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Chapter 8

Comparative Biogeography of Marine Invaders Across Their Native and Introduced Ranges

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COMPARATIVE BIOGEOGRAPHY OF MARINE INVADERS ACROSS THEIR NATIVE AND INTRODUCED RANGES

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Abstract Biological invasions continue to exert extensive environmental and economic impacts. Understanding why some introduced species become invasive is critical to their management. Determining the mechanisms underpinning invasion success has focussed on aspects of the ecology and physiology of the species in the introduced range. Through the application of biogeographic approaches, however, a growing body of research highlights insights that stem from studying invasion success as a biogeographic issue. In particular, a comparison of both biogeographic regions (i.e. the native and introduced ranges) allows exclusive insight into seven different major biogeographic hypotheses that we identified to explain invader success. These include the enemy release hypothesis, niche shifts, trait differences, the evolution of invasiveness, native allies, environmental matching and genetic diversity. All imply a difference or gradient between the ranges that may mechanistically explain an invader's differential performance. This review summarizes the support for these seven different theories underpinning the biogeography of marine invasions and also provides case studies for different theories addressing the comparative biogeography of marine invasions. Additionally, we catalogue the geographic regions of the invasive species used in biogeographic comparisons and the diversity of species, habitats and climate zones examined. Finally, we highlight critical knowledge gaps and suggest future research directions for improving our understanding of the processes driving invasion success.

Introduction

Invasive species are a major source of economic and biodiversity loss globally – costing \$100 billion annually in the United States alone (Pimentel et al. 2005, Meyerson et al. 2019). In the most extreme cases, invasive species can alter native environments, upsetting the balance of native ecosystems by displacing native biota and destabilizing microenvironments (Wright & Gribben 2008, Simberloff et al. 2013, Gribben et al. 2017, 2018). However, not all introduced species are successful, let alone problematic or invasive. Many species fail upon introduction; others form only small, localised populations. Williamson & Fitter (1996) proposed the tens rule, which stipulated that, on average, about 10% of introduced species go on to become invasive, and about 10% of those reach pest (i.e. problematic) status, although there is no quantitative rationale underpinning this rule. A recent quantitative meta-analysis suggests that the percentage of introduced species that can transition along the invasion pathway may, in fact, be much higher than this, specifically about 25%

of non-native plants and invertebrates and about 50% of non-native vertebrates (Jeschke & Pysěk 2018). Regardless, a major interest in the field of biological invasions has been to determine which species would be successful and in what places.

The field of comparative biogeography was recognised by invasion biologists as a useful tool to examine whether there were ways to predict which species perform better in their invasive range (Crawley 1987, Lonsdale & Segura 1987, Van Kleunen et al. 2010, Parker et al. 2013). Differences in species performance that were uncovered might suggest insight into the processes that enable the establishment and spread of species once introduced to a new location. Comparative biogeography also offered a means to test mechanistic theories that had been developed to explain the differential success of invasive species over natives. The gist of these biogeographical comparisons was to ask whether there were environmental or biotic differences in the native versus introduced range that might suggest a context dependency to the success of the invasive species. Such biological differences that depend on context might include a species entering an environment with fewer predators, parasites or competitors. Absent such differences, the success seemingly stemmed from innate taxonomic or physiological characteristics of the species itself, suggesting its invasion had only been hindered by a previous lack of necessary dispersal capabilities (Byers 2009).

Several mechanistic theories have been developed and tested to explain the establishment and spread of invasive species and their differential success over native species (Table 1). Some of these, like propagule pressure or quality (Marshall et al. 2003, 2006, Hollebone & Hay 2007b, Warren et al. 2012, Uyà et al. 2018), disturbance (Hobbs & Huenneke 1992, Burke & Grime 1996, Byers 2002a, Uyà et al. 2017, 2020) and their interaction (Thomsen et al. 2006, Clark & Johnston 2009, Bulleri et al. 2020), require no biogeographic comparisons and simply ask whether the presence/absence or degree of these factors in the introduced range enhances invasion. In the invasion literature, to explore successful invasion, there are three main types of comparative studies. Two of these look exclusively within the introduced ranges and compare invasive introduced species to closely related native species or non-invasive introduced species (Reichard & Hamilton 1997), examining how much relatively better performing they are. The third is the one that we focus on here, which is biogeographical comparisons of an invasive species in its native vs introduced range to ask whether an invasive species' success is related to a change in its performance between ranges and to what factors such a change might be attributed. It is common for invasive species to be non-problematic in their native range (Williamson & Fitter 1996), so determining what has released a species and is causing it to perform differently is of key interest.

To be clear, both introduced range studies and those that involve native and introduced range comparisons often investigate common processes (see Table 1). For example, changes in competition and/or predation can underpin both the escape from natural enemies (studied across both ranges) and biotic resistance (studied in the introduced range only) hypotheses, and a change in positive interactions with native species is central to both the acquisition of native allies (studied across both ranges) and biotic assistance (studied in the introduced range only) hypotheses. One could then ask, 'What is to be gained by having separate hypotheses addressing similar processes?' A key gain may be in the perspective inherent to each. Introduced range studies often emphasise how the invader compares *interspecifically* to the native species around it and also how these interactions might regulate an invader's success or impacts in its introduced range. In contrast, comparative biogeographic approaches (i.e. native-introduced range studies) often compare an invader *intraspecifically* across its two ranges to examine what traits, processes or interaction strengths may explain invasive range success. Thus, the study approach employed will be specific to the question that is being addressed. Essentially, both types of studies ask very different questions, which often do not necessarily inform each other, nor do they need to. Introduced range only studies can demonstrate why an invader is successful and impactful. But without a biogeographic context, those studies cannot speak to the specific mechanism from which such an advantage to the invader stems – for example, inherently advantageous traits, a sufficiently different biotic or abiotic environment that enables success or

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Table 1 Hypotheses for the success of invasive species and whether addressing these hypotheses requires assessment in both the native and introduced range (grey rows) or the introduced range (blue rows) only. Thus, the former category represents the true biogeographic comparisons.

Hypothesis	Definition	Ranges required	Key studies
Enemy release	Loss of natural enemies that control population growth	Both	(Keogh et al. 2017)
Acquisition of native allies	The number or strength of positive interactions with native species differs in the introduced compared with native range	Both	(Reinhart & Callaway 2006, Stout & Tiedeken 2017; Gribben et al., 2020)
Evolution of invasive success	Invaders experience rapid genetic and/or phenotypic changes to new selection pressures (biotic and abiotic) in the introduced range that enhance invasion success (e.g. via increasing competitive ability or acquisition of resources)	Both	(Blossey & Notzold, 1995, Daehler & Strong 1997, Howard et al. 2018)
Founder effects	Degree of reduction in genetic diversity in invasive population	Both	(Roman & Darling 2007, Lejeusne et al. 2014)
Traits	A shift in traits that likely reflects a change in invader fitness in the invasive range	Both	(Grosholz & Ruiz 2003, Gribben et al. 2013)
Environmental matching	Suitability of invasive range to meet the abiotic requirements of the invasive species	Both	(Iacarella et al. 2015, Cope et al. 2019)
Niche shift	Invasive species undergoes changes in environmental (abiotic and/or biotic) niche use or tolerance	Both	(Tepolt & Somero 2014, Sotka et al. 2018, Gewing et al. 2019)
Biotic resistance	The strength of negative interaction (predation and competition) by native species on invading species that slow or preclude establishment and spread of invader	Introduced	(Kimbro et al. 2013, Gribben et al. 2017, Gribben et al. 2018)
Biotic assistance	The strength of positive interaction (facilitation) by native species on invading species that aids establishment and spread of invader	Introduced	(Thomsen & McGlathery 2005, Altieri et al. 2010, Byers et al. 2012, Wright et al. 2016, Wright et al. 2018)
Superior competitive ability	Invader outcompetes native analogues to accrue niche space	Introduced	(Byers 2000, Britton-Simmons 2006, Byers 2009)
Empty niche	Invasive species utilise resources unused by native species	Introduced	(Elton 1958, Levine & D'Antonio 1999, Mack et al. 2000)
Disturbance	Invasive species are better adapted to disturbance	Introduced	(Byers 2002a, Bando 2006, Bulleri et al. 2016, Uyà et al. 2017, 2018)
Species richness	Species-rich communities are more resistant to invasion than species-poor communities	Introduced	(Stachowicz et al. 1999, Clark & Johnston 2011)
Habitat availability	Invasive population size is affected by suitable habitat	Introduced	(Byers 2002b, Gribben et al. 2015, Wright et al. 2016, Wright et al. 2018)
Propagule pressure/ quality	A metric of the intensity of introduction that is often highly positively correlated with establishment and spread of invaders	Introduced	(Clark & Johnston, 2009, Uyà et al. 2018)

Source: Adapted from Hierro et al., 2005. *Journal of Ecology* 93, 5–15.

evolutionary change that has occurred in the invader during or after introduction. Biogeographic comparisons seek such larger mechanistic understanding, and reviews of biogeographic comparisons seek common trends as a step toward predicting invasion success.

Biogeographically relevant hypotheses to explain invader success implicate favourable, and sometimes superior, aspects in the introduced versus the native range. These aspects pertain to one of three areas – 1) the abiotic environment, 2) the biological community or 3) traits of the invasive species itself. First and foremost, the abiotic environment of the invasive range must be suitable (i.e. similar) to the native range. Usually these conditions will match the native range conditions since those are the ones to which the species has adapted for thousands of years. Some studies invoke a compatible, or possibly a more favourable, abiotic environment in the introduced range as a reason for success. Habitat or niche modelling, often approached through joint probability distribution modelling like maximum entropy (maxent), has become a popular approach to determine whether a species can thrive in a new region (Kumar & Stohlgren 2009, Byers et al. 2013, McDowell et al. 2014, Jarnevich & Young 2015). Essentially, these studies examine whether an introduced region matches the native region in the fundamental niche. Data fed into these models are often mostly, if not exclusively, abiotic. Often these models are run only in the introduced range (provided the invader has spread sufficiently to supply the model with enough data for training). But effective approaches have used environmental data and presence/absence locations for a species in its native range to train a niche model and then predicted the species distribution in the introduced range (Verbruggen et al. 2013, Crafton 2015, Robinson et al. 2017).

Second, assuming the abiotic environment in the introduced range provides the proper fundamental niche, differences in the biological community may be considered next to help explain changes in the realised niche that could contribute to invasive success. Most commonly invoked in the area of biological community is the hypothesis of enemy release (Mitchell & Power 2003, Callaway et al. 2004), which refers to the fitness advantage caused by a reduction in predators, parasites, pathogens or competitors in the invasive range compared with the native range.

Often within the introduced range alone, native species richness has been examined as an important mediator of invasion success, with less diverse communities considered to offer more unexploited niche opportunities for invasive species (Stachowicz et al. 1999, Byers & Noonburg 2003, Clark 2013). Similarly, reductions in the density, cover or biomass of spatially dominant species such as foundation species (*sensu* Dayton 1972) can promote the establishment of non-native species by increasing access to limiting resources such as space and light (Valentine & Johnson 2003, Uyà et al. 2018) and by altering below-ground processes, often under microbial control, to the benefit of invasive species (Gribben et al. 2017, 2018; Bulleri et al., 2020). Many mechanisms of invasive success can be addressed without a biogeographical approach (Table 1). In fact, those studies, perhaps due to their relative ease, are far more common. To be clear, the success of an invasive species can often be shown with only evidence gathered in the invasive range. But knowing whether a species is succeeding because of inherently superior traits or because of conditions that are more favourable in the introduced range helps predict future range expansions of that species and the invasion success of other species emanating from the same region or of similar phylogeny. However, studies are rare that quantify differences in the biological community between the native and invasive ranges. Torchin et al. (2003) and Mitchell & Power (2003) compared parasite prevalence and richness patterns in animals and plants, respectively, between the native and introduced range and found substantial support for lower parasite richness in the introduced range. Fewer still are studies that document whether fitness advantages result from the observed reductions in enemies (but see Keogh et al. 2017). Addressing the question of whether invasion success is, in fact, underpinned by higher abundances and/or changes in life-history traits in the introduced compared with native ranges, and the mechanisms that may drive any such shifts, requires biogeographic approaches that incorporate biological and ecological information from both ranges. Thus, biogeographic approaches to invasion success can yield important insights that invasive range-only studies cannot resolve.

