



A framework to study the context-dependent impacts of marine invasions

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ABSTRACT

The ecological impacts of marine invasive species vary according to the spatial and temporal scale of analysis, thereby challenging the extraction of generalities about underlying mechanisms. Here, we applied a broad impact framework that addresses this scale-dependency, to test if general drivers of impacts can be identified and quantified from marine invasion experiments. This framework explains variability in impacts according to the unique (specific) and universal (general) attributes of the (1) invasive organism, (2) resident biota, (3) resource levels, and (4) abiotic conditions. In this framework, unique and universal attributes encompass the properties that are either ecologically relevant to only a few specific invasions (e.g. a unique toxin) or to most invasions (e.g. invader density, size, age or longevity), respectively. We reviewed 88 published marine invasion impact experiments, where 18 tested for effects of universal and 11 for unique attributes of the invasive organism (63 tested for presence–absence effects, where these attributes are confounded). A meta-analysis confirmed that the species identity and density (representing a unique and universal attribute, respectively) of the invader significantly predicted impacts. These attributes should, therefore, whenever possible, be treated as separate impact-modifiers. By contrast, very few experiments have tested if universal or unique attributes of the resident biota, the resource levels or the abiotic conditions modify invasion impact. This highlights a major research gap; quantitative syntheses cannot be undertaken until more factorial experiments have manipulated the invasive species and habitat-associated drivers in concert (with ≥ 2 treatments per test factor). In conclusion, to facilitate a broader understanding of marine invasion impacts, we advocate that universal and unique impact-components, whenever possible, are treated as separate test entities that should be examined for each of the four impact drivers.

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Contents

1. Introduction	322
2. Methods	323
2.1. Literature review	323
2.2. Meta-analysis of invasion impacts	323
3. Results	324
3.1. Studied populations, habitats, regions and experimental designs	324
3.2. Meta-analysis of invasion impact drivers	325
4. Discussion	325
Acknowledgement	326
References	326

1. Introduction

Invasive species have dramatically impacted marine ecosystems around the world (for recent reviews covering numerous types and forms of impacts, see Molnar et al., 2008; Byers, 2009; Crooks, 2009;

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Grosholz and Ruiz, 2009; Rilov, 2009; Thomsen et al., 2009). Despite a growing body of literature, few generalities about what influences the impacts of invasive species have emerged from marine case-studies, perhaps because broad theoretical frameworks (e.g., Parker et al., 1999; Ricciardi, 2003; Strayer et al., 2006; Grosholz and Ruiz, 2009) are rarely applied empirically. Consequently, it has recently been argued that “invasion biology as a separate discipline will continue to be questioned until we have a better framework for understanding the impacts of invasive species” (Pyšek and Hulme, 2009).

A re-occurring conclusion from marine case-studies is that invasion impacts vary depending on the spatial and temporal scale of analysis (Padilla, 2010). For example, the impact of invasive species in marine systems can vary at small spatial scales (Ceccherelli and Campo, 2002; Thomsen and McGlathery, 2006), regional scales (Bulleri et al., 2010; Thomsen et al., 2010), between seasons (Scheibling and Gagnon, 2006; Thomsen et al., 2006a, 2006b; Heiman and Micheli, 2010) and across years (Staeher et al., 2000). However, even though such findings may increase our ability to extrapolate impacts across spatio-temporal domains, space and time have no inherent causality (Hawkins and Diniz-Filho, 2004), thus they do not provide strong insight into the underlying mechanisms (Levine et al., 2003).

