

REVIEW

Biological mechanisms of marine invasions

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ABSTRACT: With expanding trade resulting in increased global transport of non-native species, a broader understanding of the mechanisms of marine invasions is becoming increasingly crucial. Yet our understanding of marine invasions lags behind that of terrestrial invasions, and this includes our understanding of fundamental biological mechanisms that influence marine invasion success. We used a systematic search of over 3000 peer-reviewed papers to review the marine invasion literature, identify overarching patterns, and help direct future research. We focus on 4 biological mechanisms: negative interactions (e.g. limiting similarity, biotic resistance, enemy release, novel weapons), positive interactions, invader traits, and post-introduction evolution, as they relate to understanding marine invasion success. A total of 470 studies (264 non-native species) were reviewed, resulting in the largest review of biological mechanisms of marine invasions to date. Negative interactions and invader traits received the majority of attention in the literature. Most negative interaction studies documented an increase in invasion success resulting from avoidance or release from competitors or consumer pressure. Consumer pressure, and predation in particular, compared to competition was more commonly documented as a mechanism that can limit invasion success. Despite limited evaluation, positive interactions and post-introduction evolution showed potential for enhancing invasion success. Invader trait studies highlighted the importance of life history and stress tolerance traits. Future studies that examine interactions at multiple scales and utilize multi-faceted approaches, molecular techniques, and predictive modeling will enhance our knowledge and ability to develop strategies to protect native ecosystems.

KEY WORDS: Species invasion · Non-native · Negative interactions · Competition · Consumer pressure · Positive interactions · Invader traits · Evolution

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INTRODUCTION

The anthropogenic transport and subsequent introduction of non-native species into new areas can change patterns of biodiversity, alter ecosystem function, and harm economies and human health (Stachowicz et al. 2002, Schlaepfer et al. 2010, Blackburn et al. 2011, Gurevitch et al. 2011). Marine invasions specifically can impair fisheries and aquaculture production, tourism, and marine infrastructure, often

affecting profit and employment in coastal economic activities (Bax et al. 2003). Invasions have been examined rigorously in terrestrial systems (Catford et al. 2009), yet systematic reviews of invasions in marine systems are still needed. Advancements have been made in testing single invasion hypotheses (biotic resistance; Kimbro et al. 2013) and the patterns and drivers of marine invasions in single geographic regions (North America; Ruiz et al. 2000), but we still lack a broad understanding of how ecological pro-

cesses shape patterns of marine invasions across the globe. This fundamental gap in the literature is likely the result of the more recent acknowledgement of invasive species in marine systems and the uncertainty surrounding the taxonomy and native ranges of many marine species (Ruiz et al. 2000). With the majority of world trade occurring by sea, and trade volume predicted to sharply increase in coming years (Kaluza et al. 2010), invasive species are a growing economic and conservation threat in marine systems (Grosholz 2002). Thus, understanding mechanisms underlying marine invasions is critical for successful mitigation and conservation of marine ecosystems.

Many theoretical frameworks have been developed for invasion biology (e.g. Parker et al. 1999, Barney & Whitlow 2008, Catford et al. 2009, Blackburn et al. 2011, Foxcroft et al. 2011, Gurevitch et al. 2011). While these frameworks differ, have their limitations, and range from simple to complex, there are 2 main points of agreement. First, invasions occur in stages: (1) transport, when species and/or propagules move from one area to another, (2) introduction, when species/propagules are released into a new system, (3) establishment, when a population of introduced organisms becomes self-sustaining, and (4) spread, when the introduced population undergoes range expansion. Second, success in any of these 4 stages of invasion depends on one or more of 3 primary factors: (1) propagule supply, which can be strongly influenced by trade frequency, (2) biological factors, including characteristics of the non-native species and the nature of their interactions with the recipient community, and (3) abiotic characteristics of the recipient ecosystem. Interestingly, the majority of these frameworks, including those intended to unify the field of invasion biology, are informed primarily by research on terrestrial systems, particularly terrestrial plants (13 of 19 frameworks reviewed by Gurevitch et al. 2011).

Although invasion frameworks from terrestrial systems may inform those in marine systems, fundamental biotic and abiotic differences between terrestrial and marine systems make it unlikely that any single conceptual framework will be able to reliably predict invasion dynamics across ecosystems. While the effects of some ecological processes, such as competition, may be similar in both ecosystems (Gurevitch et al. 1992), other processes, such as predation and the influence of regional dispersal to local communities, may be stronger in marine than in terrestrial environments (Shurin et al. 2002, Cornell & Harrison 2013). Differences in facilitative interactions among ecosystems have also emerged, as marine facilitation more commonly involves different trophic levels in com-

parison to terrestrial plant–plant facilitative interactions (Bulleri 2009). The prominence of different life histories (e.g. planktonic life stages, Strathmann 1990) and exposure to different physical forces (e.g. currents, Byers & Pringle 2006) can also affect propagule dispersal and patterns of spread in the marine environment more so than in the terrestrial environment (Kinlan & Gaines 2003, Sorte et al. 2010). The implications of these differences on invasion dynamics, however, are unclear. For example, the strength of biotic resistance mechanisms that employ competitive interactions can be stronger in terrestrial than marine environments, but consumptive biotic resistance as well as the impact of non-native consumers on native populations may be similar (Kimbrow et al. 2013, Paolucci et al. 2013). Therefore, there is a clear need to review the growing literature on marine invasions to better understand marine invasion processes and inform emerging invasion frameworks.

A large majority of invasion hypotheses, which often form the foundation of these frameworks, focus on biological factors (23 of the 29 leading invasion hypotheses reviewed by Catford et al. 2009) as opposed to propagule pressure and abiotic factors, although all 3 factors often operate in conjunction. This focus most likely occurs because propagule pressure is inherently difficult to examine in an invasion context (Levine et al. 2004), and although resource availability can be an important abiotic characteristic that promotes invasion success (Davis et al. 2000), the responses of species to the abiotic environment often hinge on biological factors. Therefore, biological factors are not only tractable to study, but also critical to the invasion process.

Four biological mechanisms (Fig. 1), viz. negative interactions, positive interactions, invader traits, and post-introduction evolution, have received significant empirical attention and are the foundation of many hypotheses for invasion success or failure. First, negative interactions between native and invasive species have been shown to either limit or enhance invasion success. Limiting similarity (MacArthur & Levins 1967) and Darwin's naturalization hypothesis (Darwin 1859) suggest that invasions are enhanced by a lack of competition because native species are functionally distinct, while the biotic resistance hypothesis (e.g. Levine et al. 2004) suggests that invasions are limited by native competitors and other natural enemies. Both the enemy release (e.g. Torchin et al. 2003) and novel weapons hypotheses (Callaway & Ridenour 2004), as well as the long-assumed positive impact of disturbance on invasions (reviewed by Lockwood et al. 2013), predict that invasive species

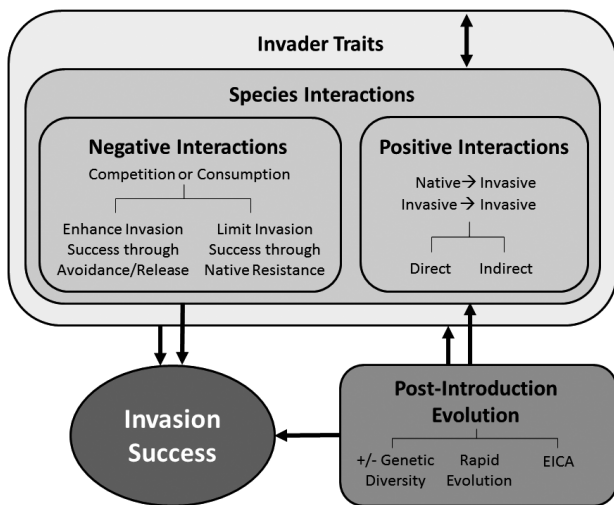


Fig. 1. Conceptual model showing the 4 focal biological mechanisms (negative interactions, positive interactions, invader traits, post-introduction evolution) and their effect on invasion success. Each mechanism is further classified, where relevant, into categories that emerged from the review of the literature. The model serves as an outline for the review, and further shows common ways in which these mechanisms and outcomes are interrelated (arrows). It is not, however, intended to show all possible relationships. Species interactions are nested within invader traits to demonstrate the inherent relationship between these 2 mechanisms.

