a community (Guo et al. 2015) because they are required for an invasive species to establish and proliferate. All else being equal, it is predicted that communities with high resource availability are most likely to be invaded (Davis et al. 2000). For example, previous work has shown that communities become more susceptible to invasion when there is an input of resources (Tyler et al. 2007) or a disturbance that reduces the abundance of established populations and increases available resources (Gross et al. 2005; Symons and Arnott 2014). Conversely, communities with low resource availability are predicted to be more resistant to invasive species (Martin and Marks 2006; Going et al. 2009). Resource levels may also affect other aspects of native–invasive interactions such as those mediated by parasites (McKenzie and Townsend 2007; Becker et al. 2015).

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Resources can influence invasions by affecting both resource competition and parasite-mediated competition (Prenter et al. 2004; Tilman 2004; Strauss et al. 2012).

Parasitism can affect species invasions through a variety of mechanisms (Prenter et al. 2004). For example, invasive species might experience reduced infection prevalence and severity in their invaded range (enemy release hypothesis; Keane and Crawley 2002) or they may carry parasites into their new range and harm native species (novel weapon hypothesis; Callaway and Ridenour 2004). Here, we focus on scenarios involving native parasites that can infect both native and invasive species. In general, the presence of a shared enemy such as a parasite should favor the less susceptible host species (Price et al. 1988). If the negative effects of a parasite on an invasive species (reduced competitive ability, higher mortality, etc.) are greater than the parasite's negative effects on a native species, then parasitism can impede invasions (a form of biotic resistance; Knevel et al. 2004; Kestrup et al. 2011). However, if the parasite has a relatively small effect on an invasive species compared to the native species (Settle and Wilson 1990; Tuttle et al. 2017), or if the invasive species amplifies the amount of parasite in the community (i.e., parasite spillback; Kelly et al. 2009), then the parasite's presence can facilitate invasions. Other factors such as resource competition and relative densities of native and invasive species can influence how shared parasites affect competition (Paterson et al. 2013; Searle et al. 2016a), highlighting the potential for interactive effects of resource availability and parasitism on species invasions.

Depending on the context and system, resources and disease can have positive or negative effects on each other. For example, an increase in resources for a host can increase infection prevalence by increasing host aggregation, host tolerance, within-host parasite production, and host population densities (Johnson et al. 2007; McKenzie and Townsend 2007; Becker et al. 2015; Civitello et al. 2015; Decaestecker et al. 2015). Conversely, higher resources can decrease disease in some scenarios by decreasing parasite exposure or parasitemia (Hall et al. 2007; Cornet et al. 2014; Becker et al. 2015). When considering the effects of disease on resources, higher infection prevalence may increase the availability of resources in a system if infected hosts have reduced per-capita foraging rates (Venesky et al. 2009; Searle et al. 2016a) or if epidemics reduce host densities (Hudson and Dobson 1989; Hall et al. 2011), but some resources may decrease in abundance if infected hosts shift their resource preferences and utilization (e.g., hosts that exhibit pharmacophagy; Smilnich et al. 2011).

We performed three experimental trials to understand the interactive effects of parasitism and resources on invasion success using a native and invasive species of zooplankton (*Daphnia dentifera* and *D. lumholtzi*, respectively). Our first experiment ("life history trial") quantified birth and death

rates of both species across a gradient of resource (algal food) levels to identify mechanisms that might influence population and community-level processes. Our second experiment ("competition experiment") was a microcosm experiment testing the effects of resources and parasitism on the native and invasive species when communities were initiated with equal densities of both species. The competition experiment helped us understand how these two species might compete under varying resource and parasite conditions. Our final experiment ("invasion experiment") also tested the effects of resources and parasitism on densities of the invasive and native species, but allowed native populations to establish before introduction of the invasive species. The invasion experiment provided us with a more realistic approximation of a natural invasion across resource and parasite treatments, and is the central focus of this study.

## Materials and methods

### Study system

Our native species, *D. dentifera*, is native to North America and is a dominant grazer in stratified lakes in the Midwestern USA (Hebert 1995). Our invasive species, *D. lumholtzi*, is native to lakes in Africa, Asia, and Australia and was introduced into North America in the early 1990s (Havel and Hebert 1993). Since its introduction, *D. lumholtzi* has spread throughout much of the eastern United States and South America and can alter the native zooplankton community structure (Kolar et al. 1997). Previous experimental manipulations of *D. lumholtzi* have shown that it is most successful at competing with native species in warmer temperatures and with the presence of predators (Fey and Cottingham 2012; Fey and Herren 2014). Hereafter, we refer to *D. dentifera* as the "native species" and *D. lumholtzi* as the "invasive species." Both species have parthenogenic life cycles and can be reared in asexual isofemale lines (hereafter, "clones") in the laboratory. Both species can also become infected with the fungus, *Metschnikowia bicuspidata* (hereafter, "the parasite") by consuming the parasite while filter-feeding. Infection causes mortality and reduced feeding rates (Ebert et al. 2000; Searle et al. 2016a).