Recently, several insightful reviews have facilitated a more detailed understanding of the impacts of marine invasions. Wallentinus and Nyberg (2007) and Crooks (2009) reviewed ‘positive’ interactions associated with habitat-provision and engineering effects, whereas Byers (2009), Rilov (2009) and Grosholz and Ruiz (2009) reviewed negative species interactions (i.e. competition, predation, and invasions as a disturbance). A few reviews have also focused on impacts associated with specific taxonomic groups such as oysters (Ruesink et al., 2005; Padilla, 2010) or seaweeds (Schaffelke and Hewitt, 2007; Williams and Smith, 2007; Thomsen et al., 2009). However, these reviews have generally emphasized post-hoc explanations rather than provided quantitative assessments. For example, we are only aware of a single marine paper to compare published disparate impact studies in a quantitative framework (Thomsen et al., 2009) and this study quantified direction and magnitude of seaweed-impacts, rather than addressing the context and their underlying drivers. In short, we are not aware of any reviews that have addressed marine invasion impacts in a quantitative mechanistic framework.

We propose that the direction and magnitude of invasion impacts depend on the properties associated with the invasive organism (e.g., their size, sex, density and species identity (Lohrer and Whitlatch, 2002b; Walton et al., 2002; Byrnes and Stachowicz, 2009)), the resident biota (e.g., the size of resident prey organisms, Walton et al., 2002), the resource levels (e.g., nutrient levels, Ceccherelli and Sechi, 2002) and the abiotic conditions (e.g., sediment levels, Piazzini et al., 2005). In this framework, the invasive organism is the primary driver and the resident biota, resource levels and abiotic conditions are secondary factors that modify invader-generated impacts (Fig. 1). Each of the four impact drivers has both “universal” (general) and “unique” (specific) attributes, reflecting attributes that are ecologically relevant for most invasions or only to a few specific invasions, respectively. For example, impacts of invasive lionfish (Albins and Hixon, 2008) may be driven by the species’ specific toxin or attack-behavior (attributes that only are relevant to measure for lionfish invasions). Impacts could also be caused by attributes associated merely with its presence as any new organism added to the resident community; thus its impact may be derived through its density, size, fitness, or longevity (attributes that are relevant to measure for all invasions). In the first example, the organism’s genetic identity is important (only the lionfish can cause the observed effects) whereas in the latter example its genetic traits are less relevant (any added organism can cause the observed effects). This distinction mirrors insights from invasion success studies that acknowledge that success depends both on invader traits (genetic properties are important;

unique attributes of an invasion) and propagule pressure (genetic properties are less relevant; universal attribute of an invasion).

Our aim is to review experimental field studies of marine invasion impacts in order to assess whether this framework can facilitate a general understanding of invasion impacts in marine systems. More specifically we ask (i) how many field-based invasion impact experiments have explicitly tested for unique or universal impacts of the basic impact drivers? (ii) what is the magnitude and direction of effects sizes for universal and unique impact attributes? and (iii) are these, on average, significantly different from zero? To answer these questions we conducted an in-depth search for published manipulative marine field experiments. We were therefore also able to highlight research areas that require additional attention, and identify taxonomic, habitat or biogeographical research biases.

2. Methods

2.1. Literature review

We searched for peer-reviewed papers where marine invaders (= primary driver) were controlled in field or outdoor mesocosm experiments (to optimize realism and causality), using standard searches in Current Contents, Web of Science and by backtracking papers from case studies and reviews. In these manipulative studies, the presence of the invader is under experimental control, and invaded plots (treatments) can be compared to non-invaded plots (controls). For each located study, we extracted information about the manipulated invasive population (taxonomy, feeding mode), habitat (elevation, substratum, coastal feature) and location (country, continent, biogeographical region), and experimental design (e.g. the number and type of treatment levels). We also identified the studies that included orthogonal tests between the primary invader-driver and secondary manipulated habitat-associated drivers. Next, we identified studies where at least two treatments were compared to the control, because these designs provide an opportunity to disentangle unique and universal impact-components. For example, comparing controls to two invasive species (of relatively similar size, age and health), or two densities or size-groups (of the same species) tests for unique and universal impact-modifications, respectively. Finally, only studies that reported an impact on the ecological performance of resident individuals and populations were included, e.g., their sizes (length, area, biomass), fitness (growth, survival, mortality, reproduction) or abundances (counts, coverage, biomass).