Third, the invasive species itself may have traits that help it operate well or better in the introduced range. The rapid spread and impacts of invasive species may be underpinned by changes in key life-history traits (e.g. larger body size) allowing higher abundances in their introduced compared with their native range (Grosholz & Ruiz 2003, Levine et al. 2003, Gribben et al. 2013). However, broad analysis has provided only mixed evidence for enhanced traits in invasive species related to reproduction, size and abundance (Parker et al. 2013). Sometimes the performance of traits is due to a fortuitous matching of the invasive species with an environment where its traits prosper; other times, heightened performance is hypothesised to be due to changes to a species that occur in the introduced range after the introduction process. Such evolution of invasiveness may give invaders enhanced resource acquisition in the introduced compared with the native range. For example, changes in traits may give invasive predators enhanced ability to capture prey. Alternatively, trait shifts may lead to an increase in competitive ability (Blossey & Notzold 1995). For invasive terrestrial plants, a relaxation of natural enemies in the introduced range can enable them to reallocate resources from defence mechanisms into growth and development, thereby evolving to grow taller, produce more biomass and yield more offspring than their native counterparts (Blossey & Notzold 1995, Daehler & Strong 1997). Sotka et al. (2018) showed that invasive species can evolve rapidly in their new environments. Specifically, with a genetically informed climatic niche shift analysis, they demonstrated that native source populations of the red seaweed *Agarophyton vermiculophyllum* occur in colder and highly seasonal habitats, while most invasive populations occur in warmer, less seasonal habitats. This climatic niche expansion predicts that invasive populations evolved greater tolerance for elevated heat conditions relative to native source populations.

As this last example demonstrates, traits may be under genetic control. Thus, many studies directly compare the difference in a species' genetic diversity between the native and introduced range. Authors do not typically link genes to traits; rather, they often infer that reduced genetic diversity compromises a species' ability to adapt well. Although theoretically, genetic bottlenecks are supposed to occur during the introduction process and decrease species' genetic potential to adapt to new environments, genetic bottlenecks in invasive species may not be as frequent as thought (Roman & Darling 2007).

Traditionally, evidence for life-history or abundance shifts of invasive species between introduced and native ranges has come from terrestrial ecosystems (Hierro et al. 2005, Parker et al. 2013). However, for marine invasive species, over the past 15 years or so, evidence for biogeographic changes in their introduced compared with native range has also been steadily increasing for numerous species. An early multispecies review of the published literature by Grosholz & Ruiz (2003) showed that 12 of 19 invertebrate species had higher body size in their introduced range. Providing additional support are the numerous intraspecific biogeographic comparative studies. Such studies clearly show differences in genetic diversity for many taxa, reduced enemies (e.g. parasites) for several invertebrates (Torchin et al. 2001, 2003), increased chemical differences in algae (Hammann et al. 2013), higher abundances and trait increases (e.g. body size; Gribben et al. 2013) of invasive species in their introduced compared with native ranges. Trait increases can also enhance the acquisition of resources. For example, higher attack rates and lower feeding times for the European green crab, *Carcinus maenas*, were related to larger claw size in crabs from some introduced compared with native populations (Howard et al. 2018). Whether larger claw size gives *C. maenas* enhanced competitive ability over native consumers of the same prey is unknown. In addition, recent studies highlight the positive effects native species can have on invader abundance in the introduced range (Rodriguez 2006, Bulleri et al. 2008, Northfield et al. 2018). As an example, Gribben et al. (2020) showed that the abundance of the porcelain crab *Petrolisthes elongatus* in its introduced range was facilitated by the presence of a habitat-forming tubeworm under boulders that was largely absent from its native range. This suggests the acquisition of native allies may also be an important process in determining shifts in the abundance of invasive species (see Reinhart & Callaway 2006, Stout & Tiedeken 2017 for terrestrial examples).

Support for these biogeographic shifts comes from an increasing number of species from a diverse range of marine taxa, including, but not restricted to, ascidians (Gewing et al. 2019), crustaceans (Torchin et al. 2001, Gribben et al. 2013), molluscs (Blakeslee et al. 2012, Riquet et al. 2013), algae (Krueger-Hadfield et al. 2016, Wang et al. 2017), plants (Allen et al. 2015, Guo et al. 2016), cnidarians (Bolton & Graham 2004, Govindarajan et al. 2017) and fish (Cure et al. 2012, Evangelista et al. 2016).

Given the burgeoning interest and increasing number of studies conducting biogeographic comparisons, it is timely to review the current state of knowledge of the evidence for demographic and population changes across native and introduced ranges. In doing so, we also investigate the support for different biogeographic theories underpinning these patterns. In the following sections, we review the current understanding of the biogeography of marine invasions by: 1) providing an overview of published studies of comparative biogeography of marine invasions (e.g. including a synthesis of the locations and habitat in which they have been described, and the species they involve); 2) summarising evidence for various mechanisms underpinning changes in life-history and population characteristics; 3) providing case studies for different mechanisms of a few well-studied examples and 4) discussing key research gaps and providing recommendations for future research into how these studies may improve our understanding of species distributions at biogeographic scales.

Overview of published introduced and native range comparisons

Literature search

We explored the evidence for the key hypotheses (e.g. the enemy release hypothesis, acquisition of native allies, shifts in resource acquisition and/or increased competitive ability, changes in traits, niche shifts, founder effects) that have been the focus of introduced/native range biogeographic comparative studies. We also determined what species were the focus of this research and explored the geographic regions across which biogeographic comparisons were made. For the search of each individual hypothesis, we included terms for native and introduced range because we wanted to capture the literature that specifically addressed hypotheses that required native-introduced range comparisons. *Thus, from our search, only papers that report both introduced and native comparisons in their abstracts were considered further.* For each search, we also included search terms to capture both marine and estuarine studies and those that used different methodologies (e.g. experimental or comparative surveys). Full search terms, and the number of papers returned under the searches, for each of our hypotheses investigated are shown in Supplementary Table 1. All searches were conducted using the Web of Science database by searching the terms in the 'All Fields' category between January 28 and February 4, 2019. Initially we captured 3647 papers, many of which were conducted in the introduced range only and were immediately excluded.

We created two separate databases for papers: one for those that measured shifts in individual, population, and trait metrics (hereafter referred to as 'IPT' papers) and one that measured shifts in genetic diversity between native and introduced ranges. We kept these two categories separate because the metric for genetic studies (genetic diversity) is distinctly different from the trait and population metrics used in the IPT papers. Also, the number of genetics papers was large, and we did not want them to overwhelm interesting physiological and ecological patterns in a combined database. For all papers, we only retained papers that used first-hand collected data from both ranges. We did not consider papers that made comparisons using previously published data. That excluded many studies in this category where, for many, the focus was largely on the introduced range, with only brief ad hoc comparisons with published data from the native range (e.g. Hollebone & Hay 2007a). For the genetics papers, we additionally excluded all those whose primary objective was to

determine source populations or range expansions and did not provide easily extractable tests for shifts in genetic diversity between native and introduced ranges. That is, it was beyond our scope to distil more sophisticated tests that compare genetic structure (e.g. discriminant analysis of principal components relationships among microsatellite genotypes).

For all papers retained, we extracted the following information: date of publication, phylum (e.g. crustacean, mollusc, plant, alga etc.), species identity, regions studied in both ranges (based on oceanographic boundaries as defined by the International Maritime Organisation) and climate zones (binned into traditional zones; Tropical = 0–23.5°; Subtropical = 23.5–35°; Temperate = 35–66.5°; Polar = 66.5–90°) in which populations were sampled in both ranges. We also extracted information on the habitat occupied (hard substrata, sedimentary or pelagic) and tidal height (intertidal, subtidal or pelagic). Hard substrata included both natural (e.g. rocky shores) and artificial substrata, and sedimentary habitats included unvegetated sediments and habitats associated with sediments (e.g. seagrass). We also noted the theory addressed. Often the theory was not explicitly stated, so we assigned theory, where possible, based on the variables measured. Finally, we also noted study type (e.g. comparative surveys, experimental or both) and whether the theory predictions were supported. Often, within papers, there were multiple measures which presented opposing evidence. In these instances, we determined whether there was overall support for the theory addressed based on all the evidence presented. We also provide case studies for individual species that have been a particular focus of biogeographic work and thus provide extended evaluation of various hypotheses.

Results

Of the 3647 papers our searches initially returned, we retained 56 IPT and 29 genetics papers (Tables 2 and 3). Most of the papers only examined species in their introduced range and therefore did not meet our criterion of a biogeographical comparison. The numbers of studies recorded for both IPT and genetics followed similar patterns, steadily increasing for the past 15 years (Figure 1).

In total, both IPT and genetics papers recorded similar numbers of native (25 and 28, respectively) and introduced (28 and 26, respectively) regions studied. For the IPT studies, the Sea of Japan (7 papers), Northwest Pacific (8 papers) and Northeast Atlantic (6 papers) and for the genetics papers the Northwest Atlantic (4 papers) were the most recorded native regions studied (Figure 2A,B; Tables

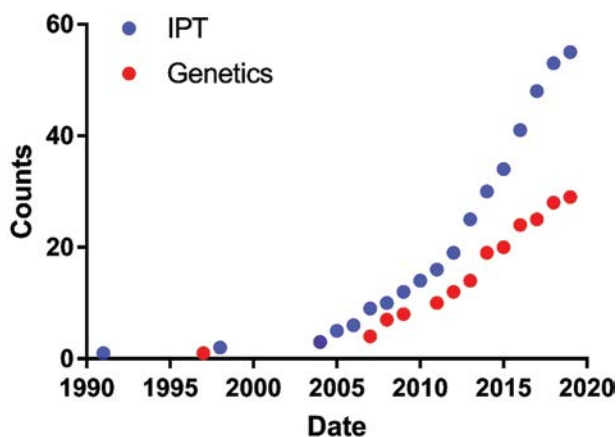


Figure 1 Cumulative list of publications over time of biogeographical comparisons meeting our criteria for inclusion in this review. The publications are categorised into two groups – those that examine individual, population and trait (IPT) metrics and genetic diversity.