A previous mesocosm study found that interactions between resources and native community structure can affect establishment of the invasive species (Lennon et al. 2003). Additionally, a microcosm experiment demonstrated that the presence of the parasite reduced densities of the native species but not the invasive species, even though the invasive species has higher susceptibility to the parasite (Searle et al. 2016a). Thus, because the parasite negatively impacts populations of the native species more than the invasive species, we predicted that the presence of the parasite would favor

the invasive species. We also predicted that higher resources would increase host densities and lead to higher infection prevalence (Hall et al. 2011; Civitello et al. 2015) due to increased rates of transmission at high host densities. These large epidemics would then reduce densities of the native species (Hall et al. 2011) and reduce individual foraging rates (Searle et al. 2016a), leading to an increase in resource availability (food resources, in particular) and an increase in the success of the invasive species.

### Life history trial

The life history trial compared birth and death rates of the native versus invasive species across a gradient of resource levels. We had three resource treatments; “low resource” treatments were fed daily with 5000 cells mL<sup>-1</sup> of the nutritious alga, *Ankistrodesmus falcatus*, “medium resource” treatments were fed 15,000 cells mL<sup>-1</sup>, and “high resource” treatments were fed 25,000 cells mL<sup>-1</sup>. Each replicate contained a single individual in a 50 mL beaker filled with 30 mL of well water. We used three clones per species (Table S1) and replicated each clone × resource treatment ten times, with the exception of one invasive clone which had six replicates per resource treatment. These clones were also used in a previous study (Searle et al. 2016a) except for one of the native clones (Table S1).

We initiated the experiment with neonates (<48 h old). Because we were interested in differences between species and not clones, we did not conduct maternal lines to produce individuals for this experiment. However, all neonates were from the third or greater clutch of adult *Daphnia* to reduce variation among replicates (Ebert 1993). Three times a week (every 2–3 days) for 32 days, we recorded the number of offspring produced by each individual, checked for mortality, and performed a full water change. We also recorded the presence of any ephippia (resting eggs) in the water; ephippia are often the source of sexual reproduction in *Daphnia*, but some species also produce them asexually (Kleiven et al. 1992). In this experiment, female adults were held individually and offspring removed every 2–3 days (male *Daphnia* of two similar species take at least 5 days to become sexually mature; Boersma et al. 1998; Winsor and Innes 2002), such that any ephippia observed would be asexually produced or nonviable. Temperatures in the laboratory were an average of 20.0 °C (±0.76) with a 16:8 light:dark cycle.

For each individual, we calculated the average number of offspring produced per day starting on day 8 (when the animals were 8–10 days old) which is when most individuals started reproducing. We only analyzed birth rate data from individuals that survived until at least day 11 (11–13 days old). We compared birth rates using a linear model with species, resource treatment, and species × resource treatment as explanatory variables, with clone nested within species.

We analyzed production of ephippia, classifying individuals as either producing or not producing an ephippium during the experiment, using a binomial generalized linear model (GLM) with clone, resource treatment, and the interaction as explanatory variables. We also compared mortality using a Cox proportional hazard model with species, resource treatment and the interaction as explanatory variables. All statistics were performed in R version 3.3.3 using the base and “survival” packages (Therneau 2015; R Core Team 2017).

### Competition experiment

We next conducted a competition experiment using a 2 × 2 factorial design, with two resource treatments (low, high) and two parasite treatments (exposed, unexposed) each replicated ten times. Low and high resource treatments were the same as in the life history trial (5000 cells mL<sup>-1</sup> and 25,000 cells mL<sup>-1</sup>, respectively, of *A. falcatus* added daily). Replicates were one-liter beakers (microcosms) filled with 800 mL of well water. We initiated the microcosms with nine individuals from each species, using three clones from each species (three individuals per clone; Table S1). We allowed populations to grow and fluctuate for 52 days (approximately seven generations; Day and Kaushik 1987). Twice a week, all microcosms received a full water change by pouring the entire contents of each microcosm through a mesh filter (which captured *Daphnia* but allowed algal cells and parasite spores to pass through) then returning the animals to their microcosm with 800 mL of clean well water. Thirteen days after the experiment began, parasite-exposed treatments were given a dose of 150 spores mL<sup>-1</sup> of the parasite; this dose is within the range that has been used to successfully infect *Daphnia* in previous experiments (e.g., Duffy and Sivars-Becker 2007; Prior et al. 2011; Searle et al. 2015).

We sampled microcosms once a week for 6 weeks beginning 4 days after parasite exposure (day 17). On sampling days, we homogenized each microcosm via standardized stirring before removing a 200 mL sample from the top of each microcosm for enumeration. For each individual in the sample, we visually identified age (adult or juvenile), sex (male or female), and infection status (infected or uninfected) using a stereomicroscope (Brooks 1957). Infections are easily identified in live animals because they turn the normally transparent hosts an opaque white color (Duffy and Hall 2008). After sampling, we returned all individuals to their microcosm.

