CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition

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Abstract. Native communities are thought to mediate the establishment and performance of invasive species through competitive and consumptive interactions, a concept referred to as "biotic resistance." We investigated the generality of this concept across ecosystems. Despite the conspicuousness of freshwater invasions, investigations of biotic resistance have focused mostly on terrestrial and, more recently, marine coastal communities. We collected in-situ studies that tested the impacts of native freshwater communities on invading primary producers and consumers. Meta-analysis demonstrated that evidence of competitive biotic resistance in freshwater habitats was not as strong as that in marine and terrestrial ecosystems. In freshwater ecosystems consumptive resistance was significantly stronger than competitive resistance and consumptive resistance appeared to be as strong in freshwater as in marine and terrestrial systems. The limited number of studies considering freshwater biotic resistance hindered our ability to understand the importance of factors including latitude, experimental duration, and method. However, the strength of biotic resistance varied among freshwater habitats; specifically, biotic resistance was strongest in lentic environments. Our analysis identifies mechanisms underlying biotic resistance in freshwater ecosystems that warrant further investigation given the potential ongoing and future impacts of invasive species in these systems.

Key words: biotic resistance; competition; consumption; freshwater; invasion; lentic; lotic.

INTRODUCTION

Biological invasions have changed community composition and ecosystem properties in a variety of habitats (Simberloff et al. 2013). The establishment, performance, and relative impact of introduced species varies among taxa and among sites. Several ecological concepts can help to understand this variation, including: enemy release, disturbance, propagule pressure, and biotic resistance. The generality of these concepts across ecosystems, however, remains unclear, due in part to the poor integration of invasion theory (Catford et al. 2009), and in part to an underrepresentation of aquatic systems in the literature (Ricciardi and MacIsaac 2011).

Biotic resistance, or the role of species interactions in limiting the success (establishment and performance) of introduced species, is interesting from both theoretical and applied perspectives (Levine et al. 2004). Invasions empirically test community assembly and coexistence

theory (Fargione et al. 2003, HilleRisLambers et al. 2012), and resource managers are interested in restoring and maintaining communities that will resist invasions (Funk et al. 2008). The concept of "biotic resistance" is often credited to Elton (1958), who suggested that species-rich communities, which are more likely to harbor strong competitors or predators, should be less invasible than species-poor communities. Nearly a hundred years before Elton, however, Darwin (Darwin 1859: Chapter 12, page 388) posited a similar hypothesis suggesting that introduced species would likely be more successful and face less competition in freshwater than more diverse terrestrial environments.

Darwin (1859) and Elton (1958) both suggested that more diverse communities should be less invasible because of increased competition or niche limitation (Davis 2009). Since then, many empirical investigations of biotic resistance have focused on the relationship between diversity and invasibility. Negative relationships between diversity and invasibility have been demonstrated experimentally at small scales; however, across larger scales that include extrinsic variation, more

TABLE 1. Theoretical reasons why the strength of biotic resistance may vary among terrestrial and aquatic (freshwater and marine) ecosystems.

Mechanism of resistance	Prediction regarding strength of resistance	Reason	Citation(s)
Competitive	weaker in aquatic communities	diversity and species density appear lower	Darwin (1859), Shurin et al. (2006), Dawson (2012)
	weaker in freshwater communities	fish communities appear unsaturated	Moyle and Light (1996), Irz et al. (2004), Smith and Shurin (2006)
	weaker in aquatic communities	more generalist and opportunistic feeding	Liem (1990), Shurin et al. (2006)
	stronger in marine and weaker in lotic communities	patterns of omnivory	Thompson et al. (2007)
Consumptive	stronger in aquatic communities	strong herbivory and top-down control	Cyr and Pace (1993), Shurin et al. (2002)
	stronger in aquatic communities	generalist predators lead to less enemy release	Shurin et al. (2006), González et al. (2010)
	stronger in lentic and benthic aquatic communities	spatial confinement increases predation intensity	McCann et al. (2005), Shurin et al. (2002, 2006)
	weaker in freshwater communities	naïveté increases vulnerability	Ricciardi and Atkinson (2004), Cox and Lima (2006)

invasive species are often found in more diverse communities (Shea and Chesson 2002, Levine et al. 2004, Fridley et al. 2007, Alofs and Fowler 2013). Small-scale experiments in both terrestrial and marine environments demonstrate resistance to invasive producers through competition increases with native producer diversity; however, the diversity effect is weaker in marine systems (Levine et al. 2004, Kimbro et al. 2013).

Freshwater, marine, and terrestrial ecosystems differ in many ways including physical structure, stoichiometry, disturbance regimes, the strength of trophic interactions, and the traits and life-histories characterizing their producer and consumer communities (Shurin et al. 2006). Understanding the differences in these factors among ecosystems should help us to predict where and under what conditions biotic resistance to invasions will be strongest. The strength of biotic resistance is primarily determined by competition and consumption (herbivory or predation), which are influenced by a number of factors (including disturbance and environmental heterogeneity). In Table 1 and the following pages we outline the theoretical reasons why we may expect the strength of biotic resistance to vary among ecosystems.