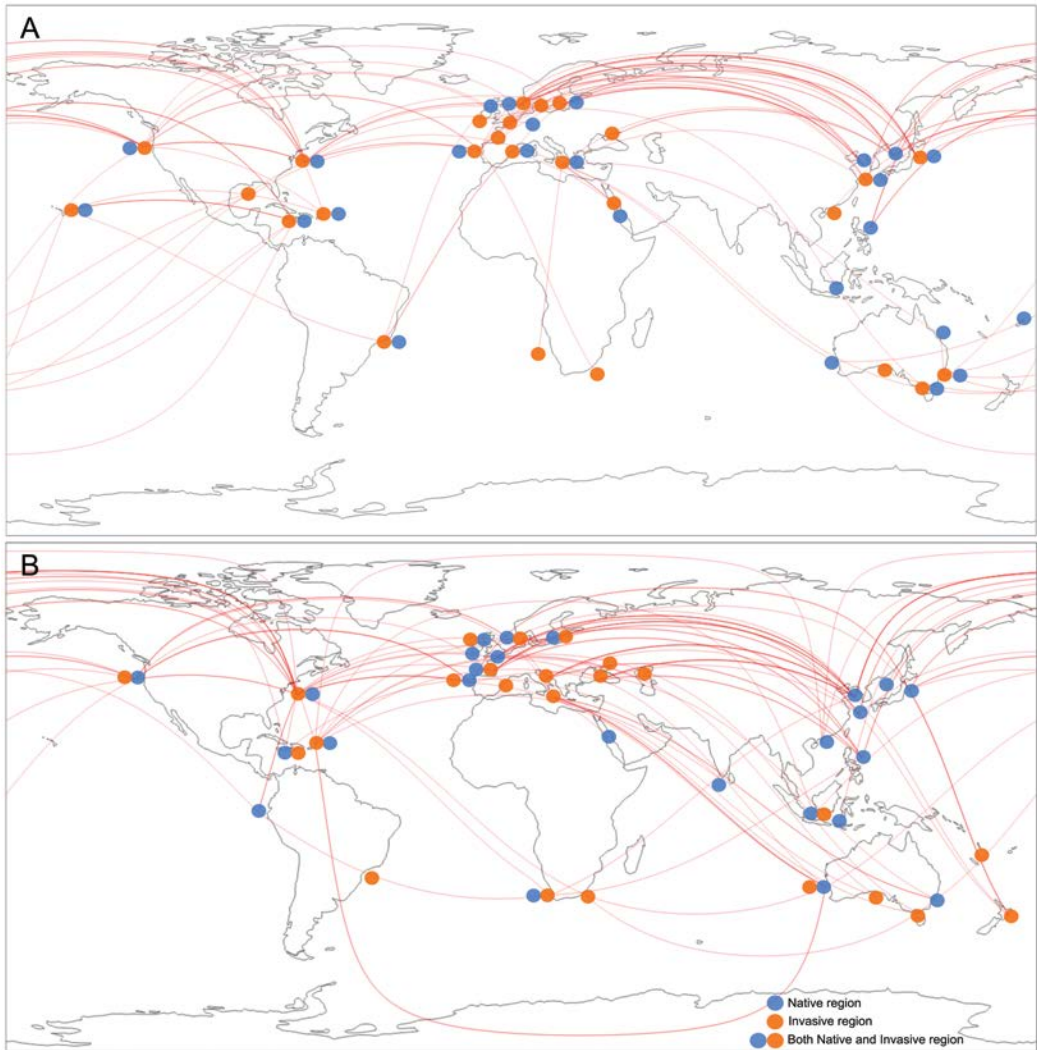


Figure 2 Maps showing native and invasive regions studied for individual population and trait papers (A) and genetics papers (B) retained in our review. For each paper, regions were counted only once if multiple populations were sampled within a region. Solitary dots highlight regions that were only found to be native species regions (blue) or invaded regions (orange) within studies. Regions with both blue and orange dots are both suppliers and receivers of introduced species. Lines always connect blue to orange dots. If it appears otherwise, it is because of a resolution issue in a region that serves as both native and introduced region. Darker lines indicating increased numbers of studies connect the native and recipient regions.

2,3). For both IPT and genetics studies, the Northeast Pacific (13 and 9, respectively), the Northwest Atlantic (13 and 8, respectively) and the Mediterranean Sea (7 and 4, respectively) were the most recorded introduced regions (Figure 2A,B; Tables 2,3).

For the IPT papers and genetics papers, algae and molluscs were the most studied taxonomic groups, respectively, accounting for ~37% of papers in each group (Figure 3A,B). For both IPT and genetics papers, crustaceans and fishes were the next most common taxonomic groups studied (Figure 3A,B). Patterns of species richness within each taxonomic group recorded (Figure 3C,D) were similar to those for number of studies on each taxonomic group.

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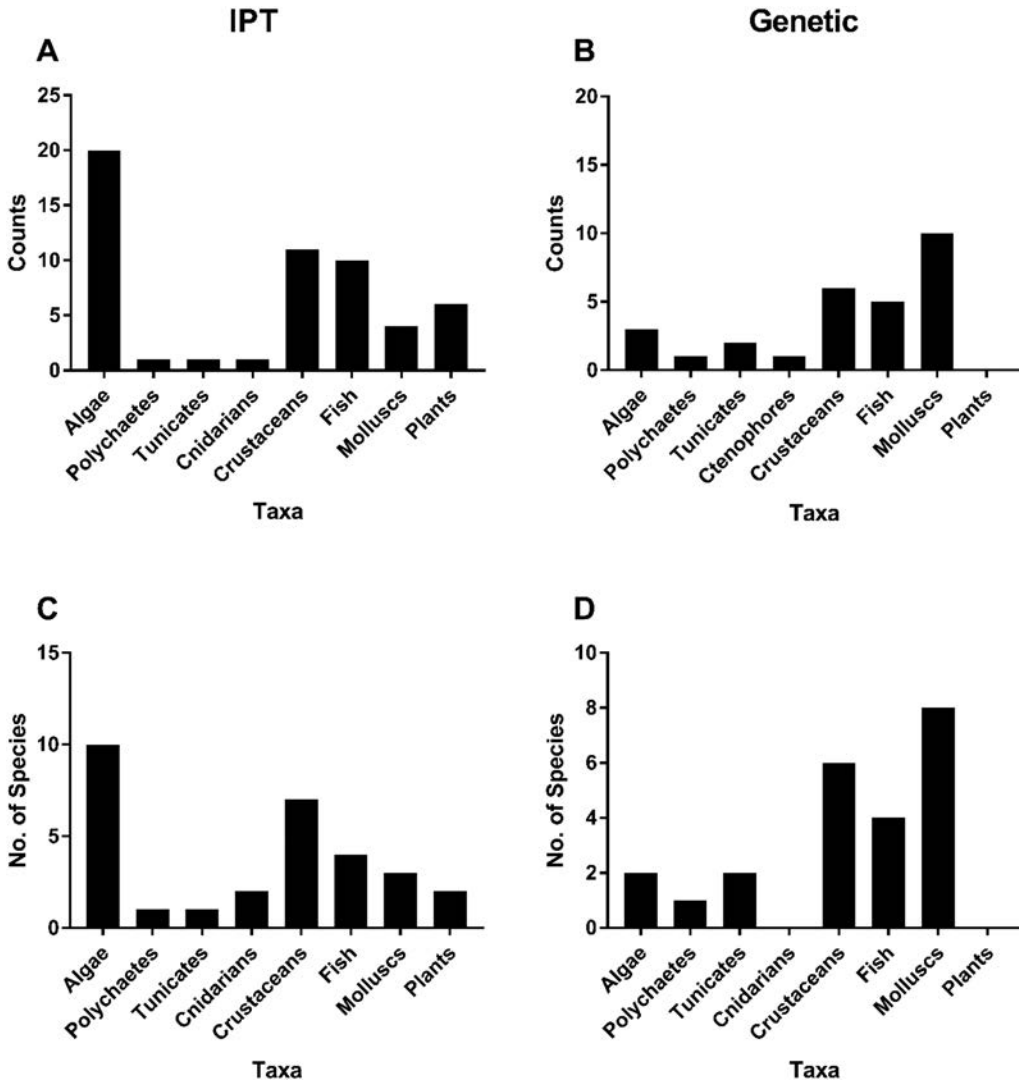


Figure 3 Number of individual population and trait (IPT) and genetic studies within taxonomic group (A,B, respectively) and diversity of species studied within each taxonomic group (C,D, respectively) investigating changes in invasive species across their native and introduced ranges.

For both IPT and genetics papers, across both ranges, most studies (~50%) were conducted in the temperate zone, followed by subtropical and tropical zones (Figure 4A,B). No studies were recorded from either range in polar regions. Within individual studies, the majority recorded similar climate regions for both the native and introduced ranges. Across all studies, there were only three instances where the climate in the native range of study was noted as temperate and in the introduced range as tropical (see Kappas et al. 2004, Riquet et al. 2013, Zanolla et al. 2015, Tables 2,3).

Most studies were conducted on hard substrata (61% and 76% for IPT and genetics studies, respectively), although there was a higher proportion of studies conducted in sedimentary environments for IPT compared with genetic studies (29% and 13%, respectively; Figure 5A,B). Studies conducted in pelagic environments were uncommon. Studies were relatively common at both intertidal and subtidal elevations and rare in pelagic environments (Figure 5C,D).

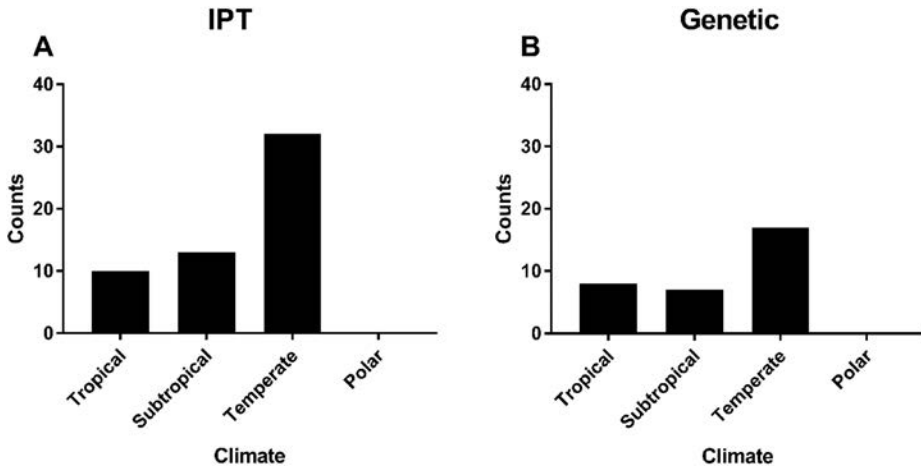


Figure 4 Number of individual, population and trait (IPT) and genetic studies according to the climatic regions of the focal species' introduced range.

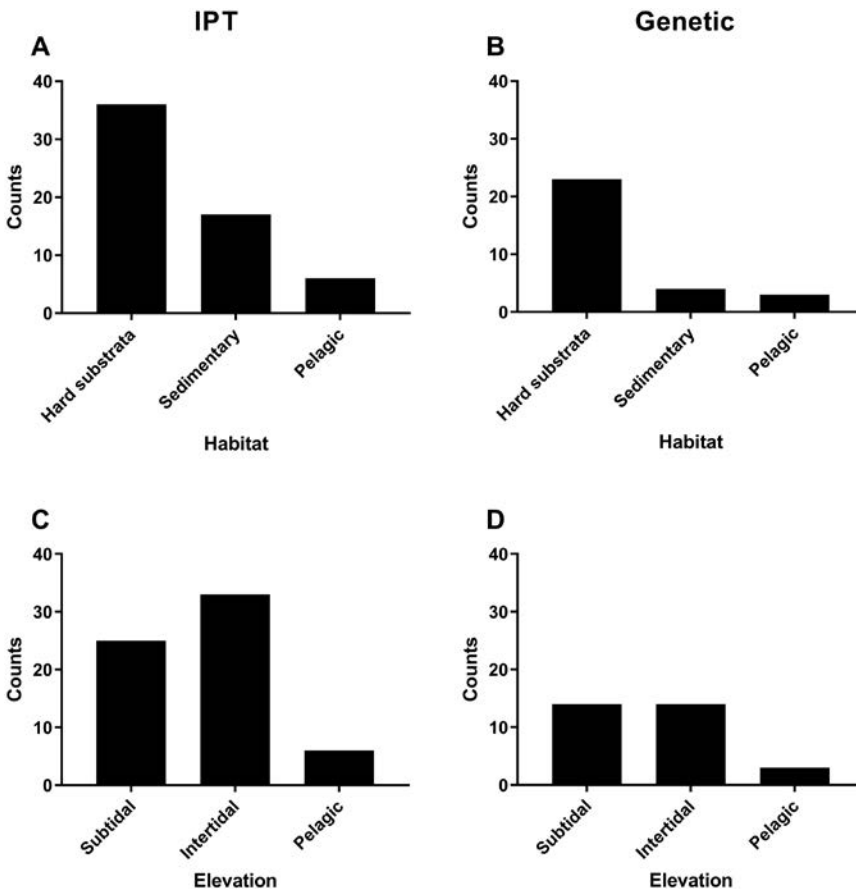


Figure 5 Habitats (A,B) and elevations (C,D) recorded for individual population and trait (IPT) and genetic studies, respectively. Hard substrata, sedimentary, subtidal and intertidal categories were used for species associated with the benthos, while species more closely associated with the water column were termed pelagic.

