REVIEW AND SYNTHESIS

Biotic resistance in marine environments

David L. Kimbro,[1,2]* Brian S. Cheng[3,4] and Edwin D. Grosholz[3,4]

Abstract

Biological invasions depend in part on the resistance of native communities. Meta-analyses of terrestrial experiments demonstrate that native primary producers and herbivores generally resist invasions of primary producers, and that resistance through competition strengthens with native producer diversity. To test the generality of these findings, we conducted a meta-analysis of marine experiments. We found that native marine producers generally failed to resist producer invasions through competition unless the native community was diverse, and this diversity effect was weaker in marine than in terrestrial systems. In contrast, native consumers equally resisted invasive producers in both ecosystems. Most marine experiments, however, tested invasive consumers and these invasions were resisted more strongly than were producer invasions. Given these differences between ecosystems and between marine trophic levels, we used a model-selection approach to assess if factors other than the resistance mechanism (i.e. competition vs. consumption) are more important for predicting marine biotic resistance. These results suggest that understanding marine biotic resistance depends on latitude, habitat and invader taxon, in addition to distinguishing between competition with and consumption by native species. By examining biotic resistance within and across ecosystems, our work provides a more complete understanding of the factors that underlie biological invasions.

Keywords

Biodiversity, biological invasion, competition, consumption, enemy-release hypothesis, evolution of increased competitive ability hypothesis, exotic species, invasion paradox, invasional meltdown, meta-analysis.

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INTRODUCTION

Anthropogenic activities are homogenising the globe's biota by transporting species beyond their historical ranges (Cohen & Carlton 1998; Mooney & Cleland 2001; Sax & Gaines 2008). Although the net consequence of this homogenisation is under debate (Sax & Gaines 2003; Vellend *et al.* 2007; Simberloff *et al.* 2012), scientists agree about the need to identify and understand the factors that limit the establishment and subsequent spread of invasive species. Whether an invasive species provides valuable services to humans in the form of food (e.g. corn, wheat and livestock; Sax *et al.* 2007) or is destructive (e.g. brown tree snake and zebra mussel; Pimentel *et al.* 2001; Wiles *et al.* 2003), knowledge about how invaders succeed is necessary to sustain ecosystem functions and services.

Among the first explanations of invasion success was that native communities contain varying abilities to prevent invasions and thus have differing levels of 'Biotic Resistance' (Elton 1958). Meanwhile, invasion success has also been addressed by other explanations such as the hypotheses of 'Enemy Release', 'Novel Weapons', 'Evolution of Increased Competitive Ability' and 'Invasional Meltdown' (Blossey & Notzold 1995; Simberloff & Von Holle 1999; Keane & Crawley 2002; Callaway & Ridenour 2004). Although these different

hypotheses involve a variety of ecological mechanisms, they all depend to some degree on the native community either resisting or failing to resist an invader. Therefore, understanding what underlies the patterns and causes of biotic resistance is fundamental to a general understanding of invasion.

Ecologists have experimentally tested biotic resistance in a variety of systems over the last quarter century (e.g. Rice 1987; Stachowicz *et al.* 1999; Levine 2000; Grosholz 2010), providing sufficient data for a synthetic approach to the question of how native communities resist invasions. We focus on experiments that address how native communities affect the success of established invaders, rather than how they influence invader establishment or how the invaders impact native communities (Levine *et al.* 2004). In most cases, particularly those involving unintentional introductions, we lack data about failed invasions and consequently cannot determine the mechanisms that underlie these failures. Nevertheless, meta-analyses of experiments on established invasions have clearly promoted our understanding of why invaders proliferate or decline, as well as the circumstances under which this outcome is influenced by resistance from native communities (Levine *et al.* 2004; Parker *et al.* 2006).

A meta-analysis of terrestrial plant experiments revealed that invasion success was typically hindered by native competitors and herbi-

[1]*Marine Science Center, Northeastern University, Nahant, MA 01908, USA*

[2]*Florida State University Coastal and Marine Laboratory, St. Teresa, FL 32358, USA*

[3]*Department of Environmental Science and Policy, University of California at Davis, Davis, CA 95616, USA*

[4]*Bodega Marine Laboratory, University of California at Davis, Bodega, CA 94923, USA*

Correspondence: E-mail: d.kimbro@neu.edu

vores, but not by native soil microorganisms (Levine *et al.* 2004). Moreover, resistance through competition increased with native plant diversity (Levine *et al.* 2004). Of course, this meta-analysis did not address the utility of equating species interactions such as consumption and competition to biotic resistance, since they negatively affect native and invasive species alike. However, a subsequent meta-analysis demonstrated that native herbivores generally reduced the fitness of invasive plants more than native plants (Parker *et al.* 2006). Thus, it is not only reasonable to equate negative species interactions with biotic resistance but it is also clear that native communities rely on multiple types of interactions for biotic resistance.

It is important to recognise that these conclusions are based solely on experiments about terrestrial plants and therefore may not apply across ecosystems. In particular, intrinsic differences between terrestrial and aquatic systems suggest that the strength and mechanism of biotic resistance may differ. For example, native primary producers (hereafter, producers) differ considerably among systems in traits such as growth rate, size and nutritional quality (Cyr & Pace 1993; Cebrian 1999; Shurin *et al.* 2002, 2006; Cebrian & Lartigue 2004). As a result, native producers are more strongly affected by consumption in aquatic than in terrestrial systems (Cyr & Pace 1993; Shurin *et al.* 2002, 2006; Cebrian & Lartigue 2004). If this variation in traits also applies to invasive producers, then biotic resistance from native consumers may be stronger in aquatic communities. In contrast, the strength of competition among native producers is similar on land and in water (Gurevitch *et al.* 1992). If the same pattern applies to competition between native and invasive producers, then biotic resistance from native competitors should also be similar among systems. Taken together, consumption may be relatively more important for biotic resistance in aquatic systems. This expectation contrasts the results from Levine *et al.* (2004) of consumption and competition contributing equally to biotic resistance in terrestrial communities.

Given this potential for ecosystem differences in biotic resistance and the high prevalence of invasion in coastal and estuarine systems (hereafter, marine; Cohen & Carlton 1998), we conducted a formal synthesis of marine invasion experiments. In our synthesis, we developed the marine database with the same data extraction and analytical methods used in each terrestrial meta-analysis to allow direct comparison of results (Levine *et al.* 2004; Parker *et al.* 2006). More specifically, our first objective was to evaluate whether competition, herbivory, and diversity from native species affect demographic variables related to the biotic resistance of invasive producers, and whether the strengths of these mechanisms differ between marine and terrestrial systems. However, 60% of the marine experiments focused on invasions of invertebrate consumers, and competition (Gurevitch *et al.* 1992) as well as consumption (Shurin *et al.* 2002) can differentially influence producers vs. consumers. As a result, the second objective of our study was to compare whether these resistance mechanisms (competition vs. consumption) differ between marine trophic levels.

To improve our understanding of the ecological processes that influence biotic resistance, we broadened our study to include a third objective. This objective used a model-selection approach to examine whether several factors in addition to resistance mechanism influence marine invasions. For organisational purposes, we introduce each of these factors under one of three categories: (1) geographic location, (2) temporal dynamics and (3) characteristics of the invader. Within geographic location, we focused on latitude because biodiversity changes with latitude and native biodiversity can increase resistance to invasion (Stachowicz *et al.* 1999). Moreover, species interactions that promote biotic resistance change in strength with latitude (Schemske *et al.* 2009; Freestone *et al.* 2011). We also examined habitat type, because invasion experiments were conducted in a diversity of habitats that have been shown to support different species interactions (Connell 1961; Paine 1966; Bertness & Ellison 1987; Peterson 1991).