Several factors suggest that competitive resistance to invasions may be weaker in aquatic than terrestrial systems. These factors include differences in diversity, community saturation and dietary specialization. Darwin (1859) argued that freshwater communities are more invasible because they have lower diversity than their terrestrial counterparts. Comparing diversity across ecosystems and trophic levels is difficult. The relative diversity of aquatic and terrestrial organisms will likely vary depending on location and taxa. Some indirect evidence, however, suggests that diversity is often higher in terrestrial than aquatic systems. For example, the most speciose plant and animal phyla are primarily terrestrial (Shurin et al. 2006). Aquatic macrophytes represent 0.5% of all bryophytes, 1–2% of all ferns and

fern allies, and <1% of all angiosperm species (Chambers et al. 2008). In contrast fish represent roughly 51% of all vertebrate species, and nearly half of this diversity occurs in the 1% of the earth's surface that is freshwater habitat (Lévêque et al. 2008). Species density (relative richness per unit of habitat volume), however, appears to be lower in marine than freshwater or terrestrial systems (Dawson 2012). Resistance to species introductions is thought to be an indication of community saturation and the importance of local ecological constraints, including competition, in determining community composition. Increases in species richness following invasion events suggest both that freshwater fish communities are not saturated with species, and that aquatic ecosystems may have limited biotic resistance (Moyle and Light 1996, Irz et al. 2004, Smith and Shurin 2006). Finally, differences in feeding by aquatic and terrestrial organisms suggest aquatic predators are more generalist and opportunistic, perhaps relaxing the strength of competition in these environments (Liem 1990, Shurin et al. 2006). However, omnivory appears to be most common in marine systems and rarest in streams (Thompson et al. 2007).

In contrast to competitive resistance, many differences between aquatic and terrestrial systems suggest that consumptive resistance, including herbivory and predation, may be strongest in aquatic communities. Aquatic herbivores remove significantly more annual primary production than terrestrial herbivores, and top-down control of producer biomass is believed to be stronger in aquatic than terrestrial systems (Cyr and Pace 1993, Shurin et al. 2002). Additionally, because many aquatic herbivores are generalists and terrestrial herbivores are specialists, introduced producers in aquatic environments are less likely to benefit from enemy release than their terrestrial counterparts (Shurin et al. 2006, González et al. 2010). In both lakes and streams, there is more evidence of predation than competition structuring fish communities (Jackson et al. 2001). Also,

spatially confined consumers appear to exert stronger top-down effects than those in less confined systems, where encounters are spread over dispersed prey populations (McCann et al. 2005). Predation, and thus consumptive resistance, may therefore be stronger in lakes than less confined marine systems or terrestrial environments (Shurin et al. 2006). Accordingly, meta-analysis has shown predation to be strongest in lentic and marine benthos and weakest in marine plankton and terrestrial systems (Shurin et al. 2002). This also suggests that the differences in consumptive biotic resistance among aquatic environments may be as great as those between aquatic and terrestrial environments.

In contrast to the expectation that consumptive resistance is stronger in aquatic systems, meta-analysis has shown that native consumers appear to resist producer invasions equally in terrestrial and marine ecosystems (Kimbro et al. 2013). Consumptive resistance may be weaker in freshwater systems than in terrestrial or marine systems because many isolated aquatic communities (including those from lakes and ponds) have evolved naively in the absence of large predators, leaving them particularly vulnerable to the effects of introduced predators (Cox and Lima 2006). Similar naïveté is thought to contribute to the impact of zebra mussels in North American communities, which had no evolutionary experience with fouling bivalves (Ricciardi and Atkinson 2004).

There are several factors that we might expect to influence the strength of biotic resistance among freshwater studies. Interacting abiotic and biotic factors can influence the strength of the species interactions that underlie biotic resistance both across ecosystems and within experiments. Kimbro et al. (2013) demonstrated that marine biotic resistance is related to latitude and habitat type. Latitude is known to influence diversity patterns and species interactions for many taxa and across habitat types, including freshwater systems (Schemske et al. 2009, Freestone and Osman 2011, Heino 2011, Kimbro et al. 2013). Within freshwater ecosystems, lotic, lentic and reservoir habitats differ in resource availability, disturbance regimes, and community composition (Palmer et al. 1996, Irz et al. 2006, Hof et al. 2008, Johnson et al. 2008), which could have considerable impacts on biotic resistance. Experimental design and duration are also known to have significant effects on the measured strength of species interactions and likely affect the strength of biotic resistance. Gurevitch et al. (1992) found greater variability in the results of studies run for shorter durations. They also demonstrated that experiments performed in enclosures reported greater competitive effects than those that were open. Additionally, the strength of competition, predation, and biotic resistance may vary among variables reflecting species establishment (e.g., survival) and performance (e.g., growth or fecundity) (Gurevitch et al. 2000, Levine et al. 2004).