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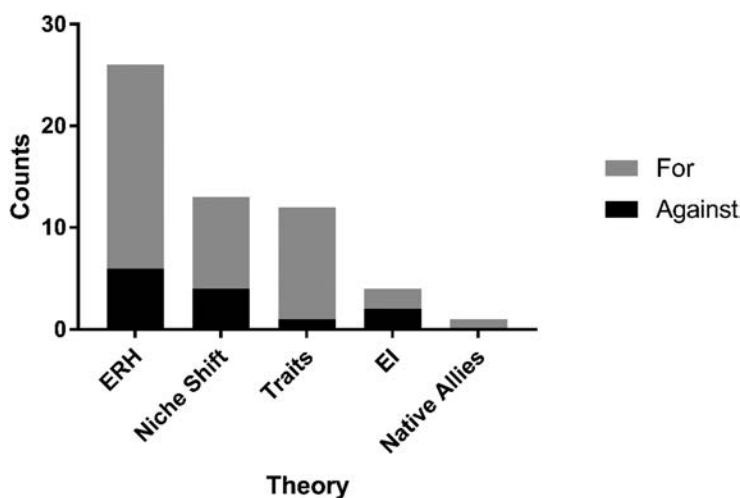


Figure 6 The number of individual population and trait (IPT) papers retained in this review investigating different comparative biogeographic theories to explain invader success (e.g. enemy release [ERH], niche shifts, traits, evolution of invasiveness [EI], and native allies). Grey and black bars indicate number of papers showing support for or against each theory, respectively.

For IPT, the enemy release hypothesis (ERH; 46% of studies) was the most common theory tested, followed by niche shifts (23% of studies) and traits (22% of studies; Figure 6). Overall, there was strong support for the ERH, niche shift and trait theories (Figure 6, Table 2). Support for evolution of invasibility was evident in two out of the four studies that addressed this theory. For the genetics studies, genetic diversity was lower (e.g. in support of founder effects) in 75% studies (Table 3). IPT studies generally employed either mensurative (29 studies) or experimental approaches (21 studies), and only in a few instances did they employ both (6 studies; Table 2). All genetics papers except one were mensurative (Table 3).

For the ERH, because of the higher number of studies recorded (Figure 6), we further explored patterns within this hypothesis. No taxonomic group was particularly over-represented across all ERH studies; however, algae (4 species across 11 studies) and fish (3 species across 8 studies) were the most common taxa studied. *Agarophyton vermiculophyllum* was the most studied alga (6 studies), whereas *Pterois volitans* and *Planiliza haematocheilus* (3 studies each) were the most studied fish species. The most common home ranges studied were the Sea of Japan (7 studies), Northeast Atlantic (5 studies) and Northwest Pacific (5 studies). The introduced ranges featuring in the highest number of studies were the North Sea (8 studies), Northwest Atlantic (6 studies), Northeast Pacific and Baltic Sea (5 studies each). Hard substrata/intertidal habitats (11 studies) were the most common habitat combination studied, followed by hard substrata/subtidal (7 studies), sedimentary/intertidal habitats (5 studies), and pelagic habitats (4 studies). Sedimentary/subtidal habitats were not recorded for any study of the ERH.

Evidence for different hypotheses explaining biogeographic shifts in invasive species

Enemy release hypothesis

The enemy release hypothesis is the most addressed biogeographic theory (Box A; *Littorina littorea*) and one of the hypotheses which received the strongest support, approximately 83%. Much evidence supports the pattern that fewer enemies are present in the introduced range, including predators,

Table 2 List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Allen et al. 2015. <i>Biological Invasions</i> 17: 3419–3432	<i>Phragmites australis</i>	Grass	NE Atlantic	Temperate	NW Atlantic Gulf of Mexico	Subtropical temperate	Sedimentary	Intertidal	Mensurative	Lipara infestation	Higher and Lower	ERH	Mixed
Allen et al. 2015. <i>Biological Invasions</i> 17: 3419–3432	<i>Lipara spp.</i>	Grass	NE Atlantic	Temperate	NW Atlantic Gulf of Mexico	Subtropical temperate	Sedimentary	Intertidal	Mensurative	Abundance	Higher	ERH	Yes
Aires et al. 2013. <i>PLOS ONE</i> 8: 11	<i>Caulerpa cylindracea</i>	Alga	SE Indian Ocean	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Bacterial communities	Higher	Native allies	Yes
Arias et al. 2013. <i>Estuarine, Coastal and Shelf Science</i> 131: 117–128	<i>Perinereis lineata</i>	Worm	Yellow Sea	Subtropical	Mediterranean	Temperate	Sedimentary	Intertidal Subtidal	Mensurative	Variation taxonomic characteristics	Lower	Trait	Yes
Bippus et al. 2018. <i>Marine Biology</i> 165: 39	<i>Agarophyton vermiculophyllum</i>	Alga	East China Sea Sea of Japan	Subtropical Temperate	NE Pacific NW Atlantic North Sea Kattegat NE Atlantic	Temperate	Sedimentary	Intertidal	Experimental	Palatability	Equal	ERH	No
Blakeslee et al. 2012. <i>Journal of Biogeography</i> 39: 609–622	<i>Littorina saxatilis</i>	Snail	NW Atlantic	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Parasite load Parasite richness	Lower Lower	ERH	Yes
Calvo-Ugarteburu & McQuaid. 1998. <i>Journal of Experimental Marine Biology</i> 220: 47–65	<i>Mytilus galloprovincialis</i>	Mussel	Mediterranean	Temperate	SE Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Parasite prevalence	Equal	ERH	No

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Cure et al. 2012. <i>Marine Ecology Progress Series</i> 467: 181–192	<i>Pterois volitans</i>	Fish	Philippines Sea N Pacific	Tropical	W Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Foraging time Prey size Foraging behaviour	Equal Higher Lower	Trait	Yes
Davidson et al. 2008. <i>Biological Invasions</i> 10: 399–410	<i>Sphaeroma quoianum</i>	Isopod	Bass Strait	Temperate	NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal	Mensurative	Population density Habitat use Salinity Range	Higher Similar Similar	Niche shift	No
Davis 2005. <i>Evolutionary Ecology</i> 19: 255–274	<i>Spartina alterniflora</i>	Grass	NW Atlantic	Subtropical	NE Pacific	Temperate	Sedimentary	Intertidal	Experimental	Reproductive effort Size at reproduction Death rate Palatability	Higher Lower	Traits	Yes
Forslund et al. 2010. <i>Fucus evanescens</i> <i>Oecologia</i> 164: 833–840	<i>Fucus evanescens</i>	Alga	NE Atlantic	Temperate	Kattegat	Temperate	Hard substrata	Intertidal	Experimental	Palatability	Lower	ERH	Yes
Gewing et al. 2019. <i>Biological Invasions</i> 21: 349–361	<i>Herdmania momus</i>	Ascidian	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Experimental	Temperature tolerance	Higher	Niche shift	Yes
Glasby, 2007. <i>Marine Biology</i> 152: 255–263	<i>Caulerpa taxifolia</i>	Alga	Coral Sea	Tropical Subtropical	Tasman Sea	Subtropical	Hard substrata Sedimentary	Subtidal	Experimental	Growth response to temperature	Lower or Equal	Niche shift	No
Gribben et al. 2013. <i>Biological Invasions</i> 5: 1877–1885	<i>Petrolisthes elongatus</i>	Crab	SW Pacific	Temperate	Tasman Sea Bass Strait	Temperate	Hard substrata	Intertidal	Mensurative	Abundance Male biomass Female biomass Sex ratio	Higher Higher Equal	Traits	Yes
Guiry & Dawes 1992. <i>JEMBE</i> 158: 197–217	<i>Asparagopsis armata</i>	Alga	Bass Strait	Temperate	Celvic Sea Mediterranean	Temperate	Hard substrata	Subtidal	Experimental	Reproductive success	Higher	Trait	Yes

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Guo et al. 2016. <i>Biological Invasions</i> 18: 2555–2561	<i>Phragmites australis</i>	Grass	Mediterranean	Subtropical	NW Atlantic	Subtropical	Sedimentary	Intertidal	Experimental	Chlorophyll concentrations	Lower	Niche shift	Yes
Guo et al. 2014. <i>Evolution and Ecology</i> 4: 4567–4577.	<i>Phragmites australis</i>	Grass	North Sea Baltic Sea Adriatic Sea	Temperate	NW Atlantic	Temperate	Sedimentary	Intertidal	Experimental	Shoot number Shoot height Biomass allocation	Higher Higher Higher	Trait	Yes
Hammann et al. 2013. <i>Marine Ecology Progress Series</i> 486: 93–101	<i>Agarophyton vermiculophyllum</i>	Alga	East China Sea Yellow Sea	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate Subtropical	Hard substrata	Intertidal Subtidal	Experimental	Biomass consumption C:N ratios	Lower Higher	ERH	Yes
Hammann et al. 2016. <i>Harmful Algae</i> 51: 81–88	<i>Agarophyton vermiculophyllum</i>	Alga	Sea of Japan Yellow Sea	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate subtropical	Sedimentary	Intertidal	Experimental	Chemical compounds	Higher	ERH	Yes
Hammann et al. 2016. <i>Marine Biology</i> 163: 104	<i>Agarophyton vermiculophyllum</i>	Alga	Sea of Japan	Temperate	Baltic Sea North Sea English Channel NE Pacific	Temperate subtropical	Sedimentary	Intertidal	Experimental	Heat stress survival HSP70 expression	Higher Higher	Niche shift	Yes

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Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Henkel et al. 2009. <i>Marine Ecology Progress Series</i> 386: 1–13	<i>Undaria pinnatifida</i>	Alga	Sea of Japan	Temperate	NW Pacific	Subtropical	Hard substrata	Intertidal Subtidal	Experimental	HSP70 expression	Equal	Niche shift	No
Howard et al. 2018. <i>PeerJ</i> 6: 22	<i>Carcinus maenas</i>	Crab	Inner Seas	Temperate	SW Atlantic NE Pacific NW Atlantic	Subtropical temperate	Hard substrata	Intertidal	Both	Foraging behaviour Morphology Prey handling time Feeding rates	Higher Higher Lower Higher	Evolution of invasibility	Yes
Kappas et al. 2004. <i>Marine Biology</i> 146: 103–117	<i>Artemia franciscana</i>	Shrimp	NE Pacific	Temperate	South China Sea	Tropical	Pelagic	Pelagic	Both	Reproductive output at high temperatures	Higher	Niche shift	Yes
Keogh et al. 2017. <i>Ecology</i> 98: 2241–2247	<i>Hemigrapsus sanguineus</i>	Crab	NW Pacific Sea of Japan	Temperate	NW Atlantic	Temperate	Hard substrata	Intertidal	Both	Parasite load Infection rate O ₂ consumption	Lower Higher Lower	ERH	Yes
Krueger-Hadfield et al. 2016. <i>Molecular Ecology</i> 25: 3801–3816	<i>Agarophyton vermiculophyllum</i>	Alga	NW Pacific	Temperate	NW Atlantic NE Atlantic NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal Subtidal	Mensurative	Life cycle complexity	Lower	Niche shift	Yes
Marquet et al. 2013. <i>Biological Invasions</i> 15: 1253–1272	<i>Mytilus galloprovincialis</i>	Mussel	NE Atlantic	Temperate	SW Indian Ocean	Temperate	Hard substrata	Intertidal	Mensurative	Endolithic infestation Mortality	Higher Higher	ERH	No
McGaw et al. 2011. <i>Marine Ecology Progress Series</i> 430: 235–240	<i>Carcinus maenas</i>	Crab	Irish Sea	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Body size	Higher	Trait	Yes

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Meyer & Dierking 2011. <i>Marine Ecology Progress Series</i> 439: 203–212	<i>Cephalopholis argus</i>	Fish	S Pacific	Tropical	N Pacific	Tropical	Pelagic	Pelagic	Mensurative	Length Biomass Growth Body condition Stomach vacuity rate	Higher Higher Higher Higher Lower	ERH	Yes
Pascual et al. 2015. <i>Marine Ecology-an Evolutionary Perspective</i> 36: 994–1002.	<i>Aurelia aurita</i>	Jellyfish	Balearic Sea	Temperate	Red Sea (Gulf of Eilat) Baltic Sea	Subtropical temperate	Pelagic	Pelagic	Experimental	Diet breadth Survival	Higher Lower or Equal Higher	Niche shift	Mixed
Pechenik et al. 2017. <i>Invertebrate Biology</i> 136: 394–402.	<i>Crepidula fornicata</i>	Snail	NW Atlantic	Temperate	North Sea	Temperate	Hard substrata	Intertidal	Mensurative	Egg capsule size Egg density Egg capsules per brood	Higher Equal Higher	Niche shift	Yes
Pickholtz et al. 2018. <i>Biological Invasions</i> 20: 3499–3512.	<i>Siganus rivulatus</i>	Fish	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Home range movement Site fidelity	Higher Lower	Trait	Yes
Pusack et al. 2016. <i>Environmental Biology of Fishes</i> 99: 571–579.	<i>Pterois volitans</i>	Fish	SW Pacific	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Total length	Higher Higher	ERH	Yes