2.2. Meta-analysis of invasion impacts

Meta-analyses were conducted using data from the studies that fulfilled our experimental design requirements. Specifically, we tested if invasion effects were affected by the density and species-identity of the invasive species (representing a universal and a unique attribute, respectively), because they were the only attributes that had been tested adequately for meta-analysis (see online appendix). We used Hedges effect-size d , corrected for small sample sizes, to standardize impacts within and between studies, by calculating d between controls and treatments (Rosenberg et al., 2000). We therefore only included studies that reported corresponding means, measures of dispersal and replication levels. The log-response ratio effect size was not used because many extracted effects included zeros (Morales and Traveset, 2009). An all-inclusive data-selection criterion was applied (Englund et al., 1999), and data that fulfilled the experimental design requirements were extracted from figures, tables and texts. Reversal markers were used when needed, (e.g. on mortality, to ensure d was negative if the invader caused a reduction in ecological performance). Details on data extraction and averaging methods used to proceed from non-independent within-study effect sizes to cumulative effect-sizes can be found in the online appendix and Thomsen et al. (2009).

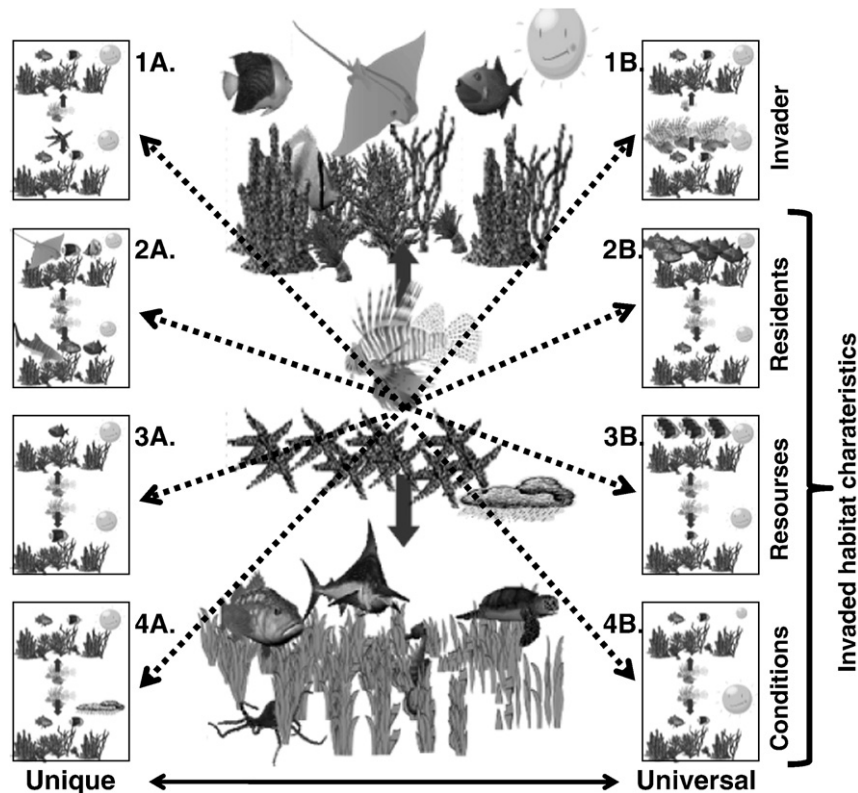


Fig. 1. Invasion impact depends on the local spatio-temporal and ecological context. For example, a single invasive lionfish will likely have different impacts on a coral reef (center-top habitat) compared to an army of seastars invading a seagrass bed (center-bottom habitat). More experimental studies should partition impact-variability into basic impact drivers (y-axis) and their unique and universal components (x-axis). Manipulative experiments are powerful tools to do this, e.g., as shown in the 8 hypothetical experiments where only a single impact driver is allowed to vary (1A–4B); 1A: species identity of invader (a seastar versus lionfish); 1B: density of invader (one versus many lionfish); 2A: species identity of resident biota (ray, butterflyfish, angelfish versus shark, grouper, triggerfish); 2B: density of resident biota (few versus many triggerfish and groupers); 3A: quality of resources (juvenile angel fish versus juvenile trigger fish = prey items); 3B: quantity of resources (density of juvenile angelfish = prey items); 4A: quality of abiotic conditions (sun versus rain); 4B: quantity of abiotic conditions (high versus low temperature).

For each individual paired response (between two density levels or between two species identities) we calculated the absolute difference as:

$$\Delta d_{\text{density}} = d_{\text{highest}} - d_{\text{lowest}} \quad \text{and} \quad \Delta d_{\text{species}} = d_{\text{invader1}} - d_{\text{invader2}}$$

(for simplicity we excluded 'absolute' value signs).

If more than 2 treatments were quantified in an experiment, we contrasted the lowest and highest d -values for the species-identity test, and the highest and lowest densities for the density test. Multiple non-independent Δd values were subsequently averaged into a single independent value per study, using equal weight for different response variables and factorial or nested within-study experiments. Finally, we used unweighted random-effect models to test if cumulative effect sizes were significantly different from zero. All analyses were conducted in Metawin 2.0 (Rosenberg et al., 2000).

3. Results

3.1. Studied populations, habitats, regions and experimental designs

We identified 88 replicated marine field-based manipulative experiments described in 78 peer-reviewed papers (that reported means, measure of dispersal and replication levels, see online appendix). A total of 93 invader populations, representing 40 species, were examined in the 88 experiments. Most species have only been tested once, although 17 have been included in multiple experiments, and four species have been tested >5 times (*Carcinus maenas* = 13,

Caulerpa racemosa = 6, *Littorina littorea* = 6, *Sargassum muticum* = 6). The 93 populations represent a diverse group of taxa including red algae ($n=6$ populations), brown algae (8), green algae (15), angiosperms (2), bivalves (10), gastropods (10), polychaetes (7), crustaceans (20), echinoderms (3), bryozoans (3), tunicates (7), fish (1) and mammals (1). The 93 populations could also be grouped into 31 plant tests, 21 filter feeder tests, 9 herbivore tests and 21 carnivore tests (online appendix).

Grouping studies by habitats revealed a near-equal emphasis on subtidal (37) and intertidal (41) environments. Likewise, there were almost equal numbers of studies conducted in high-energy open coasts (31) and low-energy estuaries (32), although fewer studies were conducted in semi-enclosed bays (in-between estuaries and open rocky coasts (8), marshes (4), and coral reefs (1)). A total of 23 studies were conducted in sedimentary habitats, 38 on rocks (including 5 on artificial substratum panels), and 17 in biogenic habitats (mussel beds, oyster reef, polychaete reefs, salt marshes, seagrass beds, coral reefs). The 78 studies were conducted in 13 different countries, dominated by the United States (38), Australia (12) and Italy (9). Most studies have been conducted in the Atlantic Ocean (45, divided into 9 NE, 23 NW, 1 SE, 3 SW, and 9 in the Mediterranean Sea) and Pacific Ocean (20, divided into 15 from the NE, 3 from NW and 2 from SW). Only 12 studies have been conducted in the Southern Ocean and 1 in the western Indian Ocean.