EICA: evolution of increased competitive ability

thrive in the recipient community because they are freed from natural enemies. These hypotheses, however, along with most other negative interaction hypotheses (e.g. the prey naiveté hypothesis, Sih et al. 2010; the global competition hypothesis, Alpert 2006) center on how invasion success is enhanced or limited via consumer pressure (predation, herbivory, or parasitism) and/or competition (single or multi-species, i.e. diversity). Secondly, positive interactions (i.e. facilitations and mutualisms) among native and invasive species (Bruno et al. 2003) can enhance the ability of invasive species to establish and potentially expand their ranges. Third, hypotheses surrounding invader traits, such as the ideal weed (Elton 1958, Baker 1965) and reckless invader hypotheses (Simberloff & Gibbons 2004), aim to identify biological characteristics of invasive species that contribute to their success. Finally, post-introduction evolution (Hastings et al. 2005), where a non-native species undergoes rapid genetic change in its introduced range, may also increase invasion success.

While terrestrial studies have suggested that these biological mechanisms are among the most fundamental of invasion biology, the extent to which these mechanisms have been studied in marine systems

has not been evaluated (but see Kimbro et al. 2013 for a recent meta-analysis of biotic resistance in marine ecosystems). Therefore, the goals of this study were to (1) review current knowledge on these 4 biological mechanisms (negative interactions, positive interactions, invader traits, and post-introduction evolution) as they relate to invasion success in marine systems, and (2) define emerging avenues of future research. In total, 470 marine studies and 264 species were reviewed (see Tables S2–S5 in the Supplement at www.int-res.com/articles/suppl/m565_p251_supp.pdf), resulting in the largest global review on biological mechanisms of marine invasions to date. Our systematic review approach provides one of the first overviews of an emerging literature on biological mechanisms of marine invasions, identifies overarching patterns in the literature, and helps direct future research.

METHODS

We employed a systematic review procedure using standardized search terms (Table S1 in the Supplement) to identify and review findings about biological mechanisms that can affect invasion success in marine systems. This search was conducted using the Web of Science in April 2014. General search terms used for all mechanisms were 'non-native * OR nonnative * OR invasi * OR introduc * OR non-indigenous OR nonindigenous OR alien OR exotic OR invade * AND estuar * OR marine OR coastal OR ocean * OR sea OR *tidal', followed by specific terms for each of the 4 focal mechanisms (see Table S1). Search results were then refined using Web of Science tools to those pertaining only to 'Marine and Freshwater Biology', and all research areas that were clearly not relevant (e.g. not biological) were excluded. All remaining papers were then individually evaluated for relevance. With the exponential rise in studies on invasion biology since the 1990s (Gurevitch et al. 2011), and the variation in how papers are cataloged in search engines, we acknowledge that standardized searches can miss relevant literature despite a broad list of search terms, which is a caveat of this approach. As such, relevant literature not captured in our search results but known to us were also evaluated in our review. Given this limitation, however, we view the papers included in this review as a large, but probably not comprehensive, sample.

We individually evaluated over 3000 papers. Of these, we identified and reviewed 470 studies that represented a broad sample of available literature

and met conceptual criteria as follows. First, the focal organism had to be a marine species that was non-native to the system in question, regardless of the time since introduction. Secondly, the focal objective of the study had to explore biological mechanisms that influence the degree of invasion success. Here, we define 'invasion success' as any increase in the survival, growth, reproduction, or dispersal of a non-native species. The factor of interest was the performance of the non-native species. Therefore, the many studies that document impacts of non-native species on a native species or community, where the response of the native species or community was the factor of interest, were excluded. All papers that were deemed relevant based on our conceptual criteria were included in the review.

We then classified relevant literature into 4 categories: negative interactions, positive interactions, invader traits, and post-introduction evolution. Studies categorized within negative interactions had to examine consumption (predation, herbivory, or parasitism) or competition (single or multi-species). To be included within positive interactions, studies had to examine a direct or indirect positive interaction (e.g. facilitations, mutualisms) between 2 or more non-native species or between a native and a non-native species. Studies that examined non-native species facilitating natives were not included because this suggested impacts on the native community rather than on invasion success. Studies categorized as invader traits were those that evaluated a specific trait, and post-introduction evolution were those studies that examined reduction or increase in genetic diversity and rapid evolution. While these mechanisms can be interrelated, studies were assigned categories based on the focus of the research. Studies that focused on more than one mechanism, however, were included in more than one category. Such cases, however, represent only 2.3% (11 out of 470 papers) of our total literature database. All studies were also categorized based on the type of research conducted (experimental, observational, meta-analysis/review, or modeling). All modeling studies (Tables S2–S5) with the exception of one (Dunstan & Johnson 2007), used empirical data to inform or test model predictions.

We report both the number of studies in each category, as well as the number of species that have been studied in each category, as a first-order examination of patterns in the literature. Many studies examined multiple species, so each species was documented separately (Tables S2–S5). While all relevant studies were included in our review, only species whose invasion success had been assessed directly were in-

cluded in our species counts. Therefore, we excluded species in our species counts that were derived from large correlative observational studies that explored the diversity of invasive species rather than invasion success of individual species. These large species lists would have inflated our estimates of the number of species that have received direct evaluation of invasion success. Studies of each mechanism were further classified into groupings that emerged during the review process and that demonstrated patterns within the literature (Fig. 1). For example, negative interaction studies were classified as enhancing or limiting invasion success based on findings from each study. A full list of studies and species included in the review, as well as their detailed classifications and associated citations are provided in Tables S2–5.

NEGATIVE INTERACTIONS

Negative interactions among native and invasive species can considerably influence invasion success. These types of interactions are the most studied species interactions in the marine invasions literature (Fig. 2). Sixty-four percent of studies on negative interactions have taken an experimental approach, 33% have taken an observational approach, and only 3% have used a review approach, meta-analysis, or modeling (Fig. 3a). Among the many hypotheses about negative interactions, 5 of the most prominent hypotheses are limiting similarity, Darwin's naturalization, biotic resistance, enemy release, and novel weapons. Limiting similarity (MacArthur & Levins 1967) and Darwin's naturalization hypothesis (Darwin 1859) suggest that invasions are enhanced by a lack of competition from functionally distinct natives,