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Qing et al. 2012. <i>Journal of Experimental Marine Biology and Ecology</i> 416: 230–236	<i>Spartina alterniflora</i>	Grass	NW Atlantic	Subtropical	East China Sea	Subtropical	Sedimentary	Intertidal	Experimental	Herbivory tolerance	Higher	ERH	Yes
Ros et al. 2014. <i>Estuarine Coastal and Shelf Science</i> 139: 88–98	<i>Caprella scaura</i>	Amphipod	SW Atlantic	Subtropical	Balearic Sea	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Diet composition	Equal	Evolution of invasibility	No
Ros et al. 2014. <i>Estuarine Coastal and Shelf Science</i> 139: 88–98	<i>Paracaprella pusilla</i>	Amphipod	SW Atlantic	Subtropical	Balearic Sea	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Diet composition	Equal	Evolution of invasibility	No
Roth-Schulze et al. 2018. <i>Limnology and Oceanography</i> 63: 459–471	<i>Caulerpa taxifolia</i>	Alga	SW Pacific	Tropical Subtropical	Great Australian Bight	Subtropical	Sedimentary	Subtidal	Experimental	Growth rate	Equal	Niche shift	No
Saha et al. 2016. <i>Journal of Ecology</i> 104: 969–978	<i>Agarophyton vermiculophyllum</i>	Alga	East China Sea Yellow Sea	Temperate	Baltic Sea North Sea NE Pacific	Temperate Subtropical	Hard substrata	Intertidal Subtidal	Experimental	Chemical defence against fouling	Higher	ERH	Yes
Sarabeev. 2015. <i>Parasitology International</i> 64: 6–17	<i>Planiliza haematochella</i>	Fish	Sea of Japan	Temperate	Mediterranean	Subtropical	Pelagic	Pelagic	Mensurative	Parasite richness Parasite assemblage size	Lower Higher	ERH	Yes

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Sarabeev et al. 2018. <i>International Journal for Parasitology</i> 48: 793–803	<i>Planiliza haematochella</i>	Fish	Sea of Japan	Temperate	Sea of Azov	Temperate	Pelagic	Pelagic	Mensurative	Monogenean prevalence	Equal	ERH	Yes
Sarabeev et al. 2017. <i>International Journal for Parasitology</i> 47: 687–696	<i>Planiliza haematochella</i>	Fish	Sea of Japan	Temperate	Sea of Azov	Temperate	Pelagic	Pelagic	Mensurative	Monogenean abundance	Higher		
Schaefer & Zimmer. 2013. <i>Marine Ecology Progress Series</i> 483: 221–229	<i>Carcinus maenas</i>	Crab	Baltic Sea	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Both	Claw size Body size Handling time	Higher Higher Equal or Lower	Evolution of inva-	Yes
Schwartz et al. 2017. <i>PLOS ONE</i> 12: e0189761	<i>Sargassum muticum</i>	Alga	NW Pacific	Subtropical	North Sea	Temperate	Hard substrata	Intertidal	Mensurative	Handling success Defence chemicals	Equal or Higher Lower	ERH	No
Schwartz, et al. 2016. <i>Marine Biology</i> 163: 13	<i>Sargassum muticum</i>	Alga	NW Pacific	Subtropical	North Sea	Temperate	Hard substrata	Intertidal	Both	Palatability Nutritional value Herbivore preference	Higher Lower Higher	ERH	No

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Shenkar & Loya. 2008. <i>Biological Invasions</i> 10: 1431–1439	<i>Herdmania momus</i>	Ascidian	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Habitat depth Length Total weight Gonad weight Egg diameter Occurrence of symbionts Reproductive season	Higher Higher Higher Lower Lower Equal Lower	Trait	Yes
Sikkel et al. 2014. <i>PLoS ONE</i> 9: 8.	<i>Pterois volitans</i>	Fish	Philippines Sea	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Experimental	Parasite susceptibility	Equal	ERH	No
Sotka et al. 2018. <i>Evolutionary Applications</i> 11: 781–793	<i>Agarophyton vermiculophyllum</i>	Alga	NW Pacific	Temperate	NE Atlantic English Channel North Sea NE Pacific NW Atlantic	Temperate	Sedimentary	Subtidal	Mensurative	Thermal tolerance Salinity tolerance	Higher Higher	Niche shift	Yes
Tepolt & Somera. 2014. <i>Journal of Experimental Biology</i> 217: 1129–1138	<i>Carcinus maenas</i>	Crab	North Sea NE Atlantic	Temperate	NW Atlantic NE Pacific	Temperate	Hard substrata	Intertidal	Experimental	Gradients in thermal tolerance Acclimation plasticity	Unclear	Niche shift	Yes
Tuttle et al. 2017. <i>Biological Invasions</i> 19: 563–575	<i>Pterois volitans</i>	Fish	Philippines Sea	Tropical	NW Atlantic Caribbean	Tropical	Hard substrata	Subtidal	Mensurative	Parasite prevalence	Lower	ERH	Yes
Vermeij et al. 2009. <i>Biological Invasions</i> 11: 1463–1474	<i>Acanthophora spicifera</i>	Alga	Caribbean	Tropical	N Pacific	Tropical	Hard substrata	Intertidal	Experimental	Herbivory pressure Growth	Lower Higher	ERH	Yes

(Continued)

Table 2 (Continued) List of studies retained in this review that use comparative approaches to measure changes firsthand in individuals, populations or traits of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence in support of the theory.

Reference	Species	Taxon	Native region	Native climate	Introduced region	Introduced climate	Habitat	Tidal height	Study type	Measure	Finding	Theory	Support
Vignon et al. 2009. <i>Parasitology Research</i> 104: 775	<i>Cephalopholis argus</i>	Fish	SW Pacific	Tropical	N Pacific	Tropical	Hard substrata	Subtidal	Mensurative	Parasite prevalence	Lower	ERH	Yes
Wang et al. 2017. <i>Journal of Ecology</i> 105: 445–457	<i>Agarophyton vermiculophyllum</i>	Alga	NW Pacific Yellow Sea	Temperate	Baltic Sea North Sea Bay of Biscay	Temperate	Sedimentary	Intertidal	Experimental	Chemical defence against biofouling	Higher	ERH	Yes
Wang et al. 2017. <i>Marine Biology</i> 164: 193	<i>Agarophyton vermiculophyllum</i>	Alga	NW Pacific	Temperate	Baltic Sea North Sea	Temperate	Sedimentary	Subtidal	Experimental	Biofouling pressure	Lower	ERH	Yes
Wikström et al. 2006. <i>Oecologia</i> 148: 593–601	<i>Fucus evanescens</i>	Alga	NE Atlantic	Temperate	Kattegat	Temperate	Hard substrata	Intertidal	Both	Herbivore assemblage preference	Lower	ERH	Yes
Wright 2005. <i>Marine Biology</i> 147: 559–569.	<i>Caulerpa taxifolia</i>	Alga	Coral Sea	Subtropical	Tasman Sea	Subtropical	Sedimentary	Subtidal	Mensurative	Thallus size Thallus density Asexual reproduction	Lower Higher Higher	Trait	Yes
Zabin et al. 2007. <i>Biological Invasions</i> 9: 523–544.	<i>Chthamalus proteus</i>	Barnacle	Caribbean SW Atlantic	Tropical	N Pacific	Tropical	Hard substrata	Intertidal	Mensurative	Habitat use Body size Fecundity	All Equal	Trait	No
Zanolla et al. 2015. <i>Biological Invasions</i> 17: 1341–1353.	<i>Asparagopsis taxiformis</i>	Alga	Coral Sea	Tropical	Mediterranean	Temperate	Hard substrata	Inter-tidal/ subtidal	Experimental	Photosynthetic plasticity	Higher	Trait	Yes

Table 3 List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Anderson et al. 2017. <i>Journal of Fish Biology</i> 91: 558–573	<i>Chromis limbata</i>	Fish	SE Atlantic	Tropical	SW Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity – number of haplotypes	Invasion dynamics	Lower	Yes
Andrew & Ward. 1997. <i>Marine Ecology Progress Series</i> 152: 131–143	<i>Sabella spallanzanii</i>	Worm	Mediterranean English Channel	Temperate	East Indian Ocean Great Australian Bight	Subtropical	Hard substrata sedimentary	Subtidal	Mensurative	Allozyme	Invasion dynamics	Lower	Yes
Blakeslee et al. 2008. <i>Mol. Ecol.</i> 17: 3684	<i>Littorina littorea</i>	Snail	Skagerrak NE-Atlantic Gulf of Biscay Celtic Sea Irish Sea North Sea English Channel	Temperate	NW Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Cahill and Viard. 2014. <i>Marine Biology</i> 161: 2433–2443	<i>Crepidula convexa</i>	Snail	NW-Atlantic English Channel	Temperate	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No
Chandler et al. 2008. <i>Molecular Ecology</i> 17: 4079–4091	<i>Rapana venosa</i>	Snail	Bolhai Sea Yellow Sea East China Sea Philippines Sea	Temperate	Black Sea Adriatic Sea Gulf of Biscay English Channel NW Atlantic	Temperate	Sedimentary	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

(Continued)

Table 3 (Continued) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Cohen et al. 2014. <i>Biological Invasions</i> 16: 1743–1756	<i>Megalobalanus coccopoma</i>	Barnacle	Eastern Pac	Tropical	NW Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No
Coleman et al. 2014. <i>Molecular Ecology</i> 23: 5552–5565	<i>Abudofduf vaigiensis</i>	Fish	Indo-Pacific	Tropical	Pacific	Tropical	Hard substrata	Subtidal	Mensurative	Genetic diversity – haplotype diversity	Invasion dynamics	Higher	Yes
Dias et al. 2018. <i>Biological Invasions</i> 20: 1749–1770	<i>Perma viridis</i>	Bivalve	Laccadive Sea South China Sea Java Sea Flores Sea	Tropical	W Atlantic	Tropical	Hard substrata	Intertidal	Mensurative	Genetic diversity – number of haplotypes	Invasion dynamics	Lower	Yes
Ghabooli et al. 2011. <i>Biological Invasions</i> 13: 679–690	<i>Mnemiopsis leidyi</i>	Ctenophore	Western Atlantic	Temperate	Black Sea Azov Sea Caspian Sea Baltic Sea	Subtropical Temperate	Pelagic	Pelagic	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Gilg et al. 2013. <i>Biological Invasions</i> 15: 459–472	<i>Perma viridis</i>	Mussel	South China Sea Laccadive Sea	Tropical	NW Atlantic Caribbean Sea	Tropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Gillis et al. 2009. <i>Diversity and Distributions</i> 15: 784–795	<i>Mytilus charruana</i>	Mussel	Eastern Pac Caribbean Sea	Tropical	NW Atlantic	Subtropical	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Gislason et al. 2013. <i>Marine Ecology Progress Series</i> 494: 219–230	<i>Cancer irroratus</i>	Crab	NW-Atlantic	Temperate	N Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No

(Continued)

Table 3 (Continued) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Hamner 2007. <i>Journal of Fish Biology</i> 71: 214–222	<i>Pterois volitans</i>	Fish	Indian Ocean	Tropical	W Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hamner 2007. <i>Journal of Fish Biology</i> 71: 214–222	<i>Pterois miles</i>	Fish	Indian Ocean	Tropical	W Atlantic	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hanyuda et al. 2016. <i>Phycological Research</i> 64: 102–109	<i>Ulva australis</i>	Alga	Western N Pac	Temperate	NE Pacific Baltic Sea NE Atlantic SE Pacific SW Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Hasselman et al. 2018. <i>Biological Invasions</i> 20: 3123–3143	<i>Alosa sapidissima</i>	Fish	Western N Atlantic	Subtropical	NE Pacific	Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Kappas et al. 2004. <i>Marine Biology</i> 146: 103–117	<i>Artemia franciscana</i>	Shrimp	Eastern N Pac	Temperate	Indo-Pacific	Tropical	Pelagic	Pelagic	Both	Haplotype diversity	Invasion dynamics	Lower	Yes
Krueger-Hadfield et al. 2016. <i>Molecular Ecology</i> . 25:3801–3816	<i>Agarophyton vermiculophyllum</i>	Alga	NW Pacific	Temperate	NW Atlantic NE Atlantic NE Pacific	Temperate	Hard substrata Sedimentary	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Martel et al. 2004. <i>Marine Ecology Progress Series</i> 273: 163–172	<i>Ocenebrellus inornatus</i>	Snail	East China Sea	Temperate	Gulf of Biscay NE Pacific	Temperate	Hard substrata	Intertidal Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Equal	No