For the category of temporal dynamics, we anticipated that experimental duration would be important, because the services provided by native species diversity that can help resist invasion tend to accrue over time (Tilman & Downing 1994; Stachowicz *et al.* 2007). We also examined the importance of experimental date relative to the date of initial invasion, because variation in the success of established invasions can include prolonged time lags. Invader populations may either grow exponentially from the beginning or there may be a time lag prior to exponential growth in which the population grows slowly for some period of time (Crooks 2005). These lags may depend on the time required for invader adaptation to native environments (Grosholz & Ruiz 2003; Holt *et al.* 2005), for native community adaptation to the invader (Carroll *et al.* 2005), and/or for environmental changes in the invaded habitat (Crooks 2005).

With respect to invader characteristics, we investigated whether the demographic variable of the invader measured in an experiment influenced the strength of biotic resistance. Existing evidence suggests that biotic resistance primarily influences the success of established invasions rather than establishment of invaders (Levine *et al.* 2004), and population biology suggests that a native community can exert such resistance by differentially impacting the recruitment, growth and survivorship of the invader. If one of these fitness components is more susceptible to native species interactions, then experimental outcomes will depend on which demographic variable is studied. Another important distinction concerns whether the taxonomic breadth of marine invaders addressed in the literature lack phylogenetic independence (Chamberlain *et al.* 2012). Invasion success may vary among taxonomic groups or trophic levels, so we tested whether biotic resistance depends on the invader's trophic level (e.g. producer vs. consumer) or on a higher taxonomic identity such as phylum.

In summary, the primary objectives of our study were to: (1) assess whether the strength of biotic resistance differs between marine and terrestrial systems and whether differences depend on the type of resistance mechanism (e.g. competition vs. consumption), (2) quantify whether the strength of each resistance mechanism depends on the trophic level of the marine invader, and (3) determine whether additional factors from experiments (i.e. geographic location, temporal dynamics, and invader characteristics) improve our understanding of marine biotic resistance.

METHODS

Data sources

Terrestrial meta-analyses
To assess how native communities generally affect the success of invasive species, we initially concentrated on two published meta-analyses. The first publication synthesised terrestrial experiments

that tested how native communities influence the establishment and performance (i.e. success) of invasive producers (Levine *et al.* 2004). Because the marine experiments of interest for our review concerned invader performance, we focused on the performance results of Levine *et al.* (2004).

The other published meta-analysis addressed a broader collection of experiments that tested whether the effects of native and invasive herbivores depend on the producer being native or invasive (Parker *et al.* 2006). A majority of these data (57%) were incompatible with our objectives, because they originated from experiments with invasive herbivores or from those with native herbivores that affected the relative abundance of native and invasive producers in multi-species assemblages (see Table S1 of Parker *et al.* 2006). Of the remaining data, most were compatible with our goals because they tested how native herbivores affect the individual performance of a terrestrial plant invader (35 experiments), of an aquatic plant invader (1 experiment), and of a native coastal plant re-colonising a salt marsh [1 experiment; see Table S2 in Parker *et al.* (2006)]. By excluding the latter two experiments, we obtained a second assessment of how native terrestrial communities affect invasive producers.

Marine meta-analysis

To test whether trends of terrestrial biotic resistance can be generalised to marine systems, we first needed to conduct a meta-analysis of published marine experiments. For a marine publication to be included in this analysis, it had to satisfy five conditions that were established by the terrestrial meta-analyses: (1) the focal organism was non-native to the system in question, (2) the assemblage of organisms that potentially influenced the invader's success was numerically dominated by native species, (3) the data concerned a manipulative experiment with both a 'control' treatment (i.e. invader exposed to the native community) and an 'exclosure' treatment (i.e. invader protected from the native community), (4) treatments were replicated so as to allow an assessment of variance of treatment means and (5) the experiment must have occurred in the natural environment rather than in the laboratory or in outdoor mesocosms. To accommodate all appropriate studies, we modified the third condition and included studies that used 'enclosure' treatments (i.e. invader confined with a native consumer or competitor) in place of 'control' treatments.

Although these requirements resembled those of the terrestrial reviews, they also differed in some important ways. For example, because of the logistical difficulties associated with larval manipulations in the field, we did not require that marine experiments begin with a focal invader at the earliest life stage (see Levine *et al.* 2004). In addition, given the physiological inability of marine organisms to remain out of water for extended time periods and given the time required to assemble experimental native communities, we included studies in which researchers assembled treatments in the laboratory before they were deployed in the field (see Levine *et al.* 2004). Finally, because the majority of native herbivores in the review by Parker *et al.* (2006) were large vertebrates that could not be enclosed in realistically sized experimental areas, their meta-analysis excluded studies that enclosed native herbivores. In contrast, we relaxed this constraint for marine experiments because the abundance of enclosed native consumers generally reflected natural abundances per unit area.

After establishing these general criteria, we searched the *Web of Science* for potential publications by using keywords and examining references within. This search identified 42 acceptable publications (Table 1). Collectively, these marine experiments addressed the success of 26 invasive species.

Data extraction

Terrestrial meta-analyses

We used GraphClick software (version 3.0) to extract the mean effect sizes (95% CI) of biotic resistance illustrated in Fig. 2b of Levine *et al.* (2004). Because the effect sizes of interest were not illustrated in Parker *et al.* (2006), we accessed this publication's raw data [see Table S2 in Parker *et al.* (2006)] and re-calculated the appropriate effect sizes. As described below, these meta-analyses used different effect size calculations. As a result, we compared our marine results to each of the terrestrial syntheses but did not compare the terrestrial syntheses to each other. Each effect size was assigned to one of three categories of biotic resistance (BR): competition (hereafter, competitive-BR), herbivory (hereafter, consumptive-BR) and competition from biologically diverse native communities (hereafter, diversity-BR). These categories represent the mechanisms by which native communities can limit the success of invasive producers. All assignments were based on those used by Levine *et al.* (2004) and Parker *et al.* (2006).

Marine meta-analysis

From each suitable publication, we extracted two types of data. The first extraction facilitated comparisons between ecosystems and between marine trophic levels. For the ecosystem comparisons, we located the appropriate figure in a marine publication and used GraphClick software to measure the mean (SE) response of the invasive producer across all experimental treatments. The replication within each experiment was obtained from the text of the publication. These data were then assigned to one of the three resistance mechanisms. To compare results between marine trophic levels, we extracted the same information from marine publications with invasive consumers. When appropriate, we also assigned the data about invasive producers and consumers to a fourth mechanism, combined competitive-BR and consumptive-BR (hereafter, combined-BR). This assignment required data to originate from an experiment with orthogonal treatment combinations of (1) an invader protected from the native community, (2) an invader exposed to native competitors, (3) an invader exposed to native consumers and (4) an invader exposed to native competitors and consumers. All designations were based on the experimental design, natural history and *Discussion* of each publication.