Here we investigate the generality of biotic resistance by examining experimental evidence of the impacts of native species on the success of invasive species. Biotic resistance has been quantitatively reviewed in meta-analyses of both terrestrial (Levine et al. 2004, Parker et al. 2006) and marine (coastal) environments (Kimbro et al. 2013). We compare biotic resistance to invasion across freshwater, marine, and terrestrial ecosystems and among freshwater studies. Many of the most conspicuous and well-known examples of biological invasions are from freshwater systems; these include *Dreissena polymorpha* (zebra mussel) in North American rivers and lakes, *Lates niloticus* (Nile perch) in Lake Victoria, and *Eichornia crassipes* (water hyacinth) throughout the tropics and subtropics (Gopal 1987, Ricciardi and MacIsaac 2011). It has been argued that invasive species in lakes and rivers have transformed freshwater communities to a greater extent than their terrestrial counterparts (Ricciardi and Rasmussen 1999, Cox and Lima 2006). The effects of exotic invasive species in freshwater environments are often magnified by other anthropogenic factors including habitat degradation, pollution, flow modification, and overexploitation (Dudgeon et al. 2006, Strayer and Dudgeon 2010, Carpenter et al. 2011). Despite the conspicuous nature of and threats imposed by invasions in freshwater systems, most studies of invasive establishment generally, and biotic resistance specifically, have been in terrestrial, rather than aquatic, systems (Puth and Post 2005, Ricciardi and MacIsaac 2011). We use meta-analysis to address (1) whether competition or consumption is more important to resistance; (2) whether there is evidence that biotic resistance is weaker in freshwater than marine or terrestrial ecosystems; and (3) what factors affect the strength of biotic resistance among freshwater studies.

METHODS

Freshwater data sources

Publications included in our freshwater meta-analysis were selected using criteria from the marine (Kimbro et al. 2013) and terrestrial (Levine et al. 2004) meta-analyses. These were: (1) the focal organism was not native to the study system; (2) the majority of the species in the community influenced by the invaders success were native; (3) the effect of the native community on the invading species was measured in a manipulative experiment with a "control" treatment (invasive exposed to native community or confined with native species) and a "protected" treatment; (4) treatments were replicated and an assessment of the variance of treatment means was possible; and (5) the experiment was run in situ. The experimental manipulation could have been performed using enclosures, exclosures, removals, or communities assembled in the laboratory and later deployed in the field. Like Kimbro et al. (2013), we included studies of invaders at any stage, whereas terrestrial studies focused on the earliest life

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stages (Levine et al. 2004). Many studies of potential freshwater biotic resistance could not be included in our meta-analysis because they were performed in greenhouses, laboratories, or mesocosms rather than in situ (e.g., Bailey et al. 2006, Doyle et al. 2007, Zukowski and Walker 2009, Carey and Wahl 2010, Njambuya and Triest 2010).

We searched *Google Scholar*, the *Web of Science*, and *PROQUEST* for publications and dissertations fitting the above described criteria by using key words (e.g., freshwater, invasion, producer, consumer, experiment, resistance, invasibility, predation, herbivory, competition, and the names of known freshwater invasives), and examining both references cited within and publications citing relevant material. By this method, we identified 48 unique studies (Appendix A: Table A1) which quantified the impacts of native biodiversity on 24 invasive freshwater species. Most invasive species were studied in fewer than three publications; however, biotic resistance to *D. polymorpha* was measured in 12 publications. Studies used a variety of measures, potentially representing different stages of invasion, to examine invasive success. We grouped these into measures of "establishment" and "performance" (as in Levine et al. 2004). A measure of establishment (e.g., survival, density, mortality) was used to measure the effect of biotic resistance in 33 of these studies. A measure of performance (i.e., biomass, condition, growth in area, length, or mass) was measured in 23 studies. Ten studies investigated biotic resistance to primary producers and 38 studies investigated biotic resistance to consumers. Eighteen studies investigated competitive biotic resistance, 31 investigated consumptive biotic resistance, and one study (Irfanullah and Moss 2004) investigated both competitive and consumptive biotic resistance in separate experiments (which remained separate throughout our analysis). There were, however, no freshwater studies that tested the effects of combined competitive and consumptive biotic resistance explicitly (as in Kimbro et al. 2013). In some cases native consumer exclosures led to increased density of potential competitors (e.g., Palmer and Ricciardi 2005, Parker et al. 2007), but the competitive effect was not explicitly measured.

We used DataThief software (Tummers 2006) to extract mean response and error measurements across control and protected treatments from each study. These data, along with sample sizes, were used to calculate effect sizes for each experiment. We also collected taxonomic, habitat, experimental location, design, and duration data from each study. Where latitude was not provided, the center of each study was estimated to the nearest decimal degree in Google Earth using site descriptions and maps. Where more than one response variable was examined in the same experiment, the most commonly presented measure (establishment) was used in our analysis (as in Parker et al. 2006). Where manipulations of competition or consumption were