(Continued)

Table 3 (Continued) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Munoz et al. 2014 <i>Hydrobiologia</i> 726: 25–41	<i>Artemia franciscana</i>	Shrimp	Eastern N Pac	Temperate	NE Atlantic Balearic Sea Mediterranean Adriatic Sea	Subtropical	Pelagic	Pelagic	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Riquet et al. 2013. <i>Molecular Ecology</i> 22: 1003–1018	<i>Crepidula fornicata</i>	Limpet	Western N Atlantic	Temperate	NE Atlantic	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Rius et al. 2008. <i>Diversity and Distributions</i> 14: 818–828	<i>Microcosmus squamiger</i>	Ascidian	SE Indian Ocean Southern Ocean Tasman Sea	Temperate	NE Pacific SW Indian Ocean NE Atlantic Mediterranean	Tropical Subtropical Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Shabtay et al. 2014. <i>Marine Biology Research</i> 10: 407–415	<i>Spondylus spinosus</i>	Oyster	Red Sea	Subtropical	Mediterranean	Subtropical	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Higher	No
Shan et al. 2019. <i>European Journal of Phycology</i> 52: 154–161	<i>Undaria pinnatifida</i>	Alga	Yellow Sea East China Sea	Subtropical	North Sea English Channel	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Smith et al. 2012. <i>PLOS ONE</i> 7: e30473	<i>Didemnum vexillum</i>	Ascidian	Western N Pac	Temperate	SW Pacific	Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

(Continued)

Table 3 (Continued) List of studies retained in this review that use comparative approaches with firsthand collected data to study changes in genetic diversity of an invasive species between native and introduced populations. Entries in the Finding column indicate the value of the measured metric in the introduced range relative to the native range. The support column indicates whether there was evidence for a shift in genetic diversity (either higher or lower; see Finding column) or not.

Reference	Species	Taxon	Native Region	Native Climate	Introduced Region	Introduced Climate	Habitat	Tidal height	Study Type	Measure	Theory	Finding	Support
Tepolt and Palumbi 2015. <i>Molecular Ecology</i> 24: 4145–4158	<i>Carcinus maenas</i>	Crab	North Sea NE Atlantic	Temperate Subtropical	NE Pacific	Temperate	Hard substrata	Intertidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Xue et al. 2018. <i>Biological Invasions</i> 20: 3297–3314	<i>Rapana venosa</i>	Snail	Philippines Sea Yellow Sea	Subtropical Temperate	Adriatic Sea Black Sea Bay of Biscay English Channel NW Atlantic SW Atlantic	Subtropical Temperate	Hard substrata	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes
Wong et al. 2016. <i>Marine Biology</i> 164: 133	<i>Charybdis japonica</i>	Crab	East China Sea Yellow Sea	Subtropical	SW Pacific	Temperate	Sedimentary	Subtidal	Mensurative	Genetic diversity	Invasion dynamics	Lower	Yes

BOX A *LITTORINA LITTOREA*. – CASE STUDY: USING THE BIOGEOGRAPHIC PATTERN OF ENEMY ESCAPE FROM PARASITES TO HELP DISCERN THE INVASIVE STATUS OF A PREVIOUSLY CRYPTOGENIC SPECIES



Because of extensive, consistent support for decreased parasite richness in introduced populations (e.g. Torchin et al. 2003), Blakeslee & Byers (2008) explored whether patterns of enemy release could be used in reverse, that is, to use parasite signatures to inform the ecological origin of a given cryptogenic host. Specifically, they tested the predictions for parasite release among three North Atlantic marine congeneric snails that were believed to have very different invasion and colonization histories in their established populations. Two species (*Littorina saxatilis* and *L. obtusata*) were thought to be naturally cosmopolitan on both sides of the Atlantic Ocean, while a third (*L. littorea*) had originally been thought to be an introduced species in North America; however, its ecological history there had recently been called into question, giving it

a cryptogenic status (Wares et al. 2002). All three snail species serve as first intermediate hosts to host-specific digenean trematode (flatworm) parasites. Although the enemy release hypothesis had been used to explain heightened invasion success and ecological impact, this study represented the first endeavour to use the hypothesis's predictions to determine the status of a cryptogenic species as either native or introduced.

Through an extensive literature review and supplemental field sampling, Blakeslee & Byers (2008) identified total trematode species richness that was 55% lower for *Littorina littorea* in North America vs Europe. Mean site-level richness was also significantly lower in North America compared with Europe, and the decline (47%) was nearly equivalent to the decline based on the total species richness (55%). This greatly reduced parasite richness in the invasive range is consistent with the expectation for enemy escape. In contrast, for the two known native species – *L. saxatilis* and *L. obtusata* – smaller, non-significant reductions in trematode species richness in North America vs Europe were demonstrated (33% and 24%, respectively). Mean site-level richness for *L. saxatilis* and *L. obtusata* also exhibited much smaller differences between North America and Europe compared with *L. littorea*. Thus, lower parasite richness in *L. littorea* compared with the other definitively native congeners (which functioned as positive controls in this study) strongly implicated *L. littorea* as an invasive species that demonstrated sizable enemy escape in its invasive North American range.

This conclusion was later corroborated with direct genetic evidence from both the *L. littorea* host snail and its parasites, which demonstrated signatures of introduction (i.e. a reduced subset of genetic diversity in the putative invasive range; Blakeslee et al. 2008). Also, Brawley et al. (2009) supported *L. littorea* as an invasive species in North America using historical records (and more genetic analyses) that furthermore documented the snail's source region within its native range to be Great Britain and Ireland.

competitors and parasites (Torchin et al. 2001, 2003). Torchin et al. (2001) sampled the crab *Carcinus maenas* around the world in its native and introduced locations and reported on parasite loads. Relative to the native European range, parasite diversity was reduced in every invasive range examined, often by large amounts, including South Africa, where *C. maenas* was parasite free. Although the pattern of ERH is well documented, the effects of having lower exposure to enemies to the fitness and establishment of invasive species is seldom examined. A positive influence of fewer enemies is often assumed, even though the enemy that is reduced in number may not necessarily have been a limiting factor on the invasive species' population abundance.

Keogh et al. (2017) document one of the only experimental approaches to ERH in marine systems. The authors surveyed the Asian shorecrab, *Hemigrapsus sanguineus*, in its native and introduced range, finding the crab in the invasive range to be parasite free. They then employed a common garden experiment in the native range in Japan using crabs from the native and introduced range and exposed them to infective stages of a castrating rhizocephalan barnacle parasite. The crabs from the introduced range were between 1.8 and 6 times more susceptible. This shows that the crabs in the introduced range were escaping their parasites ecologically but not physiologically. Furthermore, their findings imply that the cost of maintaining immune defences against infection was high, such that the crabs lost resistance to the parasite once they were not exposed to it for several generations in the invasive range. Thus, Keogh et al. (2017) provide experimental evidence of ERH and suggest a double fitness benefit from escaping the parasite – not only lower infections but also physiological savings from less investment in immunity.

Trait and niche shifts across native and introduced ranges

Trait and niche shifts are the second and third most examined biogeographic hypotheses, and support for them was high: 92% and 77%, respectively. These two are somewhat related because shifting traits can often be related to a species changing its niche. Our literature search found that all of the papers that explicitly use the term 'niche shift' refer to temperature shifts. Although niche shifts were not apparent in all studies (e.g. Glasby 2007, Davidson et al. 2008, Henkel et al. 2009), several species did have an increased tolerance to high and low temperature stress in their introduced compared with native ranges (e.g. Kappas et al. 2004, Sotka et al. 2018), and for the red alga *A. vermiculophyllum*, high temperature tolerance was associated with increased levels of heat-shock proteins (Hammann et al. 2016). Interestingly, the invasive ascidian *Herdmania momus* also had lower tolerance to cooler temperatures (Gewing et al. 2019). Gewing et al. (2019) suggested that the tropical origin of *H. momus* may limit its dispersal into cooler waters but facilitate its spread into warmer waters in introduced Mediterranean populations.

Trait and niche shift theories often employ circular logic, assuming that an observed shift in traits and niches must be positively affecting an invader. These positive shifts could happen because of a genetic bottleneck in the small, inoculating population (also possibly coupled with genetic drift), rapid selection in the introduced range or character displacement of a species expanding to fill a vacant or less crowded niche. However, trait and niche shifts need to be tested to know whether they causally affect invader fitness and advantage over natives. For example, a crab with bigger claws in the invasive range may be assumed to have a fitness advantage stemming from that trait shift. However, if untested, it might be just as likely that small claws are advantageous. Niche shift as it pertains to temperature may be more objective because a species' temperature optimum can be objectively defined and thus readily evaluated to determine whether a temperature shift has moved a species to be more aligned with the local climate. Likewise, certain traits like increased chemical defences might also allow more objective assessment of whether the direction of a shift has provided mechanistic advantage. For example, the red alga *Agarophyton vermiculophyllum* has become better defended against epiphytes and bacterial epibionts in its introduced European range compared with native populations in Asia (Saha et al. 2016, Wang et al. 2017). Indeed, constituent

chemical related changes may be generally important in explaining the invasion success of many invasive macrophytes (Wikström et al. 2006, Vermeij et al. 2009, Forslund et al. 2010, Qing et al. 2012, Hammann et al. 2013, 2016), although not all macrophytes experience palatability shifts between their native and introduced ranges (Bippus et al. 2018).

Evolution of invasiveness and acquisition of native allies

In marine ecosystems, the evolution of increased competitive ability, and evolution of invasiveness more broadly, as well as the acquisition of native allies, have been theorised about, but empirical examinations are lacking. Although most of the biogeographic comparisons on these metrics affirm their operation, there are too few studies to draw conclusions about the commonality of these mechanisms in invasion success. Facilitation is certainly a mechanism of growing interest in ecology in general (Stachowicz 2001, Kollars et al. 2016, Thomsen et al. 2018, Gribben et al. 2019); however, native allies had only a single study using a biogeographic comparison (Aires et al. 2013). Another more recent example, outside of the dates of our literature search, is Gribben et al. (2020) who demonstrated that higher abundances of the porcelain crab, *Petrolisthes elongatus*, on intertidal boulder shorelines in its introduced range of Tasmania, Australia, is due to the presence of the calcareous matrix provided by the tube-worm *Galeolaria caespitosa* on the underside of boulders, which is rare under boulders in its native range of New Zealand (see Box D for expanded *P. elongatus* case study). Positive interactions, such as facilitation, may be important drivers of changes in invader abundance across ranges, particularly when their abundance is strongly tied to habitat availability.

Three studies addressed the evolution of invasiveness, and all three examined changes in resource acquisition, with two of these studies showing that, compared with its native range, *C. maenas* has undergone behavioural and morphological (e.g. body size and claw size) adaptations that increase prey capture (Schaefer & Zimmer 2013, Howard et al. 2018). An improved amount, rate, or efficiency of resource acquisition can imply better competitive strength. However, none of these papers actually measured relative competitive abilities in the native and introduced ranges. Thus, the evolution of increased competitive ability – and evolution of invasiveness more broadly – remains a popular theory in invasion biology, but support for it here is only partial.

Environmental matching

We did not find any studies that investigated environmental matching as a mechanism behind invasion success. From a coarse perspective, we know that matching must occur to some degree, as all but three studies examined invasive species in the same climate zone in the introduced and native range. However, formal examination of environmental matching typically investigates much more finely resolved environmental attributes and also multidimensional aspects of niche apart from just temperature.