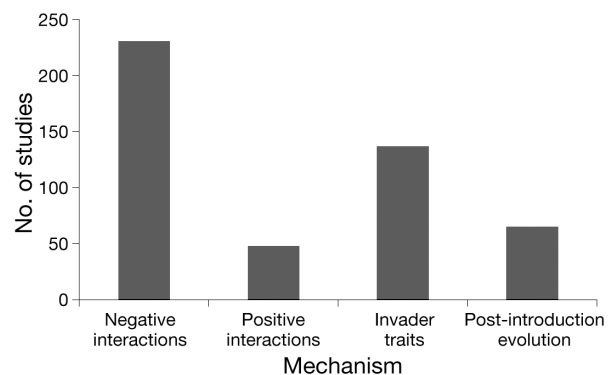


Fig. 2. Number of studies examined for the 4 focal biological mechanisms (negative interactions, positive interactions, invader traits, and post-introduction evolution). Studies total to 481 instead of 470 because some studies addressed multiple mechanisms

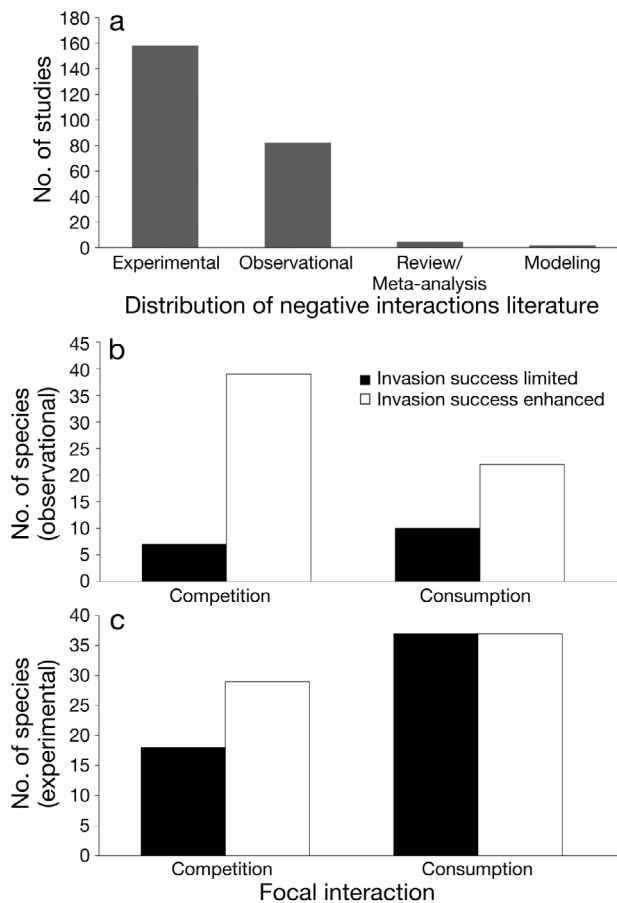


Fig. 3. (a) Distribution of the 239 negative interaction studies, classified by the type of research conducted (experimental, observational, review/meta-analysis, or modeling), and distribution of the 122 species examined in (b) observational and (c) experimental studies. Filled bars indicate where native species are superior competitors or consumers to the non-native species, and thus invasion success is limited (e.g. biotic resistance). Open bars indicate where non-native species either avoid or are released from competitive or consumptive interactions with native species (e.g. use of a different or freed resource, use of a novel weapon, release from enemies, etc.), and thus invasion success is enhanced. Studies total to 247 instead of 239 because 8 studies included experimental and observational components. Species total to 196 instead of 122 because 74 species were found to be both limited and enhanced in different studies and/or by different mechanisms (competition/consumer pressure)

while the biotic resistance hypothesis (Levine et al. 2004) suggests that invasions are limited by native competitors and other natural enemies. Both the enemy release (Torchin et al. 2003) and novel weapons hypotheses (Callaway & Ridenour 2004) predict that invasive species thrive in the recipient community because they are freed from natural enemies. Despite historically being studied separately, these and all other negative interactions hypotheses (e.g. the

prey naiveté hypothesis, Sih et al. 2010; the global competition hypothesis, Alpert 2006) are complementary in that they aim to explain the effects of competition and consumer pressure from native species on the invasion success of non-native species. We therefore frame our discussion around these 2 key factors, competition and consumer pressure, and their effects on invasion success (Fig. 1).

Competition

Competition between native and non-native species is a widely studied aspect of invasion biology. In terrestrial systems, competition from native species can often reduce invasive species establishment and performance (Levine et al. 2004). In the marine environment, however, studies suggest that competition by native species is often not strong enough to limit invasion success; 68 out of 78 invasive species that were evaluated for effects of competition demonstrated enhanced invasion success likely resulting from weak or insufficient competition from the native community (Fig. 3b,c, Table S2). Invasive species successfully established in a non-native range by invading a habitat where a functionally similar native species was absent or uncommon (Bando 2006), utilizing a resource that was different from the native species (Ricciardi & Atkinson 2004), or dispersing and spreading into habitats after disturbance, thereby filling empty niches (Erlandsson et al. 2006). Additionally, 2 meta-analyses revealed that invasive species were more successful in areas where congeners were absent. For example, 66 to 100% of successful, high-impact invaders (including fishes, algae, and plants) in San Francisco Bay, Port Phillip Bay, Chesapeake Bay, the Baltic Sea, and along the New Zealand coast were novel genera (Ricciardi & Atkinson 2004, Ricciardi & Mottiar 2006).

In contrast, fewer experimental and observational studies in the marine environment have demonstrated that specific native competitors can limit invasion success (Fig. 3b,c). For example, the invasive seagrass *Zostera japonica* and the native *Z. marina* coexisted across large spatial scales because of differences in microhabitat use (Ruesink et al. 2010), but *Z. marina* outcompeted *Z. japonica* at small scales where microhabitat use overlapped (Bando 2006). It is important to remember, however, that examples of invasions that failed because of strong competition from native species are very difficult to document and are thus likely to be underreported in the literature.

Invasive species can also face multi-species competition from native communities. Highly diverse systems have long been considered more resistant to invasion than less diverse systems (Elton 1958), since diverse systems may either utilize resources more completely (i.e. niche complementarity) or be more likely to contain a competitive dominant (i.e. sampling effect). However, the diversity–invasibility relationship is also thought to be scale-dependent in both marine and terrestrial systems: native diversity (either taxonomic or functional) is often negatively correlated with invasion success at small scales and positively correlated at large scales (Stachowicz et al. 2002, Byers & Noonburg 2003, Davies et al. 2005, Fridley et al. 2007, Mineur et al. 2008). Marine studies that did not adhere to these expected patterns often suggested that abiotic factors, resource availability, or the presence of specific competitors were more important than native richness in resisting invasions at small scales (e.g. Dunstan & Johnson 2004, Stachowicz & Byrnes 2006). The effect of native diversity on invasion success may also vary temporally and depend on life history stage. For example, native diversity was found to increase recruitment of the invasive macroalga *Sargassum muticum*, but to decrease its growth and survival as an adult (White & Shurin 2007).

Functional diversity may be more influential on invasion success compared to taxonomic diversity within a community. Three experimental studies examined the effects of functional diversity on invasion. All 3 studies concluded that the additive effects of different functional roles in communities can modify resource availability and reduce community invasibility, and that functional diversity may be more important than species richness itself (Arenas et al. 2006, Britton-Simmons 2006, Vaz-Pinto et al. 2012). Therefore, while the influence of competition on invasion success can hinge on habitat characteristics (e.g. Dethier & Hacker 2005), life stage (e.g. Hollebhone & Hay 2007), spatial scale (e.g. Osman & Whitlatch 2007, Cacabelos et al. 2013), and propagule supply (e.g. Williams et al. 2009), functional roles of both native and non-native species may help predict interaction outcomes and invasion success.