crossed with additional factors (e.g., density or environmental factors [Stewart et al. 1999, Johnson and Havel 2001, Jokela 2006, Riley et al. 2008]), we used those treatments which most closely matched ambient conditions (as in Levine et al. 2004). In enclosed competition experiments with multiple density treatments (Marks et al. 2011), we used the interspecific (native and invasive) treatment density that matched the density of the intraspecific (invasive only) treatment. Treatments manipulating environmental or biotic conditions that spanned the natural variation at different locations (e.g., conductivity substrates or rates of parasitism [Thorp et al. 1998, MacNeil 2003*a, b, c*, Bowers and de Szalay 2007, Kestrup and Ricciardi 2009, Peters and Lodge 2013]) were treated as separate experiments, and multiple effect sizes were calculated. Studies repeated in multiple seasons or years with variation in environmental conditions between years were treated as separate experiments (Dickinson and Miller 1998, Johnson and Havel 2001, Irfanullah and Moss 2004, Jokela 2006, Hidding et al. 2009, Kestrup and Ricciardi 2009). Similarly, studies replicated at multiple sites (more than a few kilometers apart) were treated as separate experiments (Hamilton et al. 1994, Sheldon and Creed, Jr. 1995, Thorp et al. 1998, Riley et al. 2008, Kestrup and Ricciardi 2009, Bajer et al. 2012, Cabrera-Guzmán et al. 2013). For studies replicated at multiple depths at the same location (Jokela 2006, Nakano et al. 2010), effect sizes were averaged across depths. Effects measured on multiple size classes of the invader were also averaged. When effects were measured several times over the period of the experiment, we used the last measurement (Traxler and Murphy 1995). Where the same invasive species was exposed to different native species or groups of species (Kupferberg 1997, Carlsson et al. 2004), these were considered separate experiments (as in Levine et al. 2004).

Several studies measured the effects of small, medium, and large native species using various sized meshes to protect invasive species from consumption by the native community (Irfanullah and Moss 2004, Bowers et al. 2005, Bowers and de Szalay 2007, Hidding et al. 2009, Nakano et al. 2010, Bajer et al. 2012). In these cases, we only included the effect of the entire native community (protected by the finest mesh vs. exposed to all potential consumers). Overall, we calculated effect sizes for 77 experiments testing the effect of freshwater biotic resistance within 48 studies (Appendix A: Table A1).

Terrestrial and marine data sources

For comparison with freshwater data, we extracted mean effect size and 95% confidence interval (CI) of biotic resistance in terrestrial and marine environments from Kimbro et al. (2013: Figs. 1 and 2) using DataThief software (Tummers 2006). Effect sizes were extracted for competitive and consumptive biotic resistance to invasive producers and consumers separately. Kimbro et al. (2013) compared marine effect sizes to a subset of
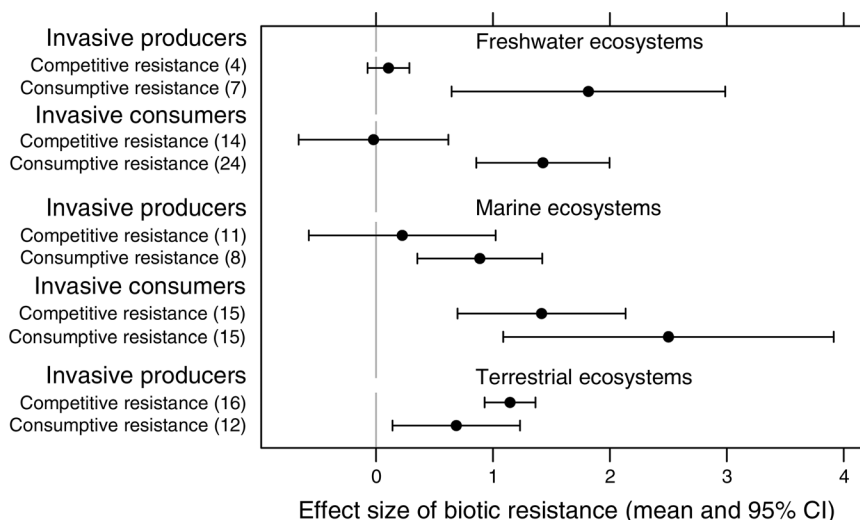
FIG. 1. The mean (and 95% CI) strength of competitive and consumptive resistance toward invasive producers and consumers in freshwater, marine and terrestrial systems. Marine results are from Kimbro et al. (2013). Terrestrial results are from Levine et al. (2004). Values in parentheses indicate number of studies in each group.