Genetic shifts

Finally, genetic change is examined a lot, and most species in our database exhibit reduced diversity in the introduced range (Box B). This reduction is parsimoniously explained by founder effects and associated genetic bottlenecks from small inoculation size. However, this finding is far from universal. Roman & Darling (2007) found an equal or even increased diversity in the introduced range of marine and freshwater species which they attributed to high propagule vectors, such as ballast water and shellfish transplantations, and multiple introductions that can infuse more heterogeneity into the introduced range and eliminate founder effects in the majority of successful aquatic invasions. What remains unclear is, even if genetic reduction occurs, whether there is a disadvantage to the invader, for example, for fitness, establishment success, or spread. Roman & Darling (2007) suggest even when diversity is low that it likely does not matter because even low-diversity introductions

**BOX B AGAROPHYTON VERMICULOPHYLLUM. – CASE STUDY:
GENETICS OF AN INVASIVE SEAWEED IDENTIFY ITS SOURCE
OF INTRODUCTION AND EVIDENCE AN ENVIRONMENTALLY
FORCED SHIFT TO ASEXUAL REPRODUCTION**

Krueger-Hadfield et al. (2017) thoroughly examined the genetics of the invasive Asian seaweed *Agarophyton vermiculophyllum* in its native and invasive range using microsatellite and mitochondrial *cox1* amplification and genotyping. The size of their sampling was impressive, with more than 2000 thalli sampled from more than 30 native sites in Asia and 35 non-native sites along the coastlines of western and eastern North America and Europe (Krueger-Hadfield et al. 2016). In doing so, they uncovered the source of the introduced populations in Europe and North America as being from the Pacific shorelines of northeastern Japan (Krueger-Hadfield et al. 2017). Based on ecological, genetic and historical evidence, they further suggested that *A. vermiculophyllum* hitchhiked with the exports of the Japanese oyster *Magallana gigas* from Japan during the 20th century, which abounded from this exact region at the same time that *A. vermiculophyllum* was introduced.

Of equal interest was their exploration of the degree of reduction in genetic diversity that often accompanies species that have founder effects, like invasive species that are introduced in small numbers. In many dimensions, invasive populations were significantly lower in genetic diversity. For example, there were significantly more unique genotypes (i.e. genotypic richness) within native sites (91%) than introduced sites (61%). But the most noteworthy aspect of the genetic diversity shift was that the native populations were 58% diploid, while the introduced populations were 81% diploid. Non-native sites were dominated by diploid tetrasporophytes as a result of asexual fragmentation. Because hard substratum is required for algal spore recruitment, the authors determined that an ecological shift from hard to soft substratum during the invasion of North American and European estuaries by *A. vermiculophyllum* resulted in a shift from sexual to asexual reproduction (Krueger-Hadfield et al. 2016). Thus, an initial colonization of a soft-sediment estuary in the non-native range by a diploid thallus meant the species was trapped in that stage, able to reproduce only asexually without a hard substratum to promote sexual reproduction. Since non-native sites were presumably the sources of inoculation for many other sites in the invasive range, it is not surprising that the predominant diploids were the stage introduced to the new secondary sites, thus perpetuating diploids as the life stage trapped in asexual reproduction throughout much of the invasive range.



have many means of avoiding the negative impact of diversity reduction. Genetic signatures that are distinctive to various parts of the native range can be used to track multiple introductions from the native range and monitor spatial and temporal changes including the mechanisms and speed of spread (Darling et al. 2008, Box C).

BOX C *CARCINUS MAENAS*. CASE STUDY: DISTINCT AND REDUCED GENETIC DIVERSITY OF AN INVASIVE CRAB IDENTIFIES ITS INVASION HISTORY AND ASYMMETRIC SPREAD WITHIN THE INVASIVE RANGE

The European green crab, *Carcinus maenas*, first appeared on the mid-Atlantic coast of the eastern United States in 1817. Over the decades, it spread northward against the mean current throughout northeastern North America until it reached Halifax, Nova Scotia, Canada, in 1964 where its upstream spread seemingly stopped (Figure C1). Byers & Pringle (2006) have demonstrated that even planktonically dispersed species like crabs can spread in an upstream direction as long as the variation in currents their larvae experience is large enough to counteract the movement in the mean current, which is by definition in the downstream direction. Methods to increase the variation in currents experienced by larvae, and thereby boost retention and upstream spread, include spawning copious larvae over long periods and decreasing larval exposure to the mean current by minimizing larval development times (and thus time spent in plankton), which are exponentially lower in warmer temperatures.



In the 1990s, *C. maenas* populations in northern Nova Scotia north of Halifax exploded (Figure C1). Roman (2006) determined that the genetic composition of the previously existing *C. maenas* populations in the United States and southern Nova Scotia were all of a single haplotype. The populations in northern Nova Scotia represented a new introduction which was composed of a suite of distinct haplotypes,

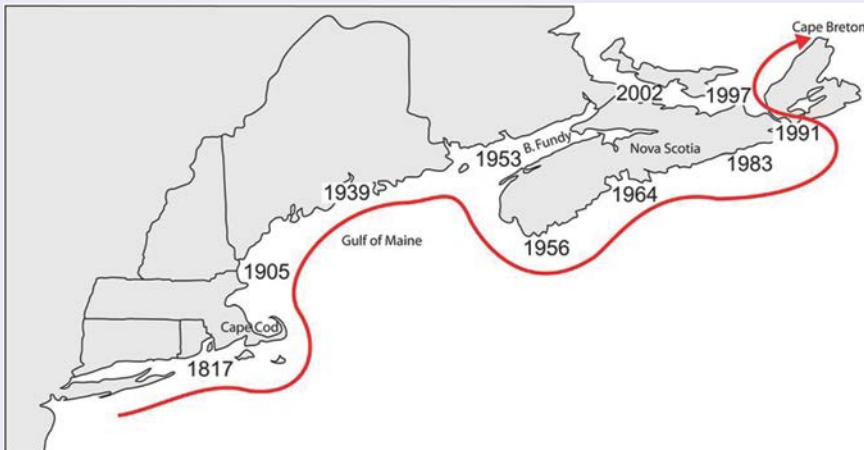


Figure C1 Dates of *Carcinus maenas* expansion northward up the coast of northeastern North America. Dates depict first record of the crab at various locations. The direction of travel is in the upstream direction throughout this domain. Red line depicts a simple proposed scenario for the crab's expansion if it had spread upstream on its own power. Adapted with permission from Roman (2006), © the Royal Society 2006, and based on a figure originally adapted from Audet et al. (2003).

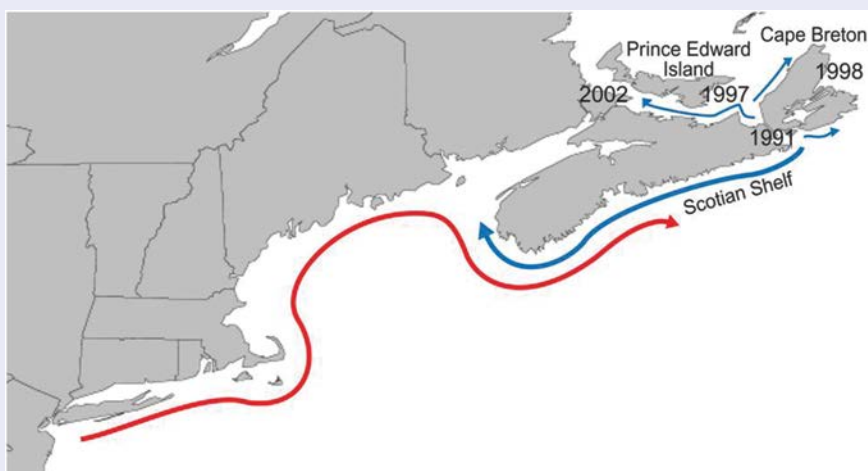


Figure C2 Hypothesised spread of the crab according to the theory of Byers & Pringle (2006). Hypothesis was tested using baseline genetic data from Roman (2006) and Pringle et al. (2011). Red represents historical invasion of *Carcinus maenas* upstream from south to north ending in Halifax, Nova Scotia. Blue represents a second introduction of *C. maenas* from a different portion of the native range to northern Nova Scotia that spread readily in the downstream direction.

most likely from the Baltic region of the crab's native European range. It was hypothesized that the northern Baltic strains were cold water adapted and therefore thriving in northern Nova Scotia. However, the theory of Byers & Pringle (2006) predicted a simpler, testable explanation – namely that *C. maenas* in North America historically had spread on its own in the upstream direction as far as it could on its own power and ceased spreading in Halifax, where the cold water temperatures meant it could no longer overcome mean advection and spread further upstream. Under this hypothesis, the new introductions were not necessarily better adapted to temperature but simply anchored in place in retention zones in northern Nova Scotia, such as the Straight of Canso and the Bras d'Or Lakes, that were not subject to the mean advective currents that sweep larvae downstream and hinder upstream establishment. However, with populations anchored in place, the crabs could easily supply larvae into coastal currents to move in the downstream direction and backfill in the portions of the range above Halifax that they could not fill on their own power (Figure C2). This prediction appears to be supported by the genetic signature of spread (Pringle et al. 2011). In fact, not only have the northern Baltic haplotypes filled in that previously unpopulated region north of Halifax, but they have continued spreading in the downstream direction, mixing with the previously homogenous single haplotype of the historical southern invasion (Figure C3). In fact, in seven years (about two crab generations), the upstream haplotypes became 20% more common throughout the entire *C. maenas* invasive range. Such downstream asymmetrical dispersal was readily observable in the genetic signature (though now introgression of haplotypes makes using the haplotypes as a tracer much harder).

Comparison with the native range indicated an originally bottlenecked North American population of *C. maenas* whose genetic homogeneity persisted for >100 years. The homogeneity was disrupted by the introduction of a novel set of haplotypes from a different part of the native range that also allowed observation of spread and subsequent mixing of genetically distinct populations within the invasive range.