Consumer pressure

Invasion success can also hinge on the strength of consumer pressure (predation, herbivory, and/or parasitism) from the native community. There is more evidence in marine systems for consumers limiting inva-

sion success than competitors; 44 out of 82 invasive species evaluated in consumption studies were limited by native consumer pressure (Fig. 3b,c). Marine communities tend to have at least one native generalist consumer (Snyder & Evans 2006, Cebrian et al. 2011), so it is not surprising that consumer pressure can limit non-native species success. The strength and influence of consumer pressure on invasion success, however, may depend on both biotic and abiotic habitat heterogeneity (e.g. Freudendahl et al. 2010, Dumont et al. 2011) and on the defense capabilities of the non-native species (Lemée et al. 1997, Lages et al. 2006). For instance, invasive species may avoid enemies (competitors or consumers) that would otherwise regulate their abundance in their introduced range by releasing novel allelopathic chemicals (Inderjit et al. 2008). In marine systems to date, these ‘novel weapons’ have been observed to increase invasion success in invasive vascular plants ($n = 1$ species) and algae (10 species), but also cnidarians (4 species), gastropods (3 species), and fish (1 species) (Table S2).

Of the 3 types of consumer pressure (i.e. predation, herbivory, and parasitism), predation was most commonly documented to limit invasion. In predation studies, 60% of invasive species studied were shown to be limited by native predation (Table S2). The other 40% of species that experienced enemy release from a lack of native predation were allelopathic (e.g. Mollo et al. 2008), had excellent chemosensory abilities to detect and behaviorally avoid native predators (e.g. Lehtiniemi & Linden 2006), or easily avoided being consumed because of native predator ‘naïveté’ (i.e. native predators not recognizing the invasive species as food, e.g. Kimbro et al. 2009).

In contrast to predation, only 38% of invasive species in herbivory studies were limited by native herbivores, and only 28% of invasive species in parasitism studies were limited by native parasites (Table S2). Of species that had enhanced invasion success resulting from a release from native herbivory, 41% were allelopathic algae (Table S2). The remaining 59% had enhanced success largely because of native herbivore preferences for native plants (e.g. Cebrian et al. 2011), but also through increasing their growth rates in response to consumption (e.g. Ruitton et al. 2006). Although parasitism is common in marine systems, most marine invasive species are transported via cargo ship ballast water during the larval stage, when individuals are relatively free of parasites that are typically present in adult stages (Ruiz et al. 2000). Consequently, marine invasive species appear to be significantly less parasitized than native species in their new

range (Torchin et al. 2002). Much of the existing research on parasite release, however, is heavily biased towards crustaceans (Table S2, Miller et al. 2006), and parasites often exhibit host-specificity (Rohde 1984). Thus, while gaps in the literature exist, studies suggest release from parasites in a non-native range may promote successful establishment (Torchin et al. 2002).

Consumer pressure may also vary geographically and have differential effects on invasion success in different regions. Few empirical studies have examined consumer pressure across large scales, but those that have indicate that native consumer pressure can limit the abundance and distribution of non-native species when they co-occur with specific predators (deRivera et al. 2005, Jensen et al. 2007), and may be strongest in tropical areas (Freestone et al. 2013). Few studies have confirmed whether enemies are important regulators of invasive species in their native ranges (Dang et al. 2009, Vermeij et al. 2009), which is a key assumption of the enemy release hypothesis and a valuable comparison to make when examining how the strength of consumer pressure influences invasion success. Examining consumption across large spatial scales and in both native and invaded ranges of invasive species would greatly increase our understanding of consumer pressure as an invasion mechanism.

Beyond experimental and observational studies, 2 reviews (Purcell et al. 2001, Troost 2010) and a recent meta-analysis of biotic resistance (Kimbrow et al. 2013) have provided useful insight into mechanisms of invasion success in relation to consumer pressure. Both reviews point to a lack of predation in invaded ranges as a major mechanism for invasion of the ctenophore *Mnemiopsis leidyi* (Purcell et al. 2001) and the bivalve *Crassostrea gigas* (Troost 2010) into Europe. The meta-analysis found that consumer pressure was a stronger biotic resistance mechanism than competition, and that native predation was a stronger mechanism than native herbivory in limiting marine invasion success (Kimbrow et al. 2013), which our findings mirror. Targeted meta-analyses examining other mechanisms of invasion and additional multi-scale studies will help clarify strength, generality, and scale dependence of the influence of negative interactions on invasion success.

POSITIVE INTERACTIONS

While negative interactions can either limit or enhance invasion success, positive interactions among

both native and invasive species can also alter invasion dynamics. Forty-eight marine studies of 35 species examined the 2 types of positive interactions that can affect invasion success: (1) invasive species facilitating other invasive species, and (2) native species facilitating invasive species (Figs. 2 & 4, Table S3). Facilitations can either be a direct interaction between 2 species, or an indirect interaction, where 2 species interact through a third species (Bruno et al. 2003). The majority of positive interactions research has been experimental (Fig. 4a), and most evidence suggests that positive interactions promote invasion success (85% of the species examined were facilitated); however, studies showing antagonistic effects between non-native and/or native species are unlikely to be reported as a failed facilitation. The few failed facilitations reported in the literature were limited to one modeling study (Wonham & Pacheřsky 2006) and 8 species studied experimentally (Fig. 4b).

Nineteen of the positive-interaction studies (18 species) demonstrated positive interactions among invasive species that enhanced invasion success; 11 studies (11 species) examined direct effects, 7 studies (7 species) examined indirect effects, and 1 study (1 species) examined both direct and indirect effects (Table S3). Invasive species directly facilitated other invasive species by providing habitat (e.g. Demopoulos & Smith 2010, White & Orr 2011) or ameliorating environmental conditions (e.g. Diederich 2006, Tsai et al. 2010). Indirect effects resulted from a facilitator indirectly increasing settlement (Demopoulos & Smith 2010), survival (Lyons & Scheibling 2008), or another life history parameter of an invasive species by increasing the available food supply (Diederich 2006) or decreasing the risk of predation (Eschweiler & Christensen 2011). Most studies examined invasion facilitation post-establishment except for one example in the dispersal stage. Resulting from its ability to tolerate anti-fouling paint, the bryozoan *Watersipora subtorquata* provided a non-toxic substrate that facilitated settlement and the subsequent transport of other ship-fouling taxa (Floerl et al. 2004). Invasive species may also have a positive feedback, where a non-native species facilitates numerous other invasions in an invasional meltdown (Simberloff & Von Holle 1999). While one observational study demonstrated invasive bryozoans facilitating the settlement and dispersal of around 25 additional invasive species (Zabin et al. 2010), evidence of invasional meltdown is limited (Simberloff 2006).