terrestrial effect sizes from meta-analyses published by Levine et al. (2004) and Parker et al. (2006). These meta-analyses used two different effect size calculations, the *d-statistic* (used in Levine et al. 2004 and described in *Calculation of effect sizes*) and the *unweighted log-response ratio* (used in Parker et al. 2006). For our analysis, we chose to exclude response ratio effect sizes because they did not incorporate sample sizes or error
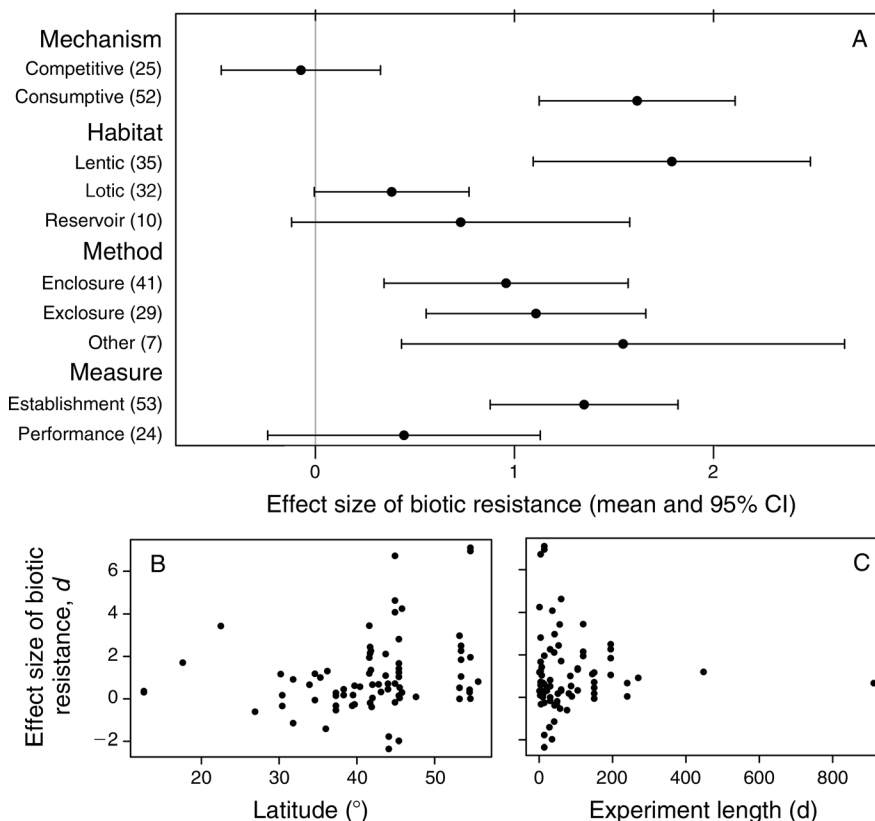

FIG. 2. The mean (and 95% CI) strength of biotic resistance toward invasive species in freshwater environments by (A) resistance mechanism, habitat type, experimental design and measure of effect, (B) location (latitude), and (C) experiment duration (days). Values in parentheses indicate number of experiments in each group.

measurements and because the effect size calculated by the *d-statistic* promoted more cross-system comparisons (as noted by Kimbro et al. 2013).

Kimbro et al. (2013) also presented a comparison of the effect of native diversity in competitive biotic resistance by calculating the *d-statistic* as a contrast of the means in the least and most diverse treatments, where invader performance was evaluated across a gradient of species diversity (effect sizes shown in Fig. 1). We found no freshwater studies where invaders performance was examined across a similar gradient, so this calculation was not included in our analysis.

Calculation of effect sizes

For comparisons across ecosystems and among freshwater studies we calculated effect size by the *d-statistic* (used in Levine et al. 2004, Kimbro et al. 2013). The *d-statistic* is calculated as

$$d = \left((\text{Mean}_P - \text{Mean}_C)/\text{SD}_{\text{pooled}} \right) \times J \qquad (1)$$

where the Mean_P is the mean of the protected treatment (i.e., invasive not exposed to competitive or consumptive effects from the native community) and Mean_C is the mean of the control treatment (i.e., invasive exposed to native community or confined with native species). The pooled standard deviation is calculated as

$$\text{SD}_{\text{pooled}} = \left[\left(\left((\text{SD}_P)^2 (n_P - 1) \right) + \left((\text{SD}_C)^2 (n_C - 1) \right) \right) \right.$$
$$\left. \Big/ \left((n_P + n_C) - 2) \right) \right]^{1/2} \qquad (2)$$

where SD_P and n_P are the standard deviation and sample size, respectively, of the protected treatment and SD_C and n_C are that of the control treatment. J in Eq. 1 differentially weights studies to correct for bias in sample size and is calculated as

$$J = 1 - \left[3 / \left(4 \times (n_C + n_P - 2) - 1 \right) \right]. \qquad (3)$$

All effects were standardized so that positive effects reflected biotic resistance, while negative effects reflected facilitation. This meant multiplying the *d-statistic* by -1 when the response variable was mortality (Hesselschwerdt et al. 2008, Gates 2012).

Data analysis

Our analysis had two parts: (1) a comparison of competitive and consumptive resistance to invasive producers and consumers across ecosystems, and (2) an examination of the factors affecting biotic resistance within freshwater studies (using a model-selection approach).

To test the significance of biotic resistance to invasions and compare the strength of biotic resistance among ecosystems, we calculated mean and 95% CIs for the effect sizes of various groups of invaders. Positive confidence intervals (not containing zero) were consid-

ered significant biotic resistance, and negative confidence intervals were considered facilitation of the invader (as in Kimbro et al. 2013). Additionally, if two groups had nonoverlapping confidence intervals, they were considered significantly different. By this method, we compared competitive and consumptive resistance to invasive producers in freshwater, marine, and terrestrial environments. Similarly, we compared competitive and consumptive resistance to invasive consumers in freshwater and marine environments. To our knowledge, resistance to invasive consumers in terrestrial systems has not been examined in meta-analysis. In all of these comparisons (presented in Fig. 1) the effect sizes for all experiments within a study were averaged before the mean and 95% CI for the group (e.g., the studies testing competitive biotic resistance to freshwater producers) were calculated. This allowed us to compare our results with the marine and terrestrial data from Kimbro et al. (2013), where confidence intervals were calculated in the same manner.