The second type of data we extracted from each publication involved seven other factors that may also explain marine biotic resistance (1–7, below). Descriptions of these factors were organised into three categories: geographic location, temporal dynamics and characteristics of the focal invader. For geographic location, we recorded the (1) the latitude (absolute value, decimal degrees), (2) the habitat type where each experiment was conducted. The spectrum of habitats included soft-sediment systems (e.g. mudflats), soft-sediment systems with foundation species (e.g. salt marsh) and hard-substrate systems (e.g. rocky intertidal and floating docks). Because of the importance of tidal height in marine systems (Connell 1961; Bertness & Ellison 1987), we further divided the latter two habitat types into intertidal vs. subtidal. For temporal dynamics, we recorded, (3) the number of years since initial invasion of each study site, (4) the duration of each experiment in days.

Table 1 Summary of publications used in our meta-analysis of marine biotic resistance

Citation	Invader	Taxon	Mechanism	Lat.	Habitat type	Invasion age (years)	Exp. length (d)	Effect size(s) N
Bando 2006;	*Zostera japonica*	Antho-phyta	Competition	46.4	Intertidal foundation	50	730	2
Britton-Simmons 2006	*Sargassum muticum*	Phaeo-phyta	Competition	48.6	Intertidal hard substrate	150	120; 270	2
Britton-Simmons and Abbott 2008	*S. muticum*	Phaeo-phyta	Competition	48.6	Subtidal hard substrate	100	150	10
Bulleri and Benedetti -Cecchi 2008	*Caulerpa racemosa*	Chloro-phyta	Competition	43.5	Intertidal hard substrate	15	120	4
Bulleri *et al.* 2009	*C. racemosa*	Chloro-phyta	Competition × Herbivory	43.5	Subtidal hard substrate	15	90	6
Caro *et al.* 2011	*Pyura praeputialis*	Chordata	Competition	−23.6	Intertidal hard substrate	200	150	24
Castilla *et al.* 2004	*Pyura praeputialis*	Chordata	Competition × Consumption	−23.6	Intertidal hard substrate	200	90	8
Cebrian *et al.* 2011	*Lophocladia lallemandii*	Rhodo-phyta	Herbivory	39.2	Subtidal hard substrate	4	280	6
Cebrian *et al.* 2011	*C. racemosa*	Chloro-phyta	Herbivory	39.2	Subtidal hard substrate	4	280	6
Ceccherelli and Cinelli 1997	*Caluerpa taxifola*	Chloro-phyta	Competition	42.8	Subitdal foundation	3	90	2
Ceccherelli and Sechi 2002	*C. taxifola*	Chloro-phyta	Competition	42.8	Subtidal foundation	3	455	2
Cheng & Hovel 2010	*Musculista senhousia*	Mollusca	Consumption	32.8	Subtidal foundation	40	7	19
Clark & Johnston 2005;	*Watersipora subtorquata*	Bryozoa	Competition	−33.9	Subtidal hard substrate	35	15	1
Clark and Johnston 2009	*Watersipora subtorquata*	Bryozoa	Competition	−34.0	Subtidal hard substrate	35	3	1
Clark & Johnston 2011;	*Watersipora subtorquata*	Bryozoa	Competition	−34.0	Subtidal hard substrate	35	3	13
Dethier & Hacker 2005;	*Spartina anglica*	Antho-phyta	Competition	48.2	Intertidal foundation	50	300	18
Dumont 2011	*Bugula neritina*	Bryozoa	Competition × Consumption	−30.0	Subtidal hard substrate	100	84	7
Dumont *et al.* 2009	*Bugula* spp.	Bryozoa	Consumption	−30.3	Subtidal hard substrate	100	120	6
Dumont *et al.* 2009	*Ciona intestinalis*	Chordata	Consumption	−30.3	Subtidal hard substrate	100	120	6
Dumont *et al.* 2011	*Ciona intestinalis*	Chordata	Consumption	−30.0	Subtidal hard substrate	30	42	4
Grey 2010	*Botrylloides violaceus*	Chordata	Consumption	48.4	Subtidal hard substrate	40	14	8
Grey 2011	*Botrylloides violaceus*	Chor-data	Competition	48.4	Subtidal hard substrate	40	605	4
Grosholz 2005;	*Gemma gemma*	Mollusca	Competition	38.3	Soft sediment	40	120	3
Grosholz 2010;	*Spartina alterniflora-foliosa*	Antho-phyta	Herbivory	37.6	Intertidal foundation	30	730	3
Hollebone and Hay 2007	*Petrolisthes armatus*	Arthr-opoda	Competition × Consumption	31.9	Intertidal foundation	10	28	2
Kushner and Hovel 2006	*M. senhousia*	Mollusca	Competition × Consumption	32.8	Subtidal foundation	40	2	18
Lopez *et al.* 2010	*Perna perna*	Mollusca	Consumption	−22.7	Intertidal hard substrate	200	60	10
Lopez *et al.* 2010	*Isognomon bicolor*	Mollusca	Consumption	−22.7	Intertidal hard substrate	20	60	10
Monteiro *et al.* 2012	*S. muticum*	Phaeo-phyta	Herbivory	41.683	Intertidal hard substrate	28	43; 60	5
Osman and Whitlach 2004	*Botrylloides violaceus*	Chordata	Consumption	41.3	Subtidal hard substrate	30	5; 90; 77	7
Osman and Whitlach 2004	*Diplosoma listerianum*	Chordata	Consumption	41.3	Subtidal hard substrate	30	5; 90; 77	7
Osman and Whitlach 2004	*Molgula manhattensis*	Chordata	Consumption	41.3	Subtidal hard substrate	30	5; 90; 77	7
Osman and Whitlach 2004	*Ascidiella aspersa*	Chordata	Consumption	41.3	Subtidal hard substrate	30	5; 90; 77	7
Osman and Whitlach 2004	*Ciona intestinalis*	Chordata	Consumption	41.3	Subtidal hard substrate	30	5; 90; 77	7
Osman and Whitlach 2007	*Didemnum* sp.	Chordata	Competition	41.3	Intertidal hard substrate	5	3	11
Reusch 1998;	*M. senhousia*	Mollusca	Consumption	32.7	Subtidal foundation	30	210	3
Reusink 2007	*Crassostrea gigas*	Mollusca	Competition × Consumption	49.0	Intertidal hard substrate	100	60	9
Rius and McQuaid 2009	*Mytilus galloprovincialis*	Mollusca	Competition	−33.5	Intertidal hard substrate	50	70	6
Sanchez and Fernandez 2006	*S. muticum*	Phaeo-phyta	Competition	43.6	Intertidal hard substrate	30	90; 240	4
Scheibling and Gagnon 2006	*Codium fragile ssp. Tomentosoides*	Chloro-phyta	Competition	44.4	Subtidal hard substrate	4	730; 165	11
Shinen and Morgan 2009	*Mytillus gallprovincialis*	Mollusca	Competition	38.3	Intertidal hard substrate	50	35	4
Shinen *et al.* 2009	*Mytillus gallprovincialis*	Mollusca	Competition × Consumption	38.3	Intertidal hard substrate	50	365	2
Simoncini and Miller 2002	*Botrylloides violaceous*	Chordata	Consumption	42.4	Intertidal hard substrate	40	6	2
Stachowicz *et al.* 1999;	*Botrylloides diagensis*	Chordata	Competition	41.3	Intertidal hard substrate	30	14	4
Stachowicz *et al.* 2007;	*Botrylloides* sp.	Chordata	Competition	41.3	Subtidal hard substrate	30	60; 1; 7	23
Stachowicz *et al.* 2007;	*Diplosoma listerianum*	Chordata	Competition	41.3	Subtidal hard substrate	30	60; 1; 7	23

(continued)

Table 1. (continued)