Positive interactions promoted invasion success in 24 studies (18 species) that examined facilitation between a native species and an invasive species. Four-

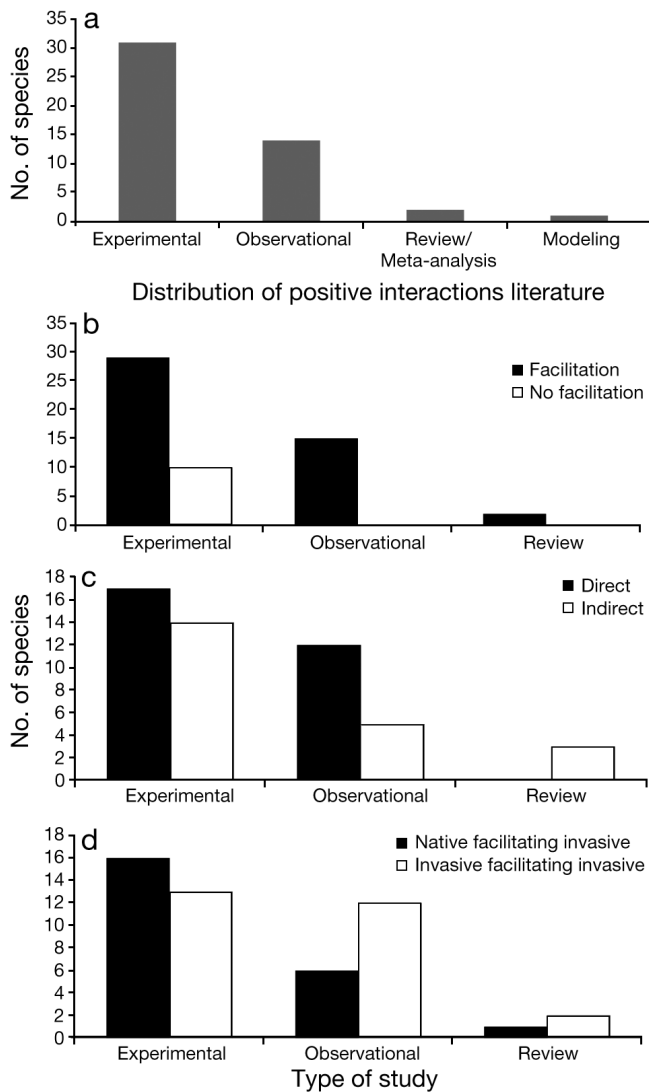


Fig. 4. (a) Distribution of the 48 positive interactions studies, classified by the type of research conducted (experimental, observational, review/meta-analysis, or modeling). (b) Distribution of the 35 species studied that were found to be facilitated (filled bars) or not (open bars). Note that only experimental studies observed a lack of facilitation. (c) Distribution of species studied that were found to be facilitated by direct effects (filled bars) and indirect effects (open bars). Two studies documented both direct and indirect effects. (d) Distribution of species studied that were found to be facilitated by a native species (filled bars) or another invasive species (open bars). Species total to 47 (panels b and d) and 43 (panel c) instead of 35 because several species were studied repeatedly

teen of these interactions (11 species) involved direct effects via habitat formation (e.g. Altieri et al. 2010) and environmental amelioration (e.g. Lopez & Coutinho 2010). One of these direct facilitations was found to be mutualistic; *Spartina alterniflora-foliosa*, a smooth cordgrass hybrid, was found to form novel

associations with native mycorrhizae which facilitated biomass production (Eberl 2011). Eight indirect facilitations (8 species) were found (Table S3), and observed mechanisms were primarily relief from abiotic stress by providing refuge from wave action (e.g. Ruesink 2007) and consumer pressure on a competitor species (e.g. Coma et al. 2011).

Although a consensus exists that positive interactions within marine communities can directly and indirectly shape species invasions and alter existing community structure, most studies examined relatively simple interactions among few species, and only one was conducted at a large spatial scale (Thomsen & McGlathery 2005). While direct facilitative effects were commonly documented to improve invasion success (Fig. 4), benefits were rarely reciprocal; only one mutualism had been studied at the time of our literature search (as described above, Eberl 2011), but other examples are emerging (Kollars et al. 2016). Additional research incorporating more complex interactions and examining larger spatial scales would aid in determining the extent to which positive interactions can promote non-native establishment and spread.

INVADER TRAITS

The outcome of species interactions, both negative and positive, may be mediated by the traits of invasive species. The first hypothesis that directly tested invader traits as a mechanism of invasion success was the ideal weed hypothesis, which proposed that invasions succeed because certain life history characteristics of invading species allow them to outcompete natives (Elton 1958, Baker 1965). The reckless invader hypothesis asserts that invader traits may be advantageous or disadvantageous, depending on environmental conditions, and is a simple theoretical extension of the invader traits concept. Both the sampling hypothesis (Crawley et al. 1999) and global competition hypothesis (Colautti et al. 2006) combine the concepts of propagule pressure and invader traits, positing that with a higher number of species introductions, there is an increased probability of an introduced species having traits that allow it to outcompete native species. The ability to recognize specific traits that contribute to invasion success is a pressing issue in invasion ecology, with important implications for understanding and managing invasions.

Invader traits are a well-studied aspect of marine invasions, with a large representation of experimental studies (Figs. 2 & 5a, Table S4), and numerous life

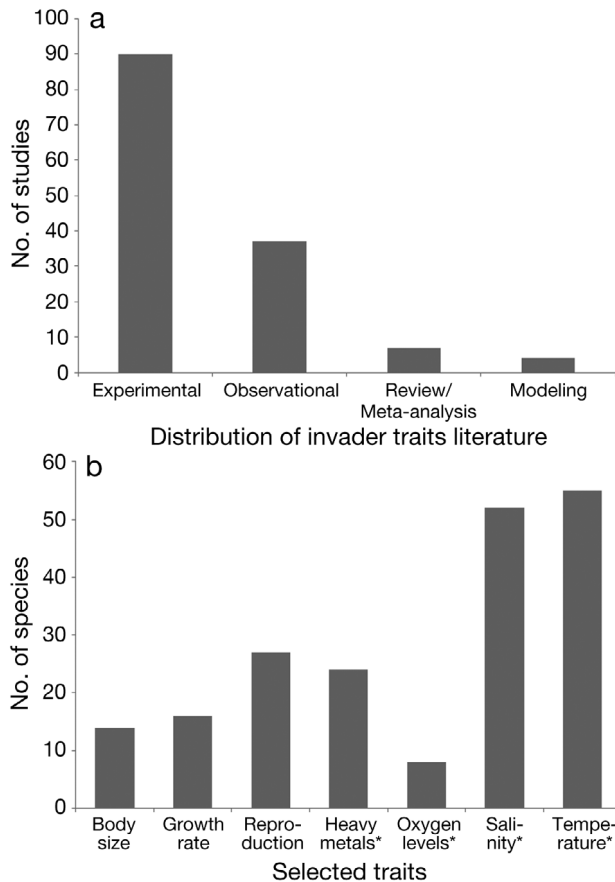


Fig. 5. (a) Distribution of the 137 invader-traits studies, classified by the type of research conducted (experimental, observational, review/meta-analyses, or modeling). (b) Distribution of species studied for a sample of 7 invader traits that received the most empirical attention. A full list of invader traits and corresponding species can be found in Table S4 in the Supplement at www.int-res.com/articles/suppl/m565/p251_supp.pdf. Asterisks indicate response or tolerance to the given stressor

history, reproductive, and stress-tolerance traits have been proposed to facilitate marine invasion success (Fig. 5b, Table S4). Life history traits such as large body size (Roy et al. 2002, Zabin et al. 2007, Ashton et al. 2010), rapid growth rates (Le Cam et al. 2009, Sareyka et al. 2011), and early maturation (Ashton et al. 2010, Sareyka et al. 2011) improve invasion success. In addition, numerous reproductive traits aid invasion success, including high fecundity (Zabin et al. 2007), polyandry (Le Cam et al. 2009), asexual reproduction, long larval durations (Dupont et al. 2007), vegetative propagation (Kahng et al. 2008), and sperm storage (Dineen et al. 2001). Traits that confer a tolerance to one or several environmental conditions have also been extensively studied in marine systems. Marine invasive species are generally tolerant of wide temperature and salinity ranges, hypoxia

(Sareyka et al. 2011), exposure to heavy metals (Piola & Johnston 2006), desiccation (Schaffelke & Deane 2005), and high levels of sedimentation (Glasby et al. 2005). Resulting from the high number of coastal and estuarine invasions (Miller et al. 2007), the role of salinity tolerance in increasing invasion success has received a fair amount of empirical attention, accounting for 38% of the 137 studies examining 110 species for marine invader traits (Figs. 2 & 5, Table S4). Many invasive species also possess traits that confer resistance to commonly employed management techniques, including UV exposure (Raikow et al. 2007), heat shock (Rajagopal et al. 2005), antifouling paint (Dafforn et al. 2009), freshwater immersion, increased salinity (Ovcarenko et al. 2006), and deoxygenation (Raikow et al. 2007). Introduced species lacking one or several of these tolerances have limited invasive potential (Urian et al. 2011) because of the harsh environmental filters imposed by transport of propagules (Raikow et al. 2007) and lack of environmental matching in the new environment (Drake et al. 2007).