Of the 88 invasion experiments, 18 included tests for universal attributes, and 11 tested for unique attributes, while the remaining 63 experiments were based on presence-absence designs where universal and unique invader attributes cannot be separated (Fig. 2). Of

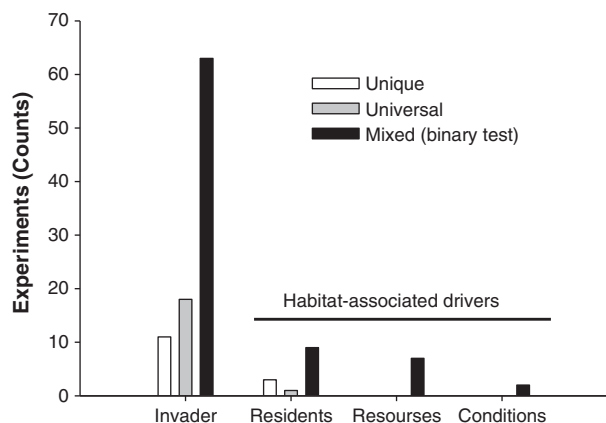


Fig. 2. Published marine experiments classified into unique, universal or mixed impact-components for four basic drivers (invader, resident organisms, abiotic resources, abiotic conditions). We identified 88 manipulative experiments from 78 peer-reviewed papers. The three habitat-associated drivers are orthogonal manipulations to the invader impact test. Unique and universal tests include a minimum of two invaded treatment levels and an uninvaded control (used in meta-analyses, cf. Fig. 3). Mixed tests correspond to binary presence-absence tests, i.e. where a single treatment is compared to the control (conflating unique and universal attributes). In addition, 44 of the 88 test included a mensurative habitat tests, i.e. an orthogonal or nested spatio-temporal component. See online appendix for details.

the 18 and 11 tests conducted on universal and unique invader properties, 17 and 9 compared impacts on the same response variables, i.e. could be used in our meta-analysis. Also, one and three experiments included orthogonal tests of universal and unique attributes of the resident biota, respectively. Invasion experiments that manipulated resource levels or abiotic conditions (orthogonally to invader manipulations) compared a single treatment to the control (e.g., with or without nutrients or sediment additions) (Ceccherelli and Sechi, 2002; Piazzini et al., 2005). Finally, half of all the experiments included at least one mensurative nested or orthogonal spatio-temporal test component.

3.2. Meta-analysis of invasion impact drivers

Meta-analytical tests have been conducted on 12 and 14 different invasive species in universal density tests and unique species-identity tests, respectively. Two crab species were particularly common study objects: *C. maenas* and *Hemigrapsus sanguineus* were used in 5 density tests, and *Carcinus* alone was included in 6 species-comparisons. Individual experiments varied widely in Δd -values for both unique and universal impact-tests. For the species-comparison, the highest Δd contrasted *Carcinus* and *Hemigrapsus* effects; $\Delta d = 23.38$ (Lohrer and Whitlatch, 2002a) and 22.75 (Lohrer and Whitlatch, 2002b) where *Carcinus* had much higher per-capita effect than *Hemigrapsus*. By contrast, the smallest Δd compared filter feeders: 0.70 comparing *Botrylloides violaceus*, *Ciona intestinalis*, *Didemnum vexillum*, *Mytilus galloprovincialis* and *Watersipora subtorquata* (Byrnes and Stachowicz, 2009), and 0.08 comparing *Sabella spallanzanii* to *Styela clava* (Ross et al., 2007). For the universal test, highest density-effects were recorded for *C. maenas* (27.85, Lohrer and Whitlatch, 2002b), *Balanus improvisus* (23.76, Kotta et al., 2006) and *L. littorea* (11.09, Lubchenco, 1983), whereas the lowest density effects were recorded for filter and deposit feeding tunicates, gastropods and polychaetes, including *S. clava* (0.19, Ross et al., 2007), *Batillaria attramentaria* (0.19, Byers, 2000) and *S. spallanzanii* (0.08, Ross et al., 2007). Despite this high data variability, cumulative Δd values were significantly different from zero for both tests (95% CL not overlapping zero i.e., $\Delta d_{\text{density}} = 4.76 \pm 4.38$, $n = 17$, Heterogeneity test; $Q_{\text{total}} = 16.00$, $p = 0.453$; $\Delta d_{\text{species-identity}} = 4.01 \pm 3.11$, $n = 9$, Heterogeneity test; $Q_{\text{total}} = 25.34$, $p = 0.001$; Fig. 3).