Citation	Invader	Taxon	Mechanism	Lat.	Habitat type	Invasion age (years)	Exp. length (d)	Effect size(s) N
Stachowicz *et al.* 2007;	*Ascidiella aspersa*	Chordata	Competition	41.3	Subtidal hard substrate	30	60; 1; 7	23
Stachowicz *et al.* 2007;	*Styela clava*	Chordata	Competition	41.3	Subtidal hard substrate	30	60; 1; 7	23
Stachowicz *et al.* 2007;	*Membranipora membranacea*	Bryozoa	Competition	41.3	Subtidal hard substrate	30	60; 1; 7	23
Sumi and Scheibling 2005	*C. fragile ssp. tomentosoides*	Chloro-phyta	Competition × Herbivory	44.4	Intertidal hard substrate	50	91	4
Vermeij *et al.* 2009	*Acanthophora spicifera*	Rhodo-phyta	Herbivory	20.8	Subtidal hard substrate	50	6	2
Vermeij *et al.* 2009	*Hypnea musciformis*	Rhodo-phyta	Herbivory	20.8	Subtidal hard substrate	50	6	2
White and Shurin 2007	*S. muticum*	Phaeo-phyta	Competition	48.9	Intertidal hard substrate	75	33; 77	6

In this table, each study is described by the following columns: *Citation* to list authors and publication year; *Invader* to list scientific name of invader; *Taxon* to list taxonomic identity of invasive species; *Mechanism* to denote which pathway of resistance was tested; *Latitude* and *Habitat Type* to describe a study's geographic location; *Invasion Age* to estimate earliest recorded date of focal invasion; *Experimental Length* to describe the number of experimental days; *Extracted effect size(s)* to list how many assessments of biotic resistance were extracted.

For invader characteristics, we recorded, (5) the measured demographic variable (i.e. abundance, survivorship, growth or recruitment), (6) the trophic level (i.e. producer vs. invertebrate consumer) and (7) the phylum of each invader.

To account for potential non-independence among experiments, we assigned multiple effect sizes from the same experiment with the same numeric identification. This resulted in 54 independent effect sizes of marine biotic resistance (Table 1).

Calculation of effect sizes

To compare the marine data with previously published terrestrial meta-analyses, we required two separate calculations of effect size. First, Levine *et al.* (2004) determined the strength of biotic resistance by calculating the *d*-statistic, which is based on the mean and standard deviation of two treatments (Gurevitch & Hedges 1993). As a result, marine effect sizes were also based on *d*.

$$d = ((\text{Mean}_E - \text{Mean}_C)/SD\,\text{pooled})^*J \qquad (1)$$

In eqn 1, Mean_E is the mean of the exclosure (E) treatment (i.e. invasive producer without native community) and Mean_C is the mean of the control (C) treatment for each experiment (i.e. invasive producer with native community). This effect size also required calculating the pooled standard deviation:

$$SD\,\text{pooled} = \sqrt{[(((SD_E)^2(n_E - 1)) + ((SD_C)^2(n_C - 1)))/((n_E + n_C) - 2))]} \qquad (2)$$

In eqn 2, SD_E is the standard deviation of the exclosure treatment, SD_C is the standard deviation of the control treatment, and *n* is the sample size. Finally, *J* in eqn 1 corrects for bias due to differences in sample size by differentially weighting studies:

$$J = 1 - [3/(4^*(n_C + n_E - 2) - 1)] \qquad (3)$$

To compare the effect of native biodiversity in biotic resistance between terrestrial (Levine *et al.* 2004) and marine systems, we used a subset of the marine data and created an additional effect size, diversity-BR. In a few marine experiments, invader performance as a function of native competition was assessed across a manipulated gradient of native species diversity. With these data, we calculated diversity-BR by using the modified equation for *d* presented by Levine *et al.* (2004).

$$d_{Diversity} = ((\text{Mean}_{\text{Min. Diversity}} - \text{Mean}_{\text{Max Diversity}})/SD\,\text{pooled})^*J \qquad (4)$$

In eqn 4, the numerator compares an invader's performance from a treatment of maximum species diversity ($\text{Mean}_{\text{Max Diversity}}$) to the invader's performance from a treatment of minimum species diversity, within the same experiment.

The second effect size calculation was required for comparison of consumptive-BR with the meta-analysis of Parker *et al.* (2006). This effect size was calculated with an unweighted log-response ratio.

$$RR = \ln(\text{Mean}_{P+H}/\text{Mean}_{P-H}) \qquad (5)$$

In eqn 5, Mean_{P+H} is the mean abundance, survival or growth of an invasive producer (P) in the presence of native herbivores (H), and Mean_{P-H} is the same response variable in the absence of native herbivores.

For each effect size, the directional outcome (+ vs. −) depended on the response variable of interest (e.g. mortality and survivorship) and on the treatments being compared (i.e. Exclosure–Control vs. Enclosure–Exclosure). As a result, we standardised the direction of resistance strength so that positive and negative estimates indicated biotic resistance vs. facilitation of invaders respectively. These effects were considered significant if the 95% CI did not overlap zero. Finally, for comparisons between marine trophic levels (Objective 2) and for identification of the factors that best explain marine biotic resistance (Objective 3), we only used the *d*-statistic. In Objective 1, the majority of the ecosystem comparisons were based on the *d*-statistic simply because the results of Levine *et al.* (2004) afforded more opportunities for ecosystem comparisons than did the results of Parker *et al.* (2006). Therefore, it seemed appropriate to use the *d*-statistic in our second and third objectives.

Data analysis

Ecosystem comparisons

This portion of our review contained two types of comparisons. First, for each mechanism, we calculated the mean (±95% CI) strength of resistance towards invasions of marine producers and terrestrial producers. A positive CI that did not contain a value of *d*

or *RR* equal to zero indicated significant biotic resistance, a CI that contained a value of *d* equal to zero indicated insignificant biotic resistance, and a negative CI that did not contain zero indicated significant facilitation of the invader.

Following this first analysis, we directly compared the strength of each resistance mechanism between ecosystems. For a mean comparison, if the ratio of the respective variances exceeded 1.0, then we used non-overlapping 95% CIs to declare significant differences. But because the use of non-overlapping 95% CIs is too conservative when variances are equal (Payton *et al.* 2003), we reduced this conservatism by basing mean comparisons with equal variances on the degree of overlap between 85% confidence intervals. The ability of the 85% CI comparison to approximate a 5% significance level was addressed by Payton *et al.* (2003). Although some mean comparisons were based on non-overlapping 85% confidence intervals, the figures only illustrate means with 95% confidence intervals.

Marine-trophic comparisons

In contrast to the ecosystem comparisons, differences between marine trophic levels were amenable to a more powerful statistical approach because we possessed replicate effect sizes for each mean value. Consequently, we used a model-selection process based on linear mixed models and R software (version 2.15.0, lme4 package). In the linear mixed models, the numeric indicator for each experiment was treated as a random effect. This designation prevented a single experiment with multiple mean comparisons – and therefore multiple effect sizes – from being over-represented in our analyses.

According to the four mechanisms of resistance, the overall marine database was partitioned into four smaller data sets. For each resistance mechanism, we compared two models: we fitted the data to a null model that included only the intercept and to a single-factor model with a term that distinguished between invasive producers and invasive consumers. Using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Burnham & Anderson 1998), we identified the best explanatory model. This identification was based on Akaike weight (w_i), which was calculated as the model likelihood normalised by the sum of all model likelihoods. Akaike weights close to 1 indicate greater confidence in the selection of the best model. In addition, two models were declared significantly different if the difference in their Δ AICc scores was greater than or equal to 2.0 (Richards 2005).