To control for variation in the timing of population growth and infection among replicates, we calculated the area under the curve for each of our response variables (population density, density of infected hosts, and infection prevalence) separating our results for each species within a replicate. For each of these response variables, we used the trapezoidal area under the curve to calculate a single

value for each replicate, which we refer to as “integrated” values. Similar methods have been used in previous studies of experimental *Daphnia* populations (Civitello et al. 2013; Searle et al. 2016a, b; Auld and Brand 2017). Since integrated values are continuous, we analyzed integrated population densities, integrated densities of infected hosts, and integrated infection prevalence using ANOVA’s with data from both species paired within a replicate. For population densities we included resource treatment, parasite treatment, species, and all two-way interactions as explanatory variables. For infection responses, we only used data from parasite-exposed treatments and included resource treatment, species and the resource x species interaction as explanatory variables. We followed significant effects with Tukey’s HSD tests.

### Invasion experiment

The invasion experiment tested the ability of the invasive species to invade microcosms with established native populations. This experiment had the same  $2 \times 2$  factorial design as the competition experiment with ten replicates per treatment, but with the invasive species introduced into the microcosms approximately half way through the experiment. We initiated populations with 15 individuals of the native species from five clones (three individuals per clone; Table S1). On day 7, parasite-exposed replicates received a dose of 150 parasite spores  $\text{mL}^{-1}$  of the same parasite isolate as in the competition experiment. On day 31, we added two, 4–5-day old females of the invasive species to each replicate. We chose to start the invasion after 31 days because this was the time when we observed high densities and visible infections in the competition experiment (Figs. S1, S2). We continued to monitor populations for 4 weeks after introduction of the invasive species, ending the experiment on day 59. Throughout the experiment, full water changes were conducted twice a week and populations were sampled once a week using the same methods as the competition experiment starting on day 10 for a total of eight sampling events (four before the invasion and four after).

We first analyzed data related to establishment and proliferation of the invasive species. We considered establishment to be successful in a microcosm if we observed invasive individuals during both of the last two sampling points (i.e., 3 and 4 weeks after introduction of the invasive species), indicating that *D. lumholzi* was persisting in the microcosms. We compared establishment among treatments using a binomial GLM with parasite treatment, resource treatment, and the parasite x resource treatment interaction as explanatory variables. We then calculated integrated population densities for the invasive species (a measure of the degree of invasion) and compared them among treatments using an ANOVA with resource treatment, parasite treatment, and

the interaction term as explanatory variables. We compared integrated densities of native hosts across treatments in the same manner. Additionally, based on the density of native hosts, we estimated available resources on the day of invasion (day 31; Fig. S4).

We compared integrated densities of infected hosts and integrated infection prevalence for each species using ANOVA’s including only parasite-exposed treatments with resource treatment as the explanatory variable. We followed significant effects with Tukey’s HSD tests. We observed infected individuals in four of our unexposed replicates (two from each of the high and low resource treatments). However, we still include these replicates in our analyses because infected individuals were only observed after the invasive species was introduced, the density of infected individuals was very low, and our statistical results are qualitatively the same whether or not we include these replicates.