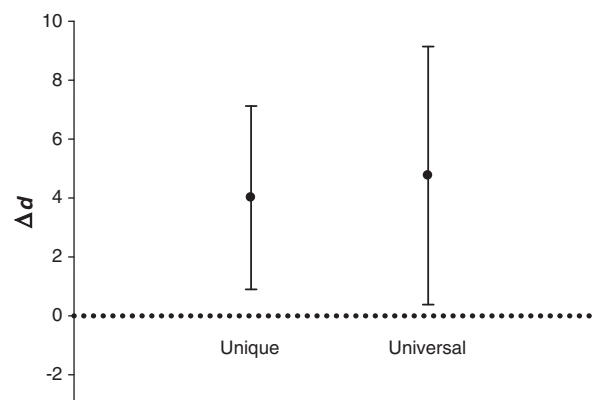


Fig. 3. Cumulative effect sizes (absolute value of the differences in Hedges d between paired responses per experiment) for unique (species-identity; $n = 9$) and universal (density; $n = 17$) impact attributes of the invader. See online appendix for details on effect size calculations.

4. Discussion

Marine invasion impact studies have progressed rapidly, building on a strong tradition of ecologists conducting manipulative field experiments. To date, close to one hundred controlled and replicated impact experiments have been published, of which about 85% have been published only within the last decade (online appendix). This provides an unparalleled opportunity to revisit past experiments to test for generalities regarding invasive species impacts and to guide future scientific activities.

We here reviewed experimental marine invasion impact studies, to investigate if these could be evaluated with respect to universal and unique attributes associated with the invasive organism, the resident biota, the resource levels, and the abiotic conditions. Our review showed that few experiments had tested how the habitat-associated factors, (i.e. the resident biota, resource levels or abiotic conditions) influence impacts. From this analysis we conclude that, although they are likely to be of critical importance, we do not have a mechanistic understanding of how marine habitat attributes modify invasion impacts. In addition, most experiments compared uninvaded controls to a single invaded treatment, making it impossible to distinguish between unique and universal impact-attributes: reported impacts can potentially be explained by any specific genotypic trait, by the invader's density, size, longevity, age, fitness, etc. (traits which all organisms possess) or by a complex combination of all these attributes. The distinction between unique and universal impact attributes may also have an applied importance. Because risk-assessments aim to identify and rank potential high-impact invaders (Dawson et al., 2009), there is an emphasis on species-specific impact-drivers, and alternative (universal) drivers may be overlooked. This may result in questionable management decisions, such as prohibiting species A and allowing importation of species B, when impacts may simply be caused by universal attributes. In short, we believe that the distinction between the universal and unique attributes is crucial to advance our mechanistic and predictive knowledge about what drives the impacts of invasion in marine ecosystems.

Our meta-analysis suggests that the isolated effects of both universal and unique attributes of marine invasive populations determine impacts despite the limitations associated with the relatively small number of case-studies and research bias (result section; online appendix). In addition, we also found indications that certain marine organisms have higher unique and universal impacts than others; for example, invasive predatory crabs (Lohrer and Whitlatch, 2002a, 2002b) differed more in effect sizes than invasive filter feeding tunicates, polychaetes and bryozoa (Ross et al., 2007;

Byrnes and Stachowicz, 2009). Similarly, effects associated with increasing invader densities were also higher for crabs than many filter and deposit feeders (Byers, 2000; Lohrer and Whitlatch, 2002a, 2002b; Ross et al., 2007). These findings indirectly support recent large-scale observations that predatory invaders across ecosystems and biomes have larger detrimental impacts compared to non-predatory invaders (Davis, 2003; Sax et al., 2007). Clearly, more manipulative experiments are needed to test this hypothesis.