Underlying factors of marine biotic resistance

To examine which of the eight factors or combination of factors best explain outcomes of marine biotic resistance, we implemented a model-selection process based on linear mixed models. This involved fitting the full marine database to the following types of models: a null model with an intercept of one, all possible single-factor models, and all possible additive combinations of the explanatory factors. However, the co-linearity between the trophic level (i.e. producer vs. consumer) and taxonomic identity of the invader prevented these two factors from occurring in the same multi-factor model. Due to an insufficient number of factorial experiments in our data set, we were also unable to analyse models with interaction terms.

After fitting all possible 89 models (see Table S1 in Supporting Information), we performed model selection using AICc (Burnham & Anderson 1998). Identification of the best explanation was based on the model or collection of models that produced an Akaike weight

(w_i) approximating a score of 0.90 of 1.0 (Johnson & Omland 2004). A significant difference between candidate models was declared if their Δ AICc scores differed by 2.0 or greater (Richards 2005).

After identifying the best model(s), we examined how the strength of biotic resistance differed within each of the explanatory factors. For a continuous independent variable, we used simple linear regression (SLR) to examine its influence on biotic resistance. For a nominal independent variable such as habitat, we calculated the mean ($\pm$95% CI) value of its different levels (e.g. soft-sediment and intertidal hard substrate) and assessed whether the confidence interval of *d* was above, contained, or less than zero. After testing for the presence of significant biotic resistance, we created subsets of the marine data and used a model-selection approach to conduct all possible mean comparisons within each nominal factor (see above section, *Marine-trophic comparisons*).

RESULTS

Ecosystem comparisons

The effectiveness of biotic resistance towards invasive producers depended on the mechanism of resistance and whether the native community was terrestrial vs. marine. For instance, when we compared our data with Levine *et al.* (2004), competitive-BR was significantly stronger in native communities of terrestrial producers than in native communities of marine producers (non-overlapping 85% CIs; Fig. 1a). Furthermore, competitive-BR failed to create significant biotic resistance towards invasive marine producers (95% CI = 0; Fig. 1a). While increasing the diversity of native producers strengthened competitive-BR in both systems (95% CI > 0; Fig. 1a), this diversity effect was significantly stronger in terrestrial communities (non-overlapping 85% CIs; Fig. 1a).

Ecosystem differences in consumptive-BR towards invasive producers depended on which terrestrial meta-analysis we examined. A comparison with Levine *et al.* (2004) illustrated that consumptive-BR was present in (95% CI > 0) and equally effective for (overlapping 85% CIs) native marine and terrestrial communities (Fig. 1b). However, a comparison with Parker *et al.* (2006) suggested that consumptive-BR affected invasive producers only in terrestrial communities (95% CI > 0; Fig. 1c). This ecosystem difference in the presence of biotic resistance was interesting, because a direct comparison of means was insignificant (overlapping 85% CIs, Fig. 1c). As a result, we inspected the raw data and found that 77% of the terrestrial studies in Parker *et al.* (2006) manipulated the vertebrate herbivores of native communities. In contrast, only 10% of the marine studies manipulated the vertebrate herbivores of native communities. When we restricted this ecosystem comparison to studies that manipulated the invertebrate herbivores of native communities, consumptive-BR was equally ineffective towards invasive producers in both systems (95% CI = 0; Fig. 1c).

Marine-trophic comparisons

Within the collection of marine experiments that we reviewed, the strengths of resistance mechanisms generally depended on whether experiments focused on invasive producers or invasive consumers. In marine experiments of competitive-BR, native communities resisted consumer invasions (95% CI > 0) but not producer invasions (95% CI = 0; Fig. 2a). A direct comparison of competitive-
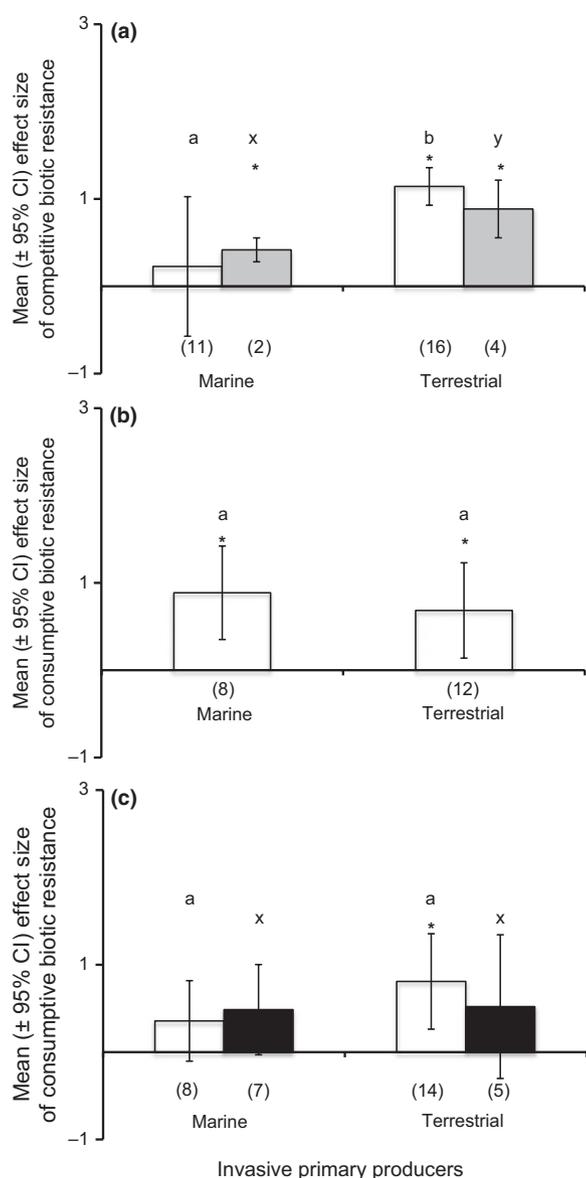
Figure 1 The mean (±95% CI) strength of biotic resistance towards invasive producers in marine and terrestrial experiments due to (a) competition from native species and (b–c) consumption by native species. In (a), open bars represent experiments with a low diversity of native species and grey bars represent experiments with a high diversity of native species. In (c), open bars indicate experiments in native communities with vertebrate and invertebrate consumers while closed bars indicate experiments with only invertebrate consumers. Values in parentheses indicate sample size, an asterisk indicates significant biotic resistance and letters designate significant mean comparison. In (a–b), terrestrial results come from Levine *et al.* (2004). In (c), terrestrial results come from Parker *et al.* (2006).

BR between trophic levels was also significant (Δ AICc = 2.0; Fig. 2a). In experiments of diversity-BR, diverse native communities equally resisted consumer and producer invasions (95% CI > 0 and Δ AICc = 0.7; Fig. 2a).