For the reasons outlined previously (see *Introduction*) we had an a priori expectation that several factors would influence the strength of biotic resistance in freshwater environments. We used a model-selection approach to examine the influence of six factors: resistance mechanism (competition or consumption), habitat type (lotic, lentic, or reservoir), response variable (establishment or performance measure), experimental design (enclosure, exclosure, or other), location (latitude), and experiment duration. Model selection involved fitting a series of linear mixed models: a null model with an intercept only, seven single-factor models, and all possible additive combinations of the seven fixed factors. Unfortunately, sample size prevented us from investigating the importance of interactions between factors. We included each of the 77 experimental effect sizes individually but assigned those from the same study a numeric identifier, which was treated as a random effect in order to prevent single studies with several experiments (multiple mean comparisons) from being over-represented in our models (as in Kimbro et al. 2013). Models were compared using Akaike's Information Criterion corrected for small sample sizes (AIC_c [Burnham and Anderson 2002]). For each model we calculated ΔAIC_c, the difference in AIC_c between each model and the best model (that with lowest AIC_c) and Akaike weight (w_i), which is the model likelihood normalized by the sum of all model likelihoods. As Akaike weight approaches 1, confidence in model selection increases (Johnson and Omland 2004). The best predictive model was generated as an average of the top (lowest AIC_c) models with a cumulative sum of $w_i s = 0.9$ (Johnson and Omland 2004). This model averaging allowed us to examine the effect of each factor on biotic resistance by comparing standardized coefficients estimates. We also compared the overall strength of biotic resistance across experiments for each categorical factor by calculating mean and 95% CIs for each level. We tested the overall relationship between biotic

resistance and continuous factors (latitude and experimental length) with simple linear regression.

All analyses were performed using R software (version 2.15.0; R Development Core Team 2012). Models were constructed using the lme4 package. Model-selection and model-averaging was performed using the MuMIn package.

Results

In freshwater ecosystems, the strength of biotic resistance to both producer and consumer invasions varied significantly by the resistance mechanism; consumptive resistance was stronger than competitive resistance (Fig. 1). We failed to find evidence of significant competitive resistance to invasive freshwater producers or consumers (95% CI includes zero). There was, however, significant consumptive resistance to both types of freshwater invaders (95% CI does not include zero). The mean strength of consumptive resistance to *D. polymorpha*, the most investigated invasive species, was not significantly different than that of other invasive freshwater consumers ($t = 1.095$, df = 22, $P = 0.285$).

In contrast to freshwater systems, there was no significant difference between competitive and consumptive resistance in marine or terrestrial ecosystems (Fig. 1). Additionally, there was significant evidence of competitive resistance to invasive consumers in marine ecosystems and to invasive producers in terrestrial ecosystems. Competitive resistance to invasive producers was significantly lower in freshwater than terrestrial ecosystems. Competitive resistance to invasive consumers was significantly lower in freshwater than marine ecosystems. In contrast, there were no significant differences in consumptive resistance among ecosystems (Fig. 1).

When we examined the factors affecting biotic resistance in freshwater habitats, all six factors (Appendix B: Table B1) were included in the nine models with the lowest AIC$_c$ (cumulative Akaike weights [w_i] = 0.90), which were averaged to produce our best model (Appendix B: Table B2). However, resistance mechanism (competitive or consumptive) and habitat type had the highest relative importance (Appendix B: Table B1) and were included in all of the top models (Appendix B: Table B2). Experimental method also had high relative importance and was included in most of the top models. Coefficients estimated by model averaging suggest that resistance mechanism, habitat type, and experimental method had the strongest effect on biotic resistance (Appendix B: Table B3). Model-averaged coefficients demonstrated that: (a) consumption increased resistance more than competition, (b) lentic habitat also increased resistance in comparison to lotic or reservoir habitat, and (c) enclosures increased resistance in comparison with exclosures. We repeated our model selection considering only consumptive effects (and excluding the relatively weaker competitive effects), and this did

not substantially change the relative importance or coefficient estimate of the other factors we investigated.

Mean comparisons showed that over all freshwater studies, consumptive biotic resistance was stronger than competitive biotic resistance (Fig. 2A). We found that mean consumptive resistance was greater than mean competitive resistance in all five phyla of freshwater invasives (Fig. 3); these differences were significant within Magnoliophyta and Arthropoda. Mean comparisons also demonstrated that there was significantly more biotic resistance to invasions in lentic than in lotic habitats (Fig. 2A). The strength of resistance in reservoirs was intermediate to these two habitats, but not significantly different from either. There were no significant overall differences in biotic resistance among experimental designs or performance measures (Fig. 2A). There was also no significant relationship between the effect size of biotic resistance and latitude or experimental length (Fig. 2B and C). Most experiments were performed between 40° and 50° latitude and lasted <100 days (Fig. 2B). Variation in effect size also appeared to decline with experiment length as illustrated by the "funnel" distribution in Fig. 2C.

Discussion

Our meta-analysis shows that in freshwater ecosystems, consumptive resistance appears to be significantly stronger than competitive resistance, and this difference is not apparent in marine or terrestrial ecosystems. Given the impacts of invasive species in freshwater systems, relatively few studies have investigated biotic resistance in freshwater environments, particularly to invasive producers. Consumptive biotic resistance, however, appears to limit the success of freshwater invaders as effectively as it does marine and terrestrial invaders. Finally, the strength of biotic resistance varies significantly between lotic and lentic habitats. However, the mechanisms underlying this difference and the influence of additional environmental or experimental factors on freshwater biotic resistance require further testing.