The framework for examining invasive species impacts has certain limitations that are worth discussing. First, the distinction between the unique (specific) and universal (general) attributes is not always apparent. These impact attributes could alternatively be interpreted along a 'generality-continuum', being relevant to only a single invasion (e.g. effects from an extremely rare and unique toxin), to a few invasions (e.g., filtering and substratum-forming capacities of certain invasive bivalves and polychaetes, Crooks and Khim, 1999; Heiman and Micheli, 2010), to most invasions (e.g., effects associated with the sex of the invader, although not all organisms have separate sexes, Walton et al., 2002), and to all invasions (e.g., the abundance, range and size of the invader, Parker et al., 1999; Griffen and Byers, 2009; Thomsen, 2010). Secondly, the generality of the impact attribute may change depending on the test-question. For example, the impacts associated with the toxin of a lion fish can be considered relevant to only a single invasion (e.g., how this toxin influences a specific resident organism), but could also be interpreted as a universal attribute if the test focuses broadly on whatever impacts are higher for invasive species with (any type of) toxins compared to invaders without toxins. Furthermore, there may be examples where attributes overlap or are not easily distinguished, such as certain morphological attributes that co-vary with size, age and genotypic traits.

Despite these limitations, the framework is a first step to reduce conflating general/universal attributes, like abundance, size, fitness/vitality/vigor, longevity, priority effects, etc. with more specific (typically genotypic) attributes. Our review highlights that most marine field impact experiments have been conducted as presence-absence experiments where impacts cannot be separated into universal and unique causal agents. Similar problems have been addressed in invasion success studies, where success was interpreted as trait-driven, when it could equally well be explained by propagule pressure (a universal attribute) (Lockwood et al., 2005, 2009; Verling et al., 2005).

We also note that the four basic impact drivers are not necessarily mutually exclusive; marine invasive predators may interact with resident biota in both a resource (living space, food) and non-resource way (interference competition, mutualism). In addition, these drivers do not operate in isolation. For example, it is often suggested that impacts are largest when marine invaders comprise a novel role or function in the invaded habitat (Parker et al., 1999; Ricciardi, 2003; Strayer et al., 2006; Thomsen et al., 2010). This hypothesis combines several impact-drivers, e.g., unique invader attack modes, uniquely naive resident biota, and low abiotic heterogeneity in the invaded habitat resulting in limited enemy escape options. Thus, factorial experiments are needed to separate these individual components. These insights highlight a logistic limitation of the framework; to disentangle universal and unique attributes of just two drivers requires at least 9 treatment-combinations (a minimum of a 3×3 design), which is probably why so few studies were available for our meta-analysis. In addition, more than three test levels will often be required to understand, for instance, density-dependency. Perhaps more marine invasion impact experiments should apply continuous impact-models (regression techniques, Byers, 2000; Kotta et al., 2006) or a combination of categorical and continuous models (Cottingham et al., 2005). Finally, an emphasis on a few general drivers only addresses impact on a very broad mechanistic level, without targeting specific ecological processes. We therefore also suggest that broad

frameworks should include relevant hypotheses, to target any ecological process that is likely to explain a specific invasion event. For example, impacts associated with the 'novel weapons hypothesis' (Callaway and Ridenour, 2004) emphasize a combination of unique traits of both the invader (unique toxins) and resident biota (evolutionary naivety), whereas impacts associated with the 'biotic resistance' hypothesis (Elton, 1958) emphasize a combination of unique and universal attributes of the resident biota.

In conclusion, only a few experiments have tested if impacts by marine invasive species are influenced by universal or unique attributes of the invasive organism. To facilitate a broader understanding of the context-dependency of invasion impacts, we advocate that universal and unique impact-components, whenever possible, are treated as separate test-entities that should be pursued for each of the four impact drivers.

Supplementary materials related to this article can be found online at doi:10.1016/j.jembe.2011.02.033.

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