In marine experiments of consumptive-BR, native communities resisted consumer and producer invasions (95% CI > 0, Fig. 2b). However, the strength of this resistance was significantly stronger towards invasive consumers than towards invasive producers (Δ AICc = 2.1; Fig. 2b). In marine experiments that tested combined-
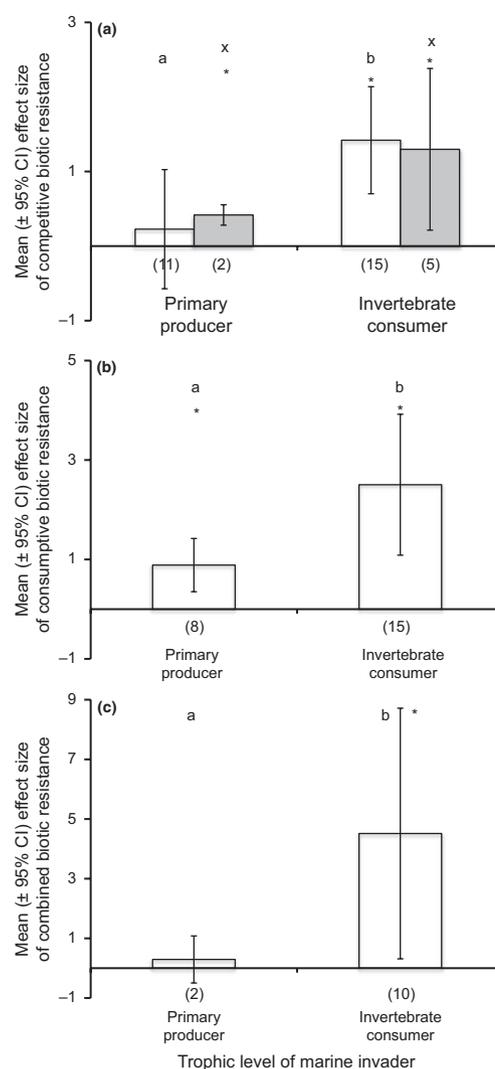

Figure 2 The mean (±95% CI) strength of marine biotic resistance towards the invasion of primary producers and invertebrate consumers as a function of (a) competition from native species, (b) consumption by native species and (c) combined competition and consumption from native species. In (a), open bars represent experiments with a low diversity of native species and grey bars represent experiments with a high diversity of native species. Values in parentheses indicate sample size, an asterisk indicates significant biotic resistance, and letters designate significant mean comparisons.

BR, native communities resisted invasions of consumers (95% CI > 0) but not producers (95% CI = 0; Fig 2c). In a direct comparison of these means, combined-BR was also significantly stronger towards invasive consumers (Δ AICc = 3.5).

Underlying factors of marine biotic resistance

Based on our model-selection analysis of marine experiments, no single model was overwhelmingly supported by the data (i.e. $w_{best\ model}$ < 0.9; Table S1). For robust estimation of parameters about marine biotic resistance, one would need the weighted average of five parameters from our top four candidate models ($w_{top\ four\ models}$ = 0.90; Johnson & Omland 2004). For each level of these five parameters, we described the degree to which biotic resistance was present (95% CI > 0) or absent (95% CI = 0). Results of

mean comparisons between the levels of each parameter are listed in Table S2.

Beginning with the parameter of resistance mechanism, native communities significantly resisted invasions of producers and consumers regardless the mechanism (i.e. 95% CIs > 0; Fig. 3a). Biotic resistance in marine experiments also depended on two parameters about the focal invader, demographic response and taxonomic identity. For the demographic parameter, biotic resistance was detected in experiments that measured invader survivorship and recruitment (95% CI > 0), but not in experiments that measured invader growth and abundance (95% CI = 0).

Because all direct mean comparisons were insignificant and because this parameter contributed minimally to the average model (i.e. AICc weight = 0.05), we do not further address these results. For the taxon parameter, native communities failed to resist Bryozoan consumers as well as Anthophyte and Chlorophyte producers (95% CI = zero). In contrast, native communities resisted invasions of Molluscan and Chordate consumers as well as Phaeophyte and Rhodophyte producers (95% CI > zero).

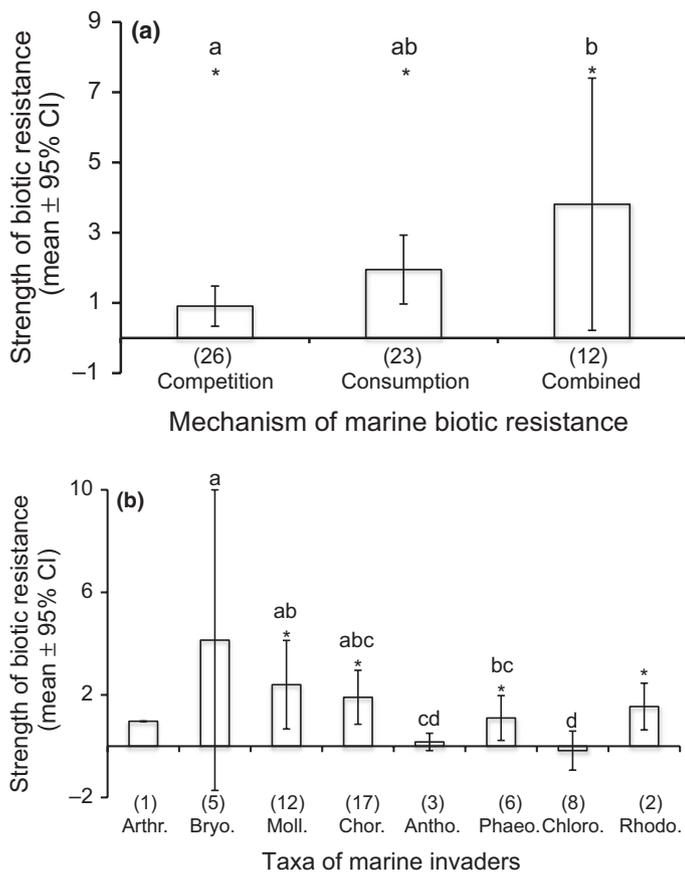The averaged model also contained two parameters about an experiment's geographic location (latitude and habitat). First, the strength of biotic resistance decreased as latitude increased ($F_{1,30} = 5.63$, $P = 0.02$; $R^2 = 0.16$; y = −0.15x + 7.68; Fig. 4a). Second, significant biotic resistance was detected in hard-substrate habitats (95% CI > 0), but not in the soft-sediment habitats regardless the presence or absence of foundation species (open bars, 95% CI = 0; Fig. 4b). Initially, tidal elevation failed to influence the presence of biotic resistance in soft-sediment or hard-substrate habitats. However, when we limited our analysis to studies within subtidal foundation habitats that contained native consumers (i.e. 5 of seven studies), we detected significant biotic resistance (95% CI > zero; closed bar, Fig. 4b).