## Results

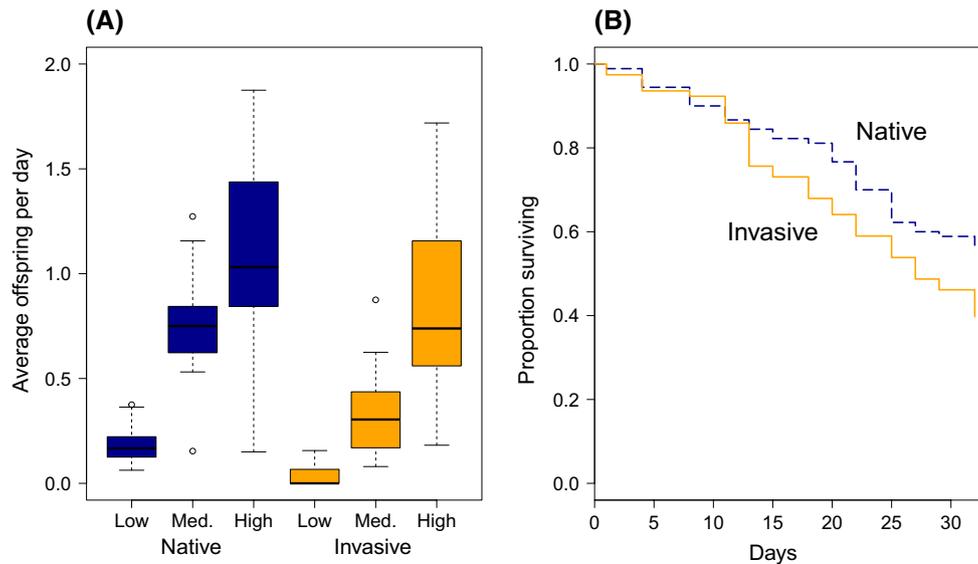
### Life history trial

The invasive species had lower birth rates than the native species ( $F_{1,133} = 46.63$ ,  $p < 0.001$ ; Fig. 1a). More resources led to increased offspring production in both species ( $F_{1,133} = 324.68$ ,  $p < 0.001$ ; Fig. 1a) and both species increased offspring production to the same degree as algal resources increased (i.e., no significant resource treatment x species interaction;  $F_{1,133} = 0.23$ ,  $p = 0.634$ ). No native individuals produced ephippia during the life history trial, but 34.3% of invasive individuals produced at least one ephippium. In the invasive species, there was no effect of clone, resource treatment or the interaction on production of ephippia ( $p > 0.05$  for all).

There was a strong trend for the invasive species to have faster mortality compared to the native species, but this was not significant at  $\alpha = 0.05$  level (hazard ratio = 2.13, 95% CI 0.99–4.60,  $p = 0.053$ ; Fig. 1b). There was no effect of resource treatment or the resource x species interaction on rates of mortality ( $p > 0.10$  for both).

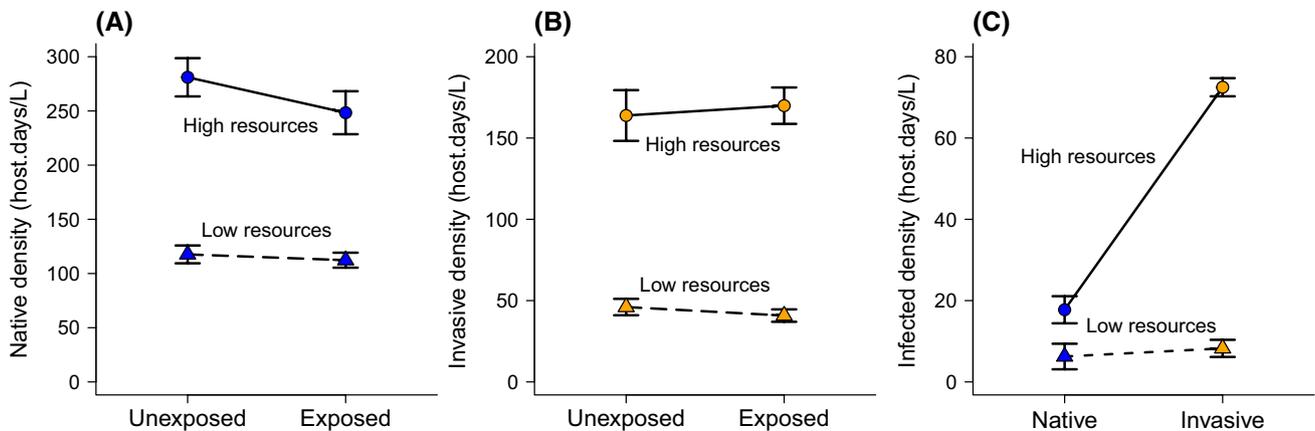
### Competition experiment

For each species, low resource treatments had lower integrated population densities ( $F_{1,66} = 9.04$ ,  $p = 0.004$ ; Fig. 2a, b) and lower integrated densities of infected hosts ( $F_{1,32} = 4.61$ ,  $p = 0.039$ ; Fig. 2c) than high resource treatments. Across treatments, integrated population densities were lower for the invasive species than for the native species ( $F_{1,66} = 21.94$ ,  $p < 0.001$ ; compare Fig. 2a–b) while integrated densities of infected hosts were higher in the invasive species ( $F_{1,32} = 5.27$ ,  $p = 0.028$ ; Fig. 2c). There



**Fig. 1** Results from the life history trial where individuals were given one of three resource treatments: low, medium (“med.”), or high. **a** Results for birth rates are shown for the native species (dark bars; *Daphnia dentifera*) versus invasive species (light bars; *D. lumholtzi*). The invasive species had lower birth rates than the native species but both species increased offspring production to the same degree as

resources increased. **b** Survival of the native species (dashed line;  $n=90$ ) and invasive species (solid line;  $n=78$ ) is shown through time with resource treatments pooled within each species. There was no effect of resource treatment on mortality, but there was a non-significant trend for the invasive species to die faster than the native species



**Fig. 2** Results from the competition experiment. High-resource treatments are indicated with circles and low-resource treatments are indicated with triangles. Parasite treatments are indicated as “unexposed” (control) or “exposed.” Each point represents ten replicates. **a** The average integrated densities of the native species (*Daphnia dentifera*) and **b** the invasive species (*D. lumholtzi*) are shown for all treatments ( $\pm$ SE). Densities were higher for both species in the high-

resource treatments and the native species had higher overall densities than the invasive species (note different y-axis scales). **c** Average integrated densities of infected hosts in the parasite-exposed treatments are shown for both species ( $\pm$ SE). Low-resource treatments had lower densities of infected hosts than high-resource treatments, and the invasive species had higher densities of infected hosts than the native species

was no effect of parasite treatment on integrated population densities ( $F_{1,66} = 0.46, p = 0.501$ ) likely because infection prevalence was relatively low in this experiment (Fig. S3). Infection prevalence was unaffected by resource treatment or species (resource:  $F_{1,32} = 0.10, p = 0.751$ ; species:

$F_{1,32} = 2.40, p = 0.131$ ). We did not find any significant interactions in any of the analyses for this experiment ( $p > 0.10$  for all). To summarize, low resource treatments had lower population densities and lower densities of infected hosts.