As a result of tradeoffs that accompany many life history and stress-tolerance traits, different invasion stages may be mediated by invasive species traits. While invasive species are often assumed to have traits generally associated with good colonizers (r-selected traits such as rapid growth, high fecundity, and extensive dispersal), they also need to cope with potentially harsh biotic and abiotic conditions in the new range, especially when invading naturally resistant communities or degraded, stressful habitats. Traits that facilitate rapid colonization often come at a cost to a competitive advantage (e.g. competition-colonization tradeoff, stress tolerance, or defense against predation; Bishop et al. 2006). For example, laboratory experiments showed that r-selected life history traits (rapid growth and early maturation) that are predicted to enhance colonization of the potentially invasive oyster *Crassostrea ariakensis* also made it susceptible to the native predatory crab *Callinectes sapidus* (Bishop et al. 2006). Tradeoffs may also explain the patchy nature of some invasions. For example, the rapid growth rate of the oyster *Crassostrea gigas* allowed it to quickly overgrow native oysters at the expense of tolerance to abiotic stress, allowing for a patchy coexistence of both species between the relatively stress-free low intertidal and the abiotically-stressful high intertidal region (Krassoi et al. 2008). Even when a clear tradeoff is not evident, certain traits may still differentially facilitate or limit certain invasion stages. For example, the heat tolerance of the mussel *Mytilus galloprovincialis*

facilitated its establishment along the Pacific coast of North America, but its lack of cold water tolerance restricted its northern spread (Lockwood et al. 2010).

The use of meta-analyses to infer the role of key traits, though currently rare in the marine literature, is proving to be useful in predicting broad invasion patterns. One such meta-analysis examined 93 species of successful and failed marine mollusk invasions based on abundance, salinity tolerance, and developmental mode and was able to successfully predict 75 to 100% of invasive species at each of 3 sites (Miller et al. 2007). Another meta-analysis compared traits among 113 species of introduced macroalgae and found that highly invasive species shared a number of simple traits such as temperature and salinity tolerance (Nyberg & Wallentinus 2005). More comprehensive approaches to understanding invader traits, such as comparing invasive and non-invasive populations of a single species (Glasby & Gibson 2007), successful versus failed invasions (Miller et al. 2007), and invasive and native populations of an invasive species (Zabin et al. 2007), may control for a variety of potentially confounding factors, and should therefore be employed in future studies.

Several other areas related to invader traits in marine systems require further study. Studies that go beyond simple correlations and identify mechanisms underlying successful traits are crucial for fully understanding marine invasions. To date, this type of approach has been best shown in studies of thermotolerance in the invasive mussel *M. galloprovincialis*, which not only found a link between thermotolerance and invasion success, but also elucidated the physiological and molecular basis for this tolerance (Lockwood et al. 2010). A final limitation of the current trait-focused research is a strong bias in the taxonomic breadth covered (Table S4). Most studies examined one of 4 major groups: mollusks (32.1% of studies), algae (25.5%), plants (14.5%), or crustaceans (16.7%), while other groups remain relatively less studied: fish (4.4%), cnidarians (2.9%), ctenophores (1.5%), and sponges (1.5%). Notably limited in the literature are studies of traits of invasive microbial organisms (with the exception of one study examining one species), despite their predicted prevalence in marine systems and the likelihood that their transport, establishment, and spread are heavily trait-mediated (Drake et al. 2007).

Although the concept that certain invader traits aid in the invasion of new regions is well-supported, several factors confound efforts to create a unified suite of predictive traits for marine species. One of the major challenges is that many invader traits are difficult to

incorporate into a generic predictive model because they are often specific to a particular invasive species, recipient community, or single-species interaction (Wonham et al. 2000, Taylor et al. 2009). Also, local conditions often dictate the impact of seemingly general traits. For example, although large body size is widely correlated with invasibility (Roy et al. 2002, Zabin et al. 2007, Ashton et al. 2010), some invasive populations were dominated by smaller size classes than found in their native ranges because of a low food supply in the invaded region (Javidpour et al. 2009). Furthermore, species that are not predicted to be highly successful invasive species based on a generic list of traits may become invasive in regions with environmental conditions to which they are pre-adapted (Schlaepfer et al. 2010). Finally, even maladaptive traits may not prevent invasion if they are part of a more complex tradeoff and are coupled with a beneficial trait, or if the species is able to quickly adapt to a new environment through evolution or plasticity (Sarà et al. 2008). Considering the wealth of empirical data on marine invader traits, a focus on more comprehensive (e.g. comparison of invasive and non-invasive introduced species) and synthetic approaches (e.g. meta-analysis) would better advance our understanding of trait-mediated invasion dynamics.

POST-INTRODUCTION EVOLUTION

Most studies view invasive species as 'static entities,' but rapid evolution following introduction is common (Lee 2002, Prentis et al. 2008, Whitney & Gabler 2008) and may influence invasion success. Invasive species can undergo rapid genetic change in response to novel environmental conditions and pressures, resulting in population increases and changes to species traits (Booth et al. 2007, Gilchrist & Lee 2007). Despite the importance of rapid evolution in the establishment and spread phases of invasions, the evolutionary aspects of biological invasions remain understudied (Blair & Wolfe 2004, Gilchrist & Lee 2007). Between 1997 and 2001, less than 5% of the invasion ecology literature considered evolutionary processes (Parker et al. 2003). Sixty-five studies (examining 42 species) investigated the invasion success of marine species resulting from rapid evolution and/or genetic change after introduction to a new environment (Figs. 2 & 6a,b, Table S5). In addition to a handful of examples of rapid evolution, the majority of studies address 2 primary areas of evolutionary research in invasion ecology: (1) the factors that decrease or increase genetic diversity (bottlenecks and

hybridization, respectively) and their impact on invasion success, and (2) the emerging hypothesis of evolution of increased competitive ability (EICA) (Fig. 6b). Unlike the other 3 invasion mechanisms discussed, the majority of post-introduction evolution studies have been observational (40 out of the 65 studies, Fig. 6a), likely because of the inherent difficulty of experimentally examining evolution. While evolution of natives in response to invasive species can also occur (Freeman & Byers 2006, Strauss et al. 2006), we focus our discussion on evolution of non-native species.