DISCUSSION

Ecosystem comparisons

Our study suggests that the ability of native communities to limit the success of established invaders differs in important ways
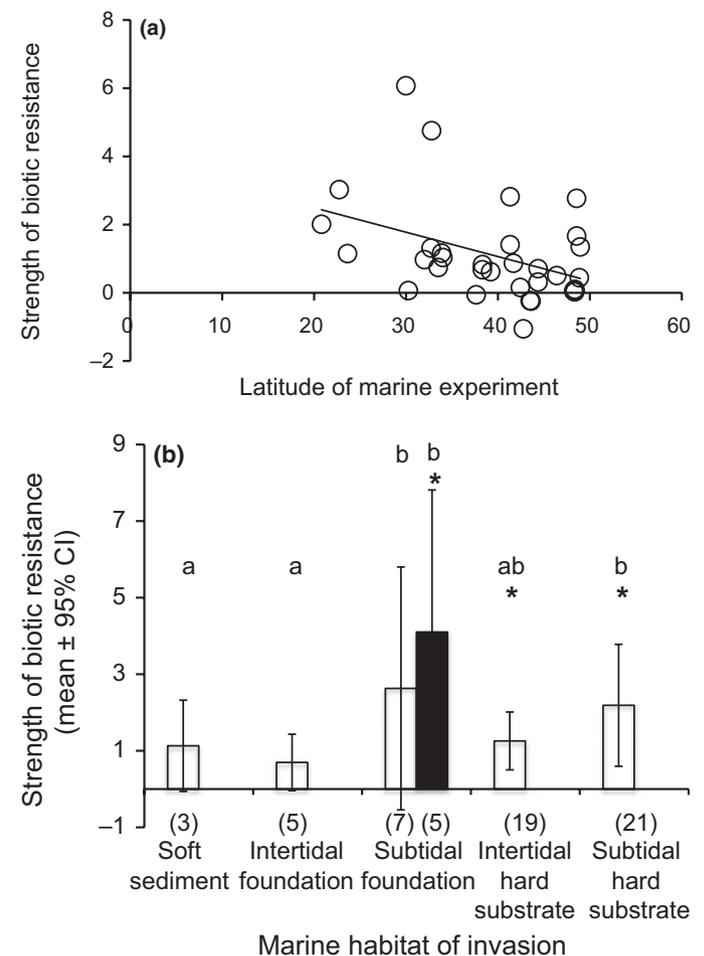

Figure 3 In (a), we present the mean (± 95% CI) strength of marine biotic resistance as a result of different species interactions from native communities. In (b), we present the mean (± 95% CI) strength of marine biotic resistance towards the different phyla of invaders. Values in parentheses indicate sample size, an asterisk indicates significant biotic resistance, and letters designate significant mean comparisons. From left to right, abbreviations on the x-axis represent the phyla of Arthropoda, Bryozoa, Mollusca, Chordata, Anthophyta, Phaeophyta, Chlorophyta and Rhodophyta.

Figure 4 (a) The relationship between the strength of marine biotic resistance and the latitude at which the experiment was conducted. (b) The mean (± 95% CI) strength of biotic resistance from experiments in different marine habitats. In (b), the closed bar represents the mean of subtidal foundation habitats with native consumers and the adjacent open bar represents this habitat's mean both with and without native consumers. Values in parentheses indicate sample size, an asterisk indicates significant biotic resistance, and letters designate significant mean comparisons.

between marine and terrestrial systems. Beginning with competitive biotic resistance towards invasive producers, it is generally accepted that competition from native terrestrial communities significantly limits producer invasions, and that this resistance strengthens with increasing diversity of native producers [Fig. 1a; Levine *et al.* (2004)]. In contrast, we found that competitive-BR in marine communities fails to resist producer invasions unless the communities contain many native producer species. Furthermore, the influence of native diversity was significantly weaker in marine than in terrestrial systems. While these last two differences about native diversity may be important, they currently require cautious consideration because of low sample size.

This ecosystem variation in competitive-BR may be best understood by considering a previous meta-analysis of field experiments within non-invaded communities. In this review, Gurevitch *et al.* (1992) found that competition among producers was moderately strong within terrestrial, aquatic, and marine experiments. Presumably, this is moderated by local mechanisms of species coexistence (Gurevitch *et al.* 1992). Accordingly, the ecosystem difference in competitive-BR illustrated by our review (Fig. 1a) may reflect ecosystem differences in the degree to which invaders disrupt local coexistence mechanisms of community diversity. For instance, marine systems are generally more open and have higher producer turnover relative to terrestrial systems (Carr *et al.* 2003). Also relative to terrestrial systems, the community structure of marine systems is influenced more strongly by regional than by local processes (Cornell & Harrison 2013). In fact, studies of epifaunal marine communities demonstrated that regional patterns of species diversity explain as much as 75% of local diversity patterns (Witman *et al.* 2004). Given that local marine communities are not saturated and that membership is less constrained by local processes than terrestrial communities, invading producers would be less likely to experience competitive-BR in marine systems. This is consistent with our result of producer invasions confronting less competitive-BR in marine than in terrestrial systems.

Our hypothesis is tangentially supported by another ecosystem difference in the effect of native species diversity on competitive-BR towards invasive producers, which we refer to as diversity-BR. But before proceeding, we highlight that this ecosystem comparison and our following points are based on small sample sizes. In agreement with theory (Elton 1958, Stachowicz *et al.* 1999), we found that native marine communities with high producer diversity significantly resisted invasions of non-native producers (Fig. 1a). Because low diversity communities in the same marine systems failed to resist invasive producers, we speculate that the ecosystem differences in competitive-BR and diversity-BR may reflect variation in these two systems' dependence on local coexistence mechanisms. But despite a significant effect of native marine diversity, large differences in competitive-BR persisted between marine and terrestrial systems. Future work needs to resolve whether this cross-system variation is simply an artefact of low sample size. If the difference persists with increasing sample size, then it is worthwhile to investigate why competitive-BR remains unequal between ecosystems regardless of native species diversity.

Ecosystem differences in consumptive biotic resistance were less clear: the comparison with Levine *et al.* (2004) resulted in no difference but the comparison with Parker *et al.* (2006) detected significant consumptive-BR only in terrestrial communities (Figs 1b,c). While assessing the relative accuracy of these two metrics was not our goal, we can reconcile the discrepancy by considering that our comparison with Parker *et al.* (2006) primarily reflected a difference between the effects of invertebrate (marine) and vertebrate (terrestrial) herbivores. When only invertebrate herbivores were considered, we no longer observed an ecosystem difference in consumptive-BR and this result matched that of our comparison with Levine *et al.* (2004). Still, it is interesting that the metric of Levine *et al.* (2004) resulted in biotic resistance for both systems and the metric of Parker *et al.* (2006) did not. But because the effect size calculation (*d*) used by Levine *et al.* (2004) promoted more cross-system comparisons, we limit the rest of our discussion to results based on *d*.

To understand the broader implication of consumptive-BR being equally strong in both systems, we must recognise that native marine and terrestrial producers have fundamentally different traits. Relative to terrestrial producers, marine producers generally have faster growth rates, smaller sizes, higher nutritional quality, and fewer defenses (Strong 1992; Shurin *et al.* 2002, 2006). According to previous reviews, these differences promote stronger consumer effects on producers in aquatic than in terrestrial systems (Strong 1992; Cyr & Pace 1993; Cebrian 1999; Shurin *et al.* 2002, 2006; Cebrian & Lartigue 2004). Curiously, this does not seem to be the case for invasive producers. An absence of ecosystem variation in consumptive-BR may be due to multiple features of invasive producers including selection for low palatability and faster growth rates (Grosholz 2010), lack of recognition by consumers (Cox & Lima 2006), and lower diversity of introduced vs. native producers.

Marine-trophic comparisons

Our review also uncovered important differences in biotic resistance between marine trophic levels (Fig. 2). Except for diversity-BR, all mechanisms of resistance were significantly stronger towards invasive consumers than towards invasive producers. Because the sample size for diversity-BR towards primary producers was low, we will not discuss this non-significant comparison. The other significant comparisons, however, are consistent with previous reviews demonstrating that native consumers are more strongly affected by competition and consumption than are native producers (Gurevitch *et al.* 1992; Shurin *et al.* 2002). We also know that native consumers negatively affect invasive producers more strongly than native producers (Parker *et al.* 2006). Therefore, the marine-trophic differences in biotic resistance that we documented may be due to invaders experiencing more intense negative interactions with native species (Parker *et al.* 2006) and to these interactions more strongly affecting consumers than producers (Gurevitch *et al.* 1992; Shurin *et al.* 2002).