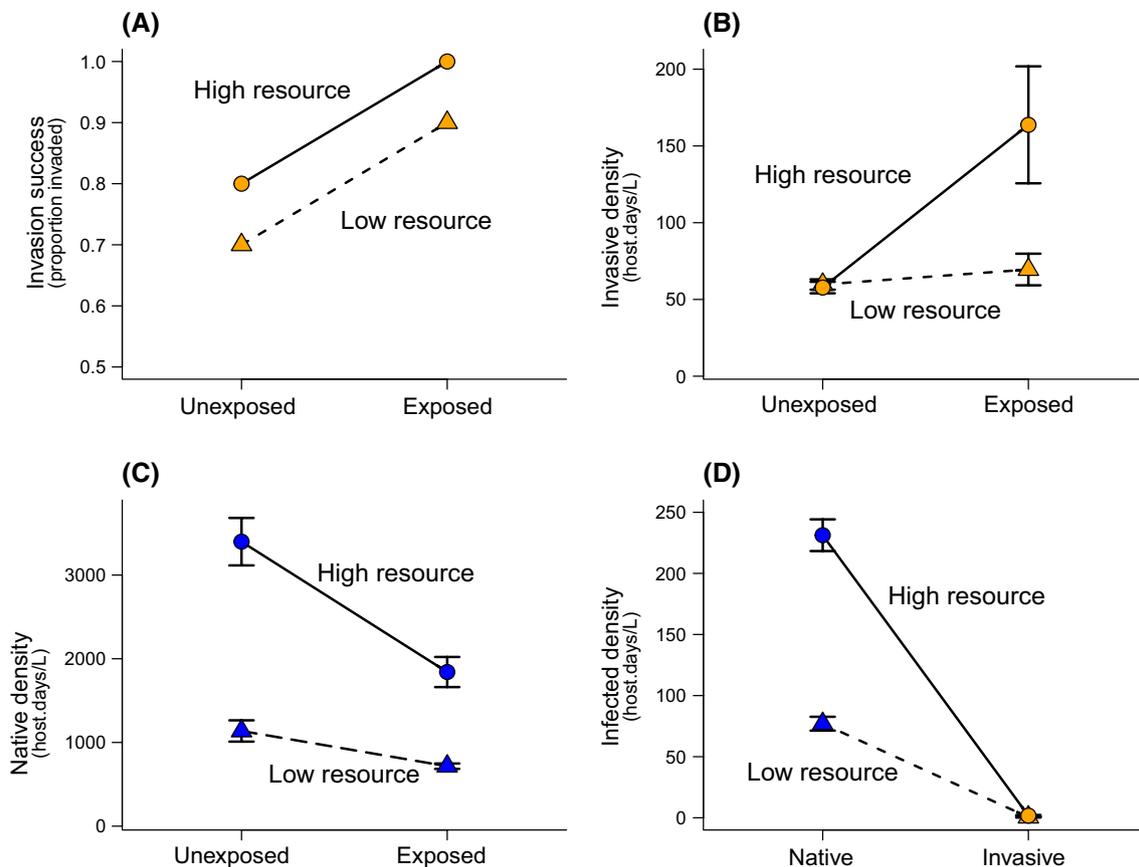
## Invasion experiment

The invasive species established in all but six replicates in the invasion experiment. Five of these failed invasions were in unexposed replicates; there was a non-significant trend for establishment to be higher in the parasite-exposed treatments ( $X^2 = 3.38$ ,  $p = 0.066$ ) but there was no effect of resource treatment or the resource  $\times$  parasite interaction ( $p > 0.10$  for both; Fig. 3a). For integrated population densities of the invasive species, there was a significant resource  $\times$  parasite treatment effect ( $F_{1,36} = 5.85$ ,  $p = 0.021$ ; Fig. 3b). In the high resource, parasite-exposed treatments, integrated population densities of the invasive species were an average 164.4% higher than all other treatments (Figs. 3b, 4c, d).