Bottlenecks and hybridization

Loss of genetic diversity can occur when a population undergoes a bottleneck, such as when an invasive population is founded by only a few individuals

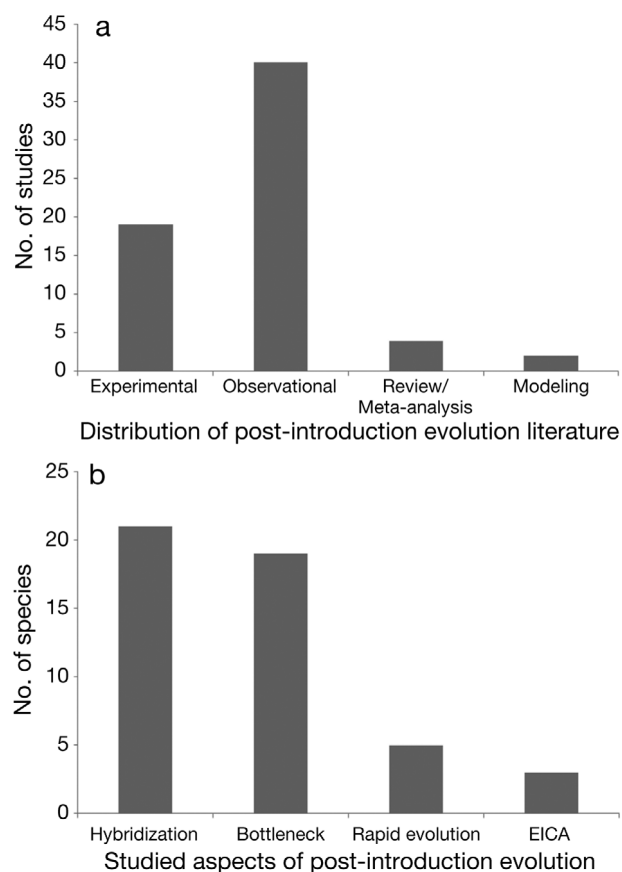


Fig. 6. (a) Distribution of the 65 post-introduction evolution studies, classified by the type of research conducted (experimental, observational, review/meta-analyses, or modeling). (b) Distribution of species studied across 4 aspects of post-introduction evolution. Species total to 48 instead of 42 because of species being included in more than 1 category. EICA: evolution of increased competitive ability

(Prentis et al. 2008). Although bottlenecks are often associated with reduced fitness, studies of post-bottleneck populations indicate that genetic variation might not always be critical to invasion success in marine species (Booth et al. 2007, Roman & Darling 2007, Chandler et al. 2008). Of the 20 studies (19 species) from several continents, habitats, and taxonomic groups examining the effect of bottlenecks on marine invasion success, 9 studies (9 species) found evidence of successful population spread despite a reduction in genetic diversity (Table S5). It remains unclear, however, how vectors of marine invasions, such as hull fouling or ballast water discharge, may influence patterns of propagule dispersal and the likelihood of bottlenecks, and thus affect genetic flow and genetic diversity of invasive populations.

In contrast to the reduction of genetic diversity caused by bottlenecks, hybridization (Allendorf & Lundquist 2003, Booth et al. 2007) introduces new genetic variation into populations of invasive species. In marine systems, hybridization was the most-studied mechanism of post-introduction evolution in marine systems, with a total of 39 studies on 21 different species across 7 phyla (Table S5). All of these studies found evidence of hybridization, and 17 studies (examining 17 species) found that hybridization increased invasion success by enhancing reproductive fitness and rate of spread (Ayres et al. 1999, Nehring & Hesse 2008). Notably, all studies of invasive hybridization in marine systems involved hybridization between an invasive and native species, despite the possibility that invasive–invasive hybridization may also occur. Recent advances in genetic tools (Turon et al. 2003) that can distinguish new mutations from pre-invasion genetic variation (Prentis et al. 2008) will undoubtedly contribute to our understanding of genetic variability and invasion success.

Evolution of increased competitive ability

While evolutionary change certainly occurs within populations of invasive species, studies that document the specific ecological consequences of this change are exceedingly rare. The EICA hypothesis was proposed to explain the difference in success between high- and low-impact invasive species. This hypothesis emerged in response to observations that some invasive plants grow more vigorously and reach larger sizes in their introduced range (Blossey & Notzold 1995). EICA is also known as the competitive release hypothesis (Sorte et al. 2010) or simply as rapid

genetic change, causing a shift from a low- to a high-impact invasion. EICA originally specified that invasive plants freed from herbivores via enemy release will undergo selection for improved competitive abilities (higher biomass and fecundity) rather than herbivore defense (Blossey & Notzold 1995). The EICA hypothesis continues to expand, and has been applied to observed increases in species' biochemical weapons against consumers (also known as allelopathic advantages against resident species; Callaway & Ridenour 2004). Rigorous empirical studies of EICA in marine systems are nearly absent in the literature; one experimental study of EICA examining 3 invasive species of macroalgae found little evidence to support the hypothesis (Hill 2006). Four marine studies on invasive fishes have investigated post-introduction changes in genetic variability (reviewed by Hanfling 2007), and 5 studies of rapid evolution showed increased invasion success through phenotypic plasticity (Raimondi 1992, Smith et al. 2004) and genetic differentiation among invasive populations of the same species (Bjorklund & Almqvist 2010). None of the studies, however, addressed enemy release or increased competitive ability. Thus, EICA is an open avenue for research in marine systems.

CONCLUSIONS

Considering the urgent conservation concerns regarding marine invasions, a greater empirical understanding of the biological mechanisms that drive marine invasion dynamics is needed. This study provides the first review of biological mechanisms that influence the success of marine invasive species (Fig. 1). We found negative interactions and invader traits to be the most heavily studied biological mechanisms of marine invasion, with the greatest number of species studied in the context of negative interactions (Fig. 2, Tables S2–S5).

Several broad patterns were observed in the literature. First, most negative interaction studies documented an increase in invasion success resulting from avoidance or release from competitors or consumer pressure in the non-native habitat (Fig. 3). In contrast, consumer pressure, and predation in particular, compared to competition was more commonly documented as a mechanism that can limit invasion success (Fig. 3). The extent to which negative interactions result in the complete exclusion of non-native species and a failed invasion, however, is difficult to study and not commonly reported in the literature. Second, more experimental and observational studies

of positive interactions documented direct interactions rather than indirect interactions (Fig. 4), which likely resulted from the relative ease of documenting direct interactions in comparison to more complex dynamics. Interestingly, nearly the same numbers of studies have documented native species facilitating the invasion of non-native species (22 studies, 18 species) and non-native species facilitating other non-natives (18 studies, 20 species), suggesting that roughly equivalent attention has been paid to both alternatives (Fig. 4). Third, the field of invader traits has undergone a recent and rapid expansion, with the large majority of studies occurring in the past decade (Table S4). These advances highlight the particular importance of reproductive, life history, and stress-tolerance traits aiding in establishment, and thus may assist in predicting large-scale invasion patterns (Fig. 5). Fourth, post-introduction evolution has the strong potential to enhance non-native species establishment and spread. While current studies suggest that hybridization may be particularly common, EICA remains largely unexplored (Fig. 6b). Post-introduction evolution was also the only one of our 4 focal mechanisms of invasion for which the large majority of studies were observational, rather than experimental (Fig. 6a). It is worth noting that while these patterns emerged from the literature, we cannot conclude that these patterns indeed reflect the frequency of these mechanisms in nature, or simply a bias in the types of studies that are undertaken or published.

Interestingly, our findings highlight differences between biological mechanisms that influence invasion success in marine compared to terrestrial systems. For instance, while allelopathy has mainly been observed in plants in the terrestrial literature, just as many marine allelopathic animal invasions have been documented as algal invasions (Table S2). Also, many widely documented marine invader traits relate to stress tolerances to abiotic conditions that are more common in, if not unique to, marine and aquatic systems, including salinity, dissolved oxygen levels, and desiccation (Table S4). These examples highlight the need to evaluate and synthesize findings from the marine literature to inform a more comprehensive understanding of invasion dynamics across different ecosystems.