Underlying factors of marine biotic resistance

In the preceding portions of this review, we demonstrated that biotic resistance mechanisms towards invasive producers differ in important ways between marine and terrestrial systems (Fig. 1). Moreover, the strengths of these mechanisms differed between marine trophic levels (Fig. 2). However, we contend that the relative importance of these differences cannot be assessed without first considering whether factors other than mechanism (e.g. competitive-BR vs. consumptive-BR) help explain experimental outcomes of marine biotic resistance.

In the third objective of this study, our mixed model comparison analysis found that marine biotic resistance is linked to four factors. First, even when additional factors were considered, the type of biotic resistance mechanism remained important (Fig. 3a). For instance, and without distinguishing between invasive producers and invasive consumers, the ability of native communities to resist invasions was significantly strongest when both resistance mechanisms were present (i.e. combined-BR). Given the significant difference between competitive-BR and combined-BR, we suggest that research on biodiversity-ecosystem function (Loreau & Hector 2001) and multiple predator effects (Sih *et al.* 1998) can offer a falsifiable hypothesis for future studies: multiple species interactions maximise a native community's ability to resist invasion. In other words, greater diversity of native functional groups may increase the likelihood that functional groups can individually or interactively reduce the spread of an invasive species.

Understanding marine biotic resistance also depends on the taxonomic identity of the invader with respect to phylum or similar levels of organisation (Fig. 3b). Of course, we cannot rule out that this factor's significance reflects a sampling bias, nor can we conclude that such a bias is insignificant. But at the same time, these results may reflect conclusions based on reviews of experiments with only native species, which showed that negative interactions attenuate from higher to lower trophic levels (Gurevitch *et al.* 1992; Shurin *et al.* 2002). On the one hand, if life history characteristics of producers (e.g. above- and below-ground biomass, regenerative tissue growth, asexual reproduction) promote resilience to competitive exclusion and consumer pressure, then the inconsistent presence of these traits in invertebrates may explain why invertebrate taxa were often more negatively influenced by native communities than were producer taxa (2/3 of all mean comparisons, Table S2). But on the other hand, many of the significant differences in how native communities impact invasions of invertebrates vs. producers may be an artefact of low sample size.

The remaining two influential factors of marine biotic resistance concerned experimental locations. First, the ability of native communities to resist established invasions increased as latitude decreased (Fig. 4a). Interestingly, independent studies showed that latitude inversely correlates with species diversity and species interaction strength (Pianka 1966; Schemske *et al.* 2009; Freestone *et al.* 2011). While these previous findings and the correlative result from our review may be independent, it is also reasonable to assume that increasing biodiversity mechanistically strengthens species interactions and thus biotic resistance. For example, biodiversity-ecosystem function research suggests that diversity promotes biotic resistance by increasing complimentary use of resources (Loreau & Hector 2001; Cardinale *et al.* 2007), by decreasing variability in community and ecosystem properties (Stachowicz *et al.* 2007; Loreau & de Mazancourt 2013), by increasing the probability that the system contains a dominant consumer or competitor (i.e. sampling effect; Tilman 1999; Cardinale *et al.* 2006), and/or by facilitating multiple predator effects and in turn consumer pressure (Sih *et al.* 1998; Byrnes & Stachowicz 2009). Regardless of the mechanism, native diversity may dictate the outcome of various invasion hypotheses by decreasing the likelihood that a native community will be naïve to an invader, will lack an effective enemy, or will be susceptible to novel invasive weapons. It follows that changes in diversity and species interaction strengths across latitude may then produce corresponding patterns of biotic resistance.

The type of marine habitat was another important location factor that provides interesting parallels between invasion biology and marine community ecology (Fig. 4b). On the basis of positive interaction theory (Bruno *et al.* 2003), we expected native communities to resist invasions from intertidal soft-sediments, but not from habitats created by foundation species. This is because foundation species often benefit associated species by ameliorating competition and predation. All of these soft-bottom habitats, however, lacked significant biotic resistance. Although the absence of resistance in soft-sediments may be due to low sample size, this result may also reflect a habitat that is vulnerable to invasion. Given that competitive exclusion among native benthic invertebrates is largely absent in soft sediments (Peterson 1991), the latter interpretation seems reasonable.

Because resistance from native communities was stronger in subtidal than in intertidal foundation habitats, we reviewed the experiments conducted within these soft-substrate habitats. We found that soft-sediment and intertidal foundation experiments contained only native competitors and that most subtidal foundation experiments (71%) contained native consumers. Furthermore, this latter subset of studies resulted in significant biotic resistance (Fig. 4b). This tidal trend suggests that significant biotic resistance is due to consumptive-BR from native consumers and competitive-BR from the foundation species. In addition, our data show that combined-BR is the most effective resistance mechanism (Fig. 3a). On the basis of these details, we think that the variability of biotic resistance between intertidal and subtidal foundation species aligns with principles that were studied along rocky shores. In particular, rocky shoreline communities are regulated by physiological tolerances at higher tidal elevations and by competition and predation at lower elevations (Connell 1961; Paine 1966; Menge & Branch 2001). Therefore, variation between intertidal and subtidal foundation habitats may be due to both the direct effects of tidal elevation on native consumers (i.e. less consumption at higher tidal elevations) and/or the indirect effect of tidal elevation on native consumers via benefits to the traits of subtidal foundation species that attract consumers (i.e. positive interaction theory). Still, if tidal elevation influences biotic resistance in soft-substrate habitats, then it would be productive to test why native communities resisted invasions on hard-substrates regardless of tidal elevation.

Our meta-analysis has two important limitations. First, the sample size of the existing data set on marine invasion experiments does not enable us to test whether multiple-factor models with interaction terms explain results of biotic resistance better than multiple-factor models with only additive terms. Because interactions between factors (e.g. latitude × resistance mechanism) could be common, our understanding of marine biotic resistance suffers from a lack of factorial experiments and from studies that utilised the comparative experimental approach (e.g. Menge *et al.* 2003). Second, a number of elegant experiments illustrate how invasions are influenced by physical disturbance and by resource supply (Sanchez & Fernandez 2006; Clark & Johnston 2011). Consequently, factorial and comparative experiments on biotic resistance must integrate these two factors across gradients in location and invasive traits.

In summary, our study makes three important contributions to a broader understanding of biological invasion. Our first point is that most invasion hypotheses depend to some degree on the ability of the native community to resist invaders. By highlighting that the relationships between biotic resistance and other invasion hypothe-

ses are bi-directional, we identified a common framework with which to link predictions from a diversity of invasion hypotheses. The second contribution concerned our highlighting the clear differences in biotic resistance between marine and terrestrial systems. Our explanations of these differences provide testable hypotheses for future studies. Finally, our third contribution concerns the conclusion that biotic resistance can be influenced by several other and previously unidentified factors. Earlier meta-analyses illustrated how consumption and competition from native species limits the success of established invaders. But the relative influence of latitude, habitat type, taxonomic identity and other factors had not been previously investigated. Ultimately, we suggest that biotic resistance is not a static quantity, even within a specific system, and that the ability of communities to resist invaders may truly be a function of where and when an invasion takes place.

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AUTHORSHIP

EG proposed study; DK, BC, and EG identified literature for inclusion in database; DK, BC, and EG developed the decision framework for inclusion of studies and data types; DK performed data extraction, model development and statistical analysis; DK wrote the first draft while BC and EG edited and contributed to subsequent drafts.

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