Integrated population densities of the native species were lower in low-resource conditions ( $F_{1,36} = 883.43$ ,  $p < 0.001$ )

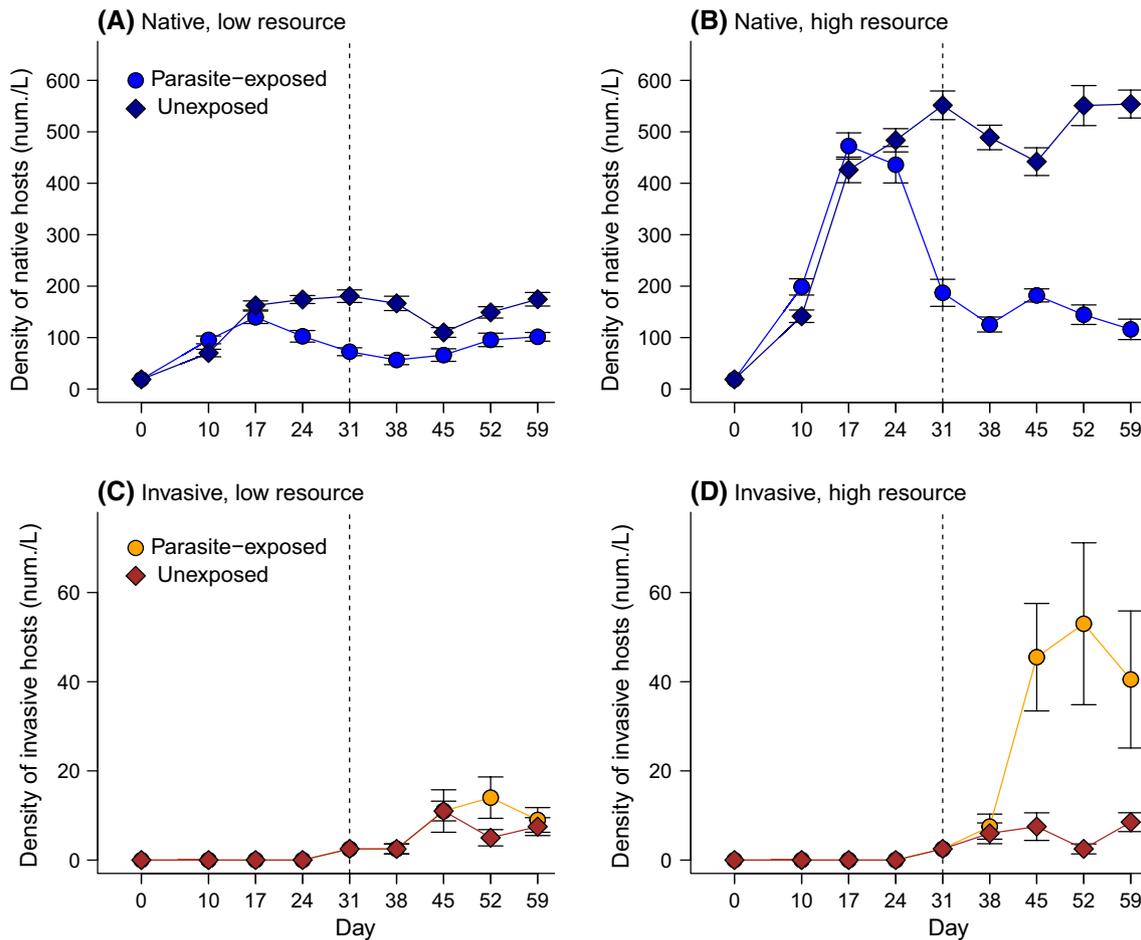
and in parasite-exposed treatments ( $F_{1,36} = 301.45$ ,  $p < 0.001$ ; Fig. 3c). Additionally, there was a significant resource  $\times$  parasite treatment effect on the integrated population densities of the native species ( $F_{1,36} = 99.47$ ,  $p < 0.001$ ; Figs. 3c, 4a, b); the presence of the parasite caused a greater reduction in native population densities in high-resource conditions (an average 45.8% reduction) compared to low-resource conditions (an average 37.0% reduction; Fig. 3c).

Integrated density of infected hosts and integrated infection prevalence of the native species were lower in low-resource treatments compared to high-resource treatments (density of infected hosts was an average of 66.7% lower:  $F_{1,18} = 118.71$ ,  $p < 0.001$ ; Fig. 3d; infection prevalence was an average of 29.7% lower:  $F_{1,18} = 13.21$ ,  $p = 0.002$ ). Infection in the invasive species (measured as integrated density or integrated prevalence) was very low and did not differ



**Fig. 3** Results from the invasion experiment. High-resource treatments are indicated with circles and low-resource treatments are indicated with triangles. Parasite treatments are indicated as “unexposed” (control) or “exposed.” Each point represents ten replicates and all values are averages  $\pm$  SE. **a** Establishment of the invasive species (*Daphnia lumholtzi*), measured as the proportion of replicates in each treatment where the invasive species established. There was a non-significant trend for establishment to be higher in parasite-exposed treatments. **b** Integrated population densities of the invasive species. There was a significant resource  $\times$  parasite treatment interac-

tion where population densities of the invasive species were highest in the high resource, parasite-exposed treatment. **c** Integrated population densities of the native species (*D. dentifera*). There was a significant resource  $\times$  parasite treatment interaction where the presence of the parasite caused a greater reduction in native population densities in high-resource conditions compared to low-resource conditions. **d** Integrated infected densities for both species in the parasite-exposed treatments. In the native species, the density of infected hosts was lower in low-resource treatments. Infection was very low in the invasive species and did not differ between resource treatments