AVENUES FOR FUTURE RESEARCH

Despite these advances, several key research areas need empirical attention, specifically the roles of positive interactions and post-introduction evolution in

invasions. Of the total 470 marine invasion studies included in this review, fewer studies (and species studied) investigated positive interactions and post-introduction evolution than the more widely-studied negative interactions and invader traits (Fig. 2). The inclusion of positive interactions in community ecology has lagged behind that of negative interactions more generally (Bruno et al. 2003), and this lag may help explain the more recent appreciation for positive interactions as a driver of invasion success. Further development of post-introduction evolution as a biological mechanism of marine invasions will benefit from recent molecular advances that have great potential to illuminate the evolutionary dynamics underlying successful invasions.

The data available to inform both a theoretical understanding of invasion success and an applied strategy for management for many taxonomic groups is also still limited, as only 11% of known non-native marine species have been studied in the context of these biological mechanisms (Fig. 7). However, the top 3 phyla with the most known non-native species (arthropods, mollusks, and chordates) also have received the most empirical attention (Fig. 7, and see Byers 2009), with an emphasis on experimentally tractable mollusk species (Tables S2–S5). Interestingly, although only 16 non-native and cryptogenic vascular marine plants have been reported worldwide, most have received empirical study (Fig. 7),

probably because of the ease of obtaining and studying marine plants given their shallow coastal distribution. The least studied phyla are the cryptic flatworms, dinoflagellates, and diatoms (Fig. 7), for which basic ecological information is lacking. Scientists may focus efforts on more conspicuous species on the assumption that less-detectable organisms have minimal impacts, but this assumption may be misguided (see Torchin et al. 2002 for a discussion on introduced parasites). Future studies targeting poorly known and functionally distinct species may provide novel insights into mechanisms of invasion.

Future research should also examine invasions across multiple spatial scales. Larger spatial scales encompass heterogeneous environments that affect community structure, patterns of diversity, and strength of species interactions, and could differentially influence invasion dynamics (Freestone et al. 2013). Determining how invasion dynamics vary with spatial scale will aid in predicting the broader impacts of invasive species, from local abundances to global patterns of spread. Additional studies are also needed that compare multiple biogeographic regions of the invader; such comparisons are critical to key invasion mechanisms including enemy release, novel weapons, invader traits, and post-introduction evolution.

Future studies can also more effectively capitalize on recent advances in community phylogenetics, which show promise for clarifying mechanisms underlying invasion success (Strauss et al. 2006, Schaefer et al. 2011). Examining phylogenetic relatedness would provide a way to identify and predict which invasive species, and the traits they possess, might negatively impact native communities (Strauss et al. 2006, Cavender-Bares et al. 2009). In particular, phylogenetic comparisons may yield new insights on how relatedness and functional similarity limit or enhance invasion success. As molecular data become more common and accessible, phylogenetic comparisons can be more effectively utilized to inform marine invasion hypotheses. Coupling both manipulative experiments and community phylogenetic approaches (e.g. Weber & Agrawal 2012) across multiple spatial scales would reveal the relative importance of functional and phylogenetic similarity in limiting the establishment of invasive species, identifying both a

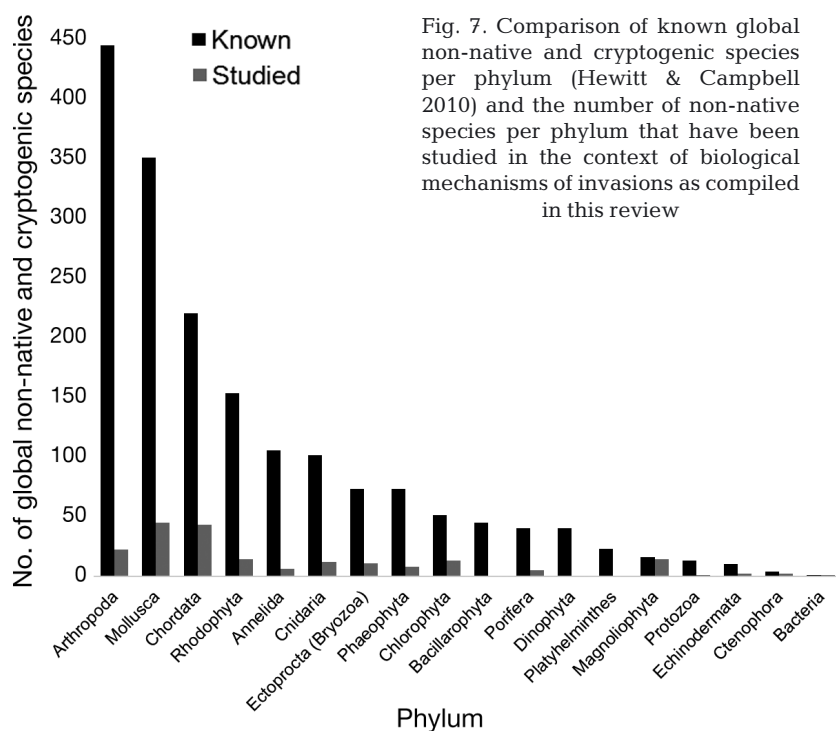


Fig. 7. Comparison of known global non-native and cryptogenic species per phylum (Hewitt & Campbell 2010) and the number of non-native species per phylum that have been studied in the context of biological mechanisms of invasions as compiled in this review

gap in the literature as well as an opportunity for future research.

Studies have also been limited in scope, reducing their power to fully disentangle the ecological complexity inherent in invasion biology. Many studies to date have tested a single invasion hypothesis or mechanism and single stage of invasion. This approach, while experimentally tractable in a simplified system, renders little insight into the relative importance of each mechanism in nature, where many biotic factors influence processes simultaneously. Studies that test multiple hypotheses in conjunction across multiple stages of invasion would not only identify mechanisms of invasion but also their interactive effects (e.g. Noonburg & Byers 2005, Rius et al. 2014). To further develop a conceptual understanding of marine invasion, future research should more explicitly target alternative hypotheses, multiple stages of invasion, and a broader suite of inter-specific interactions.

A final avenue for future research is the development of more comprehensive approaches to predictive modeling in a marine invasion context. Niche models can greatly aid in determining what functional traits restrict the distribution of potentially invasive species in their current range and offer the capability to predict novel or expanding invasions based on environmental factors (Herborg et al. 2009, de Rivera et al. 2011). These models, however, usually employ data on traits and the abiotic environment, and have generally not addressed broad suites of species interactions and transport vectors (propagule supply). An approach that integrates these processes more explicitly would unify many of the mechanisms discussed in this review and may be particularly powerful in informing predictions about future establishment and spread of non-native marine species.

Invasive marine species are establishing in our coastal waters at an accelerating rate (Ruiz et al. 2000), with many more species being transported among environments at a global scale. Understanding the mechanisms that underlie successful or failed invasions is inherently complex, testing the ability of ecologists to apply knowledge of local, regional, and global dynamics to understand and predict the result of countless introductions of propagules. We focus here on biological mechanisms of marine invasions, recognizing that these factors do not operate in isolation and rather are dependent on both abiotic characteristics and propagule supply. Future studies can leverage existing knowledge as well as emerging approaches and technologies to further advance under-

standing of marine invasions and aid in the development of management and prevention strategies to protect our marine ecosystems.

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