Competitive resistance in freshwater ecosystems was relatively weak both in contrast to marine and terrestrial ecosystems and in contrast to consumptive resistance in freshwater ecosystems. The difference between competitive and consumptive resistance in freshwater habitats matches well with the observation that there is more evidence of predation than competition structuring fish communities (Jackson et al. 1992, 2001). It also appears that consumptive resistance may be stronger than competitive resistance across a range of invasive freshwater taxa including producers and consumers. Because consumptive resistance does not significantly differ among ecosystems, it appears that the difference between competitive and consumptive resistance within freshwater ecosystems is due to the weakness of competition in these communities rather than the strength of consumption. Importantly, Gu-
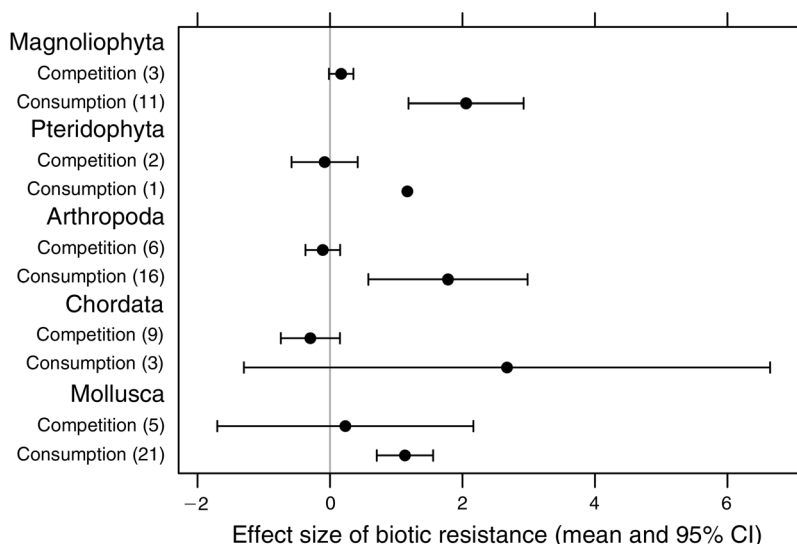
FIG. 3. The mean (and 95% CI) strength of biotic resistance toward invasive species in freshwater environments separated by phyla and resistance mechanism. Values in parentheses indicate number of experiments in each group.

revitch et al. (2000) found that there was a significant interaction between competition and predation; we could not address the influence of this interaction on biotic resistance because of the lack of freshwater studies that tested both effects. Consumptive resistance to invasive freshwater producers was congruent with the strong influence of herbivores in these systems (Cyr and Pace 1993, Shurin et al. 2002). There was also significant consumptive resistance to invasive freshwater consumers despite the perceived naïveté of these native communities (Ricciardi and Atkinson 2004, Cox and Lima 2006).

In accordance with Darwin's (1859) prediction that invaders would more easily establish in less competitive freshwater communities, competitive resistance to invasive producers was stronger in terrestrial than in freshwater studies. Lower competitive resistance in freshwater ecosystems may be a consequence of lower diversity or the lack of saturation in freshwater communities (Irz et al. 2004, Shurin et al. 2006, Smith and Shurin 2006). However, we only examined four studies of competitive resistance to invasive freshwater producers and none explicitly addressed diversity or saturation (despite a concerted effort to identify more studies of biotic resistance to aquatic invasive producers for this study). Kimbro et al. (2013) suggested that invasive producers may also face less resistance in marine than terrestrial environments because marine communities are less saturated. However, we did not find significant differences in competitive resistance to invasive producers between marine and terrestrial or between marine and freshwater communities (with 95% CIs).

We found that competitive resistance to invasive consumers was significantly stronger in marine than freshwater environments. This conflicts with the idea that competition may be most relaxed amongst marine consumers due to the prevalence of omnivory in marine communities (Thompson et al. 2007). In many freshwater studies, particularly with vertebrate invaders, competition appeared to facilitate invasion rather than hinder it (for five of seven studies of competitive resistance to vertebrate invaders effect size, d, was less than zero). Frequently, these experiments measured the effect of interspecific competition (between native and invasive species) in contrast to intraspecific competition (between individual invaders), while keeping the density of individuals in the two treatments constant. The lack of competitive biotic resistance to freshwater consumers, therefore, may be related to weaker interspecific competition than intraspecific competition. Niche or stabilizing processes, which cause invasive species to limit themselves more than their competitors, are thought to favor coexistence and limit the impacts of invasive species (Chesson 2000, MacDougall et al. 2009). Competitive biotic resistance may also be moderated by native species density (Smith et al. 2004, Alofs and Fowler 2013) and invasive propagule pressure (Von Holle and Simberloff 2005, Miller et al. 2014); however, we focused on effects measured at ambient density where possible (see *Methods*).