**Fig. 4** Average density through time (day) for each host species across treatments ( $\pm$ SE) in the invasion experiment. Results for the native host are shown in low (a) and high (b) resource treatments. Each treatment was replicated ten times. Invasive population densities are shown in a similar manner in low (c) and high (d) resource treatments. Circles represent parasite-exposed treatments while diamonds are unexposed treatments. Two invasive individuals were introduced

to each replicate on day 31, indicated with the dashed vertical line. Data shown were used to calculate the area under the curve (“integrated”) values in Fig. 3b, c. For the native species, the presence of the parasite caused a greater reduction in density in high-resource conditions compared to low-resource conditions. For the invasive species, the high resource, parasite-exposed treatment had higher densities than any other treatment

between resource treatments (density of infected hosts:  $F_{1,18} = 3.95$ ,  $p = 0.062$ ; infection prevalence:  $F_{1,18} = 1.28$ ,  $p = 0.273$ ; Fig. 3d).

### Discussion

It is well-established that both resources (Davis et al. 2000) and infectious disease (Prenter et al. 2004) can influence invasions, but little is known regarding interactive effects of these two factors. In our life history trial, we found that both species increased offspring production to the same degree as algal resources increased, suggesting that changes in resources would have similar effects on both species. In our competition experiment, we found that higher resources led to higher population densities of both species and higher

densities of infected hosts. Finally, in our invasion experiment, we found that resources and disease had greater-than-additive effects on the invasion; the density of invasive hosts was greatest in treatments with both high resources and the presence of the parasite, but not for each of the conditions alone. Together, these results demonstrate that different scales and timing of experimental manipulations can influence experimental outcomes, and that resources and parasitism can have interactive, non-additive effects on invasions.

The greater-than-additive effects of increased resources and parasitism on the density of invasive hosts can be explained by changes in the densities of the native hosts. In the invasion experiment, high resources initially led to an increase in the density of the native hosts (Fig. 4a, b). In our study and in previous work, higher densities of the native host increased infection prevalence and the density

of infected hosts (Figs. 2c, 3d; Hall et al. 2011), presumably due to an increase in transmission rates. Therefore, the parasite caused a greater reduction in densities of the native host in high-resource environments (Figs. 3c, 4a, b). The invasive species was introduced shortly after this reduction in the density of native hosts occurred (Fig. 4), allowing the invasive species to take advantage of the subsequent increase in available resources (Fig. S4) even though it is more susceptible to infection than the native host (Fig. 2c; Searle et al. 2016a). Thus, in this system, we found the highest densities of the invasive species in high resource, parasite-exposed treatments, but not for each of these conditions alone (Fig. 3b).

Establishment of *D. lumholtzi* (a measure of invasibility) was not significantly different across our treatments (Fig. 3a), although we did find a non-significant trend for higher establishment in parasite-exposed treatments. This lack of effect may be due to the high success of the invasive species at invading microcosms (establishing in 85% of the microcosms; Fig. 3a), making it difficult to statistically tease apart treatment effects. We do not know if establishment of *D. lumholtzi* is equally high in the field, because unsuccessful invasions can be difficult to document. However, our results suggest that interactions between resources and parasites may have a greater impact on the degree of invasion (measured as the density of the invasive species) than on the establishment of an invasive species.

While the main focus of our study was the invasion experiment, we can use results from the life history and competition experiments to understand patterns of invasion in this system. For example, in the life history trial, we found that the native species had higher birth rates than the invasive species and that both species increased birth rates to the same degree as resources increased (Fig. 1a). Additionally, there was a non-significant trend for the invasive species to have greater mortality across treatments compared to the native species (Fig. 1b). This information can explain our competition experiment results for population densities where the native species was in higher abundance than the invasive species. We also found that the effects of parasitism were different in the competition versus invasion experiments. In the competition experiment, we did not observe any effect of the parasite on population densities of either species (Fig. 2a, b), likely because we had relatively low infection prevalence throughout this experiment (Figs. S2, S3). In contrast, the invasion experiment had higher densities of infected individuals and higher infection prevalence (Figs. S5, S6) and the parasite treatment was a significant predictor of several variables (Fig. 3). The different timing of parasite exposure in these two treatments or the use of different clones may have caused higher infection in the invasion experiment than the competition experiment.

Since priority effects are known to influence many aspects of communities (e.g., Shulman et al. 1983; Alford and Wilbur 1985), it is likely that altering the timing of species introduction and parasite exposure drove at least some of the differences in our results across experiments. In the invasion experiment, *D. lumholtzi* was added to microcosms shortly after the densities of the native species were reduced due to the parasite (Fig. 4a, b). If the invasion had happened before this epidemic or after the population recovered, the effects of the parasite would likely be diminished. In the competition experiment, both species were added to the microcosms at the same time, so the invader was not able to take advantage of the parasite-driven reduction in the densities of native hosts since it was also experiencing high rates of disease (Fig. 2c). Furthermore, it is possible that the presence of the parasite would have eventually limited the densities of the invasive species if the experiment had continued for longer. However, a previous microcosm experiment found that the parasite did not reduce densities of *D. lumholtzi* (Searle et al. 2016a), suggesting that population densities of the invasive species can be stable even with large epidemics.

There are several mechanisms by which infectious disease may affect invasive species in our system. It is possible that *D. lumholtzi* experiences reduced regulation from parasites in its invaded range (i.e., enemy release) because we did not find any evidence that the native parasite reduced densities of the invasive species (Figs. 2b, 3b). It is also possible that *D. lumholtzi* could carry other microorganisms (e.g., bacteria, fungi) that have detrimental effects on the native species (i.e., a novel weapon), but we did not detect any parasites besides *M. bicuspidata* in our experiments. Additionally, there is no evidence of biotic resistance or parasite spillback in our system (Searle et al. 2016a). Instead, we found evidence of another mechanism where the parasite acted as a form of disturbance, reducing the densities of the native species and allowing the invasive species to establish and proliferate during the epidemic (Fig. 4). Because natural epidemics in the native species are seasonal (Hall et al. 2011), the timing of introduction of the invasive species is likely critical for its establishment. Thus, our results suggest that populations are more susceptible to species invasions when they are experiencing epidemics.

*Daphnia lumholtzi* has been a successful invader in North and South America (Havel et al. 1995; Hiskey 1996; Kotov and Taylor 2014). Our results show that it has lower birth rates and higher death rates than the native species (Fig. 1), and lower densities than the native species in every treatment in the competition experiment (Fig. 2a, b). However, despite low population densities, a previous study found that the invasive species is a strong interspecific competitor, causing a greater reduction in the densities of the native species than vice versa (Searle et al. 2016a). Additionally, *D. lumholtzi* individuals often produced ephippia in our life history

experiment, while none of the native individuals produced ephippia. The production of ephippia likely contributes to invasion success, as dispersal of zooplankton often occurs via movement of ephippia (Havel and Shurin 2004). Thus, despite low densities and low birth rates of the invasive species in our experiments, *D. lumholtzi* can still successfully invade native communities and suppress populations of native species (Kolar et al. 1997; Searle et al. 2016a).

It is unknown if the interactive effects of resources and disease that we observed are also found in natural systems. *Daphnia lumholtzi* is common in manmade reservoirs (Havel et al. 1995; Dzialowski et al. 2000), which tend to have higher disturbance regimes than inland lakes (Havel et al. 2005), potentially facilitating invasions through frequent increases in available resources. Additionally, a survey of the invasive species in Missouri found that invaded lakes tended to have higher levels of nitrates and nitrites than uninvaded lakes (Havel et al. 1995). However, in a survey and mesocosm study, *D. lumholtzi* was more likely to establish in environments with low nutrients (Dzialowski et al. 2000; Lennon et al. 2003). The varying effect of nutrients on the invasive species may be due to differences across sites in the biotic environment, including the presence or absence of parasites.

Both resources and infectious disease are known to influence invasions in many systems (Prenter et al. 2004; Guo et al. 2015) and the interactions between these two factors may lead to different results than observed in our system. For example, native parasites preferentially harm invasive species in some systems (e.g., oomycetes in freshwater amphipods; Kestrup et al. 2011, soil-borne pathogens in dune grasses; Knevel et al. 2004) so an epidemic caused by increased resources could inhibit invasive species in these systems. Alternatively, because high resource availability can reduce infection prevalence or severity in some systems (e.g., avian malaria in birds; Cornet et al. 2014, blood parasites in lace monitors; Jessop et al. 2012) increasing resources could reduce the effect of infectious disease on invasions (whether positive or negative). Thus, it is necessary to understand the individual effects of both resources and infectious disease in a system to predict the joint impacts of these factors on invasive species.

## Conclusions

We found that our invasive species was the most successful in conditions with a combination of high resources and the presence of a parasite. Previous studies have shown that eutrophication of aquatic systems can benefit invasive species (Byers 2002; Chase and Knight 2006) and that infectious diseases can influence the outcome of an invasion (Prenter et al. 2004). These factors also alter community

structure (Buck et al. 2016). Thus, our results indicate that eutrophication of freshwater systems may facilitate invasions through a direct increase in resources or as an indirect effect, mediated through parasites. Ultimately, understanding how resources and parasites interact to influence invasions can help ecologists predict which communities are most at-risk from species invasions and to create management plans that minimize the chances of a species successfully invading native communities.

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**Author contribution statement** CLS designed the experiments and analyzed the data. BRH, AMM, JKI, and MAW performed the experiments. CLS wrote the manuscript; all other authors provided editorial advice.

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