After resistance mechanism, habitat type appeared to have the strongest influence on the strength of biotic resistance in freshwater environments. Lentic communities had significantly greater biotic resistance than their lotic counterparts. There is some evidence that species interactions are stronger in lentic than in lotic habitats. For example, Shurin et al. (2002) showed that benthic predators in lentic habitats had a significantly stronger effect on herbivores than those in lotic habitats.

Disturbance is thought to increase the strength of regional processes (e.g., dispersal) relative to local species interactions (including competition and consumption) in determining community composition (Harrison and Cornell 2008). Accordingly, introduced species would be less likely to establish in lentic communities than lotic communities, which are more frequently disturbed by unpredictable flood and drought conditions (Resh et al. 1988, Palmer et al. 1996). Testing the strength of biotic resistance along a disturbance gradient within one habitat type would help to disentangle the impact of disturbance from other differences that occur between freshwater habitats (including productivity and microhabitat structure).

We found that the mean effect size of biotic resistance in reservoir habitats was about half that in lentic habitats, but the two were not significantly different by 95% CIs. Coefficients estimated by model averaging, however, suggest that reservoirs are less resistant than lentic habitat. Reservoirs have been considered as intermediate to lotic and lentic habitats in terms of morphology, hydrology, nutrient supply, and community composition (Irz et al. 2006). In contrast, Johnson et al. (2008) suggested that the relatively recent assembly of reservoir communities following impoundment may weaken biotic resistance in these habitats and make them more prone to invasions.

Model averaging also suggested that experimental method may influence the measured effect of biotic resistance; specifically, that biotic resistance appears stronger when enclosures are used instead of exclosures. Gurevitch et al. (1992) found experiments performed in enclosures often report greater competitive effects. The difference between enclosure and exclosures, we found, however, appears to be driven by consumptive rather than competitive biotic resistance experiments (only one experiment measured competition in exclosures and competitive resistance in enclosures was relatively weak; see *Results*).

Several factors that we expected to influence biotic resistance in freshwater environments were not significant. Kimbro et al. (2013) showed that the strength of biotic resistance to invasions in marine environments declines with latitude, as may be expected if diversity also declines with latitude. Latitudinal gradients in diversity have been demonstrated for some freshwater species and habitats (e.g., fish and lotic habitats) but not others (e.g., stoneflies and lentic habitat [Hof et al. 2008, Heino 2011]). We found no significant relationship between latitude and the strength of biotic resistance in freshwater environments. The freshwater studies we analyzed spanned a greater range of latitude than the marine studies in the analysis by Kimbro et al. (2013); however, the studies included in our analysis did not evenly sample a large range of latitudes. Biotic resistance was also not significantly related to experiment duration, but there was greater variability in effect sizes in shorter experiments (funnel shape; Kimbro et al. 2013:

Fig. 4f). This could reflect that shorter studies are less reliable indicators of the true effect of biotic resistance, or that biotic resistance weakens over time or across seasonal variation. Alternatively, the greater number of short-duration experiments could include more variable taxa, environmental conditions, and species interactions (Gurevitch et al. 1992).

For native species, meta-analysis has shown that removing competitors has more positive effects on an organism's performance (growth and mass measures) than removing predators (consumers), while removing predators improved survival more than removing competitors (Gurevitch et al. 2000). Similarly, Levine et al. (2004) demonstrated that herbivory produces stronger biotic resistance to invasive establishment (primarily germination and early survivorship) than competition, but the same was not true for resistance measured by invader performance. In our meta-analysis, more studies examined establishment than performance, which may have influenced the observed strength of competitive effects; however, we found no significant difference in effect sizes compared between measures.

Our meta-analysis demonstrates the relative effect of biotic resistance both across ecosystems and within freshwater habitats. We feel that further understanding the generality of this concept and the mechanisms underlying biotic resistance will require (1) performing more in-situ experimental studies, particularly over longer time scales and in the tropics; (2) performing more aquatic studies of invasive producers and terrestrial studies of invasive consumers; (3) examining competitive and consumptive resistance in the same experiments and investigating their interactions; (4) testing resistance across gradients of freshwater diversity, particularly functional diversity (which is known to influence resistance to both terrestrial and marine invasions [Britton-Simmons 2006, Funk et al. 2008]); and (5) testing resistance along disturbance gradients. Additionally, it has been shown in terrestrial systems that propagule pressure can overwhelm biotic resistance and should be controlled for when trying to understand resistance to invasions (Von Holle and Simberloff 2005, Miller et al. 2014). To understand the overall importance of biotic resistance in freshwater systems it will be important to investigate the relative effects of propagule pressure and biotic resistance in different habitats and across taxa.

The strength of biotic resistance that we found in relatively few freshwater studies suggests that this is a promising avenue of research. Understanding the mechanisms of biotic resistance will be important for predicting how environmental changes that impact local diversity may make communities more vulnerable to future invasions. In contrast to terrestrial systems, evidence in aquatic ecosystems suggests that climate change is likely to favor nonnative species over native species (Sorte et al. 2013). Finally, biotic resistance has been proposed as an important component of effective

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terrestrial restoration (Funk et al. 2008). Our review suggests that biotic resistance could play an equally important role in aquatic restoration and conservation. However, more basic research is needed to understand the factors controlling biotic resistance in freshwater environments.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-0060.1.sm