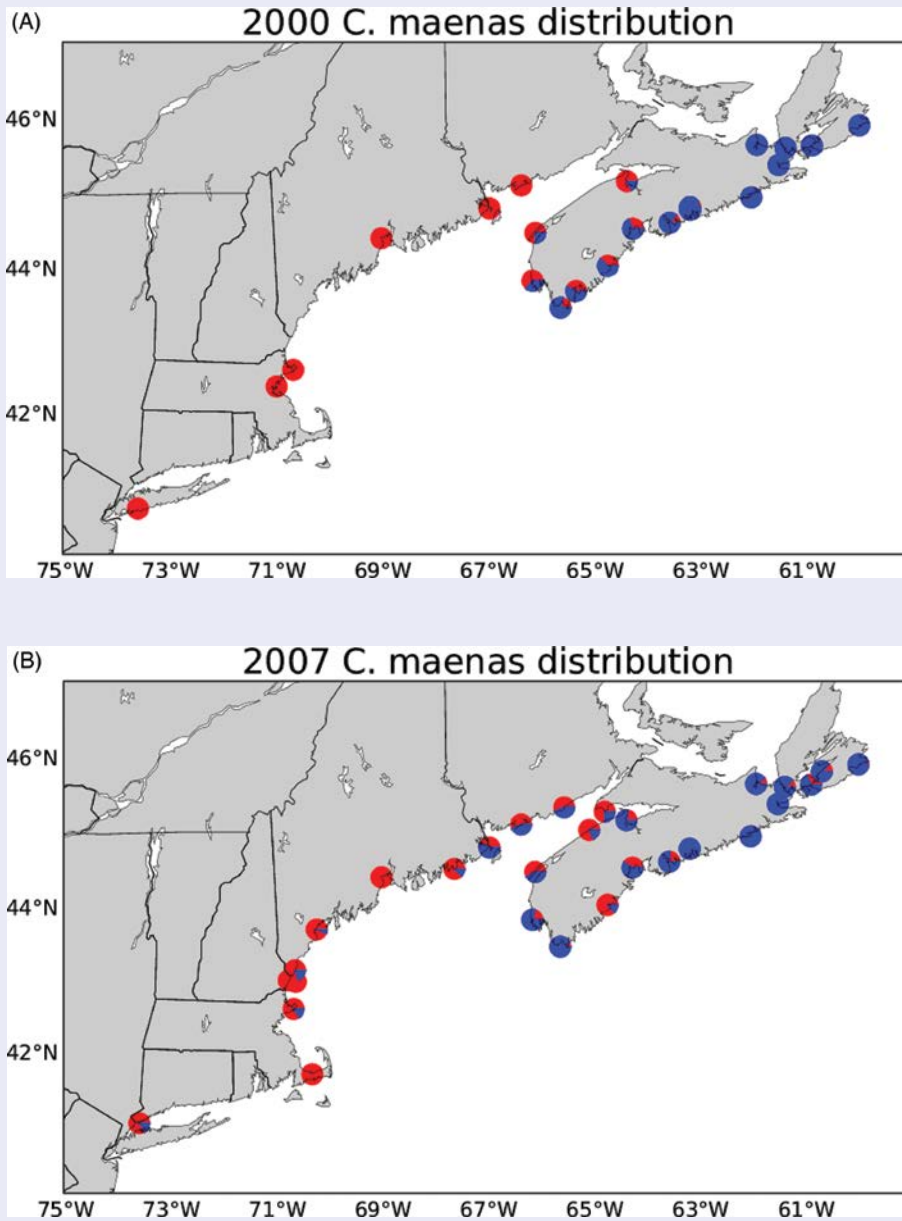


Figure C3 (A) Original haplotype distribution of *Carcinus maenas* in 2000 from Roman (2006). Red represents the haplotype of the older historical invasion to the US that spread north to Halifax. Blue is the haplotype suite that was introduced in the 1990s to northern Nova Scotia. Note these data were collected almost a decade after the introduction(s) of *C. maenas* to northern Nova Scotia, and spread away from the point of introduction has already occurred. (B) Within seven years, the upstream (blue) haplotype suite has begun to displace the red haplotype downstream and was 20% more abundant throughout the domain. The northern haplotypes have even passed to the south of major biogeographic boundaries like Cape Cod (Pringle et al. 2011). Adapted from Pringle et al. (2011).

Knowledge gaps

What role for increased competitive ability?

The evolution of increased competitive ability (EICA, Blossey & Notzold 1995) predicts that enemy release should result in introduced species losing costly traits that confer resistance to native enemies, with a subsequent reallocation of resources to other traits (e.g. body size or reproduction) that may be under greater selection in the introduced range (Hierro et al. 2005). While tests are equivocal (e.g. Blossey & Notzold 1995, Maron et al. 2004, Felker-Quinn et al. 2013), in terrestrial ecosystems, invasive plants can undergo evolutionary changes through the invasion pathway which can give them increased competitive ability in their introduced compared with native ranges (Blossey & Notzold 1995). We could find no studies that have addressed this hypothesis for marine ecosystems. However, there are several reasons the EICA may play an important, yet underappreciated, role in invasion success in marine ecosystems. First, competition has strong effects on the structure of marine ecosystems, particularly rocky intertidal ones. Because of this, it has been a focal process of study in marine environments (Branch 1984, Byers 2009). Second, studies show that invasive marine species can undergo phenotypic (morphological and behavioural) changes and that those changes, in some instances, increase their acquisition of resources in their introduced compared with native range (Schaefer & Zimmer 2013). Moreover, separate studies show that invasive species can be better at acquiring resources than native competitors (Byers 2000, Hendrickx et al. 2015). However, no study has approached this using a biogeographic framework to test the importance of EICA in explaining the success of marine invasive species.

What role for associated microbes in controlling the biogeography of marine invasions?

In terrestrial ecosystems, plant-soil-feedbacks (PSFs; Bever 1994) play an important role in regulating community succession, coexistence and invasiveness (Van der Putten et al. 1993, Klironomos 2002, Bever 2003, Callaway et al. 2004, Kulmatiski et al. 2008). There is mounting evidence that different PSFs experienced by invasive plants in their introduced compared with native range are also critical to their invasion success. Invasive success of plants can be enhanced by leaving behind below-ground enemies or by encountering stronger soil mutualists or having enhanced competitive ability through stronger allelopathic effects in the introduced compared with native range (Callaway 1995, Callaway & Aschehoug 2000, Reinhart et al. 2003, Vivanco et al. 2004, Reinhart & Callaway 2006, Callaway et al. 2008). Despite invasive marine plants and algae that colonise soft sediments constituting some of the most damaging invaders globally, the role of changes in PSFs across their native and introduced range in contributing to their success remains relatively unexplored. However, by manipulating microbial communities from native seagrass sediments, Gribben et al. (2017) demonstrated that the presence or absence of a sediment microbial community from the native seagrass *Zostera muelleri* inhibited and promoted success, respectively, of the invasive alga *Caulerpa taxifolia*. Manipulation of the sediments occupied by *C. taxifolia* had the opposite effect. Moreover, field experiments show, compared to disturbed sediments, intact sediments from native seagrasses have similar strong negative effects on the growth of reducing fragment growth of invasive *Caulerpa* spp. fragments in the Mediterranean and Australia (Gribben et al., 2018; Bulleri et al. 2020). Success (or not) of both *Caulerpa* spp. was linked to microbial control of sediment sulphur cycles. In another example, Chen et al. (2020) found that soil properties of native *Spartina* marshes depressed freeze tolerance of range-expanding tropical mangrove competitors. These studies demonstrate an emergent role for PSFs in controlling the success of invasive soft-sediment macrophytes, similar to that demonstrated for terrestrial plants.

Changes in surface-associated ‘epibacteria’ on invasive macrophytes between native and introduced ranges may also influence invasion success. The results may be positive or negative

depending on how the host benefits from the microbial community it acquires in the introduced range. For example, some epibacteria can be virulent or promote the settlement of fouling organisms, or they contribute to anti-fouling defence or provide essential nutrients (Egan et al. 2001, Dobretsov et al. 2009, Goecke et al. 2010, Fernandes et al. 2011, 2012, Egan et al. 2014, Wichard 2015). We suggest that understanding changes in microbial communities, and the processes they control, across native and introduced ranges of macrophytes will be a critical avenue of future research for fully explicating the mechanisms behind their success.

Integrating hypotheses to determine mechanisms

Many of the comparative biogeographic theories to explain invader success overlap. Also, multiple theories likely operate at once, especially due to the correlation of ecological processes and traits. For example, a niche shift in the introduced range could easily involve a shift in traits. The evolution of invasiveness might involve traits that shift in the absence of certain enemies in the introduced range. Traits shifts in particular are very likely to be operating with other processes, since trait changes in and of themselves do not always imply a mechanism of success. For example, changes in macrophyte traits (e.g. chemistry) are potentially neutral but could indirectly enhance invasion success if shown to reduce herbivore pressure (Wikström et al. 2006). Thus, splitting hairs regarding which hypothesis fits a study or species could rapidly become futile. Instead, the overlap among various potential mechanisms should be viewed in a positive light since it lends itself to integrated theory and approaches. For example, an integrated theory of biogeographic success by an invader might invoke advantages from the evolution of invasiveness and enemy release, despite lower genetic diversity.

Towards a mechanistic understanding using experimental approaches

Somewhat surprisingly, our review indicated that experimental approaches were almost as frequent as mensurative surveys when investigating biogeographic shifts in the biology and ecology of invasive species between their native and introduced ranges (Table 2). Studies using experimental approaches mostly use common-garden experiments where the experimenter brings introduced and native-range individuals together in a common setting, usually in the lab. Such experiments provided robust tests for niche shifts via, for example, changes in temperature tolerances (Krueger-Hadfield et al. 2016, Gewing et al. 2019) or a reduction in natural enemies via reduced palatability or parasites (Vermeij et al. 2009, Keogh et al. 2017), benefitting invasive species in their introduced ranges.

In addition to common-garden experiments, another approach to experiments is through *in situ* experiments conducted in both the introduced and native range. Although this approach is theoretically possible, no such papers appeared in our database. Likely this is influenced by ethical considerations that place strict limits on where invasive species can be moved. This is part of the reason common-garden experiments have been so useful – native and invasive species can be transported between ranges under controlled conditions. Comparative biogeographic experimental approaches whereby equivalent experiments in an invader's native and introduced range provide a useful alternative for elucidating shifts in the net strength of species interactions (e.g. predation, competition) or tolerances across ranges (Hierro et al. 2005), although they are confounded by different species pools and/or environmental conditions in the native and introduced ranges.

However, there are creative ways to employ unconfounded *in situ* experiments of factors testing the biogeography of invader success. Gribben et al. (2020) provide one such example (Box D). In this case, surveys indicated that higher abundances of *Petrolisthes elongatus* in its introduced range were due to the presence of a habitat-forming tube worm that forms a calcareous matrix underneath rocks that was largely absent from its native range, and this was confirmed in replicated biogeographic experiments with habitat mimics in both ranges (see Box D for more detail). Where invasion success

BOX D *PETROLISTHES ELONGATUS* – BIOGEOGRAPHIC CASE STUDY: THE ROLE OF POSITIVE INTERACTIONS IN PROMOTING HIGHER ABUNDANCES OF AN INVASIVE CRAB

Native to New Zealand, the porcelain crab *Petrolisthes elongatus* was introduced into Tasmania, Australia, in the early 1900s via ballast rock or the live oyster trade between the two countries (Dartnall 1969, King 1997). Following its introduction, *P. elongatus* spread rapidly and is now widespread and a dominant member of intertidal rocky shore communities, where it reaches high abundances (up to 2000/m²) under boulders (Gribben et al. 2015, Wright & Gribben 2017). Throughout Tasmania, high abundances of *P. elongatus* are associated with strong shifts in



community structure (Gribben et al. 2015, Wright et al. 2016). Higher overall abundances of *P. elongatus* in the introduced compared with native range were shown in two separate studies which surveyed crab abundances throughout the invasive range in Tasmania (Gribben et al. 2013, 2020). In the introduced range, the abundance of *P. elongatus* is positively correlated to habitat availability (i.e. the amount of boulder material available for colonisation; Gribben et al. 2015, Wright et al. 2018). However, higher abundances of *P. elongatus* in the introduced range are not simply explained by greater habitat availability because surveys of habitat characteristics (amount of boulder material, boulder sizes) indicated no difference among the two ranges (Gribben et al. 2020). Instead, these surveys showed a high presence of habitat-forming tube worm *Galeolaria caespitosa* under rocks in Tasmania – where it is known to enhance recruitment of *Petrolisthes elongatus* compared with rocks without the tube worm – compared with New Zealand, where it was virtually absent (Wright et al. 2016). Deploying mimics of rocks with and without worms at three sites in both the native and invasive range, Gribben et al. (2020) experimentally demonstrated that rocks with worm structure facilitated crab by at least 50% in both the native and introduced ranges. This study was novel for two main reasons. First, it is an unconfounded *in situ* experimental test of the mechanism explaining higher abundances of invasive species in their introduced range, and second, it shows that positive interactions are an important mechanism explaining differences in the abundance of an invasive species between its native and introduced ranges. In this example, the higher cover of a native habitat-forming species facilitates higher abundances of an invader in its introduced range, possibly because the presence of this habitat-former reduces temperature stress (Wright & Gribben 2017).



is linked to changes in the physical environment, such as changes in habitat structure, structural mimics may provide a particularly powerful tool for conducting unconfounded *in situ* experiments at biogeographic scales.

Comparative studies that do not involve experiments can still be valuable. Two aspects that will boost their value are enhanced replication and proper spatial spread of sampling points. Often studies only examine a few sites in the native and introduced range to make comparisons. But, especially for species with wide ranges, capturing the effect of within-region heterogeneity is important for a fair comparison. That is, to know that there is a real difference between regions, you need adequate replication in both ranges. Alternatively, if the exact region of the native range from which the inoculating invasive individuals were drawn is known, as it is for several prominent invasive species (Brawley et al. 2009, Krueger-Hadfield et al. 2017), then that area of the native region should be sampled exclusively for comparisons since variation in other parts of the native range is moot. Diversity studies need equal sample sizes in both ranges (or rarefaction techniques to control for unequal sample size) (e.g. Blakeslee & Byers 2008) since species richness scales with sampling effort.

Another goal for future studies is to diversify our taxonomic exploration. We know, for example, that many species traits vary with phylogeny, for example, larval duration and temperature tolerance. As most reviews of invasive species have found (e.g. Ruiz et al. 2000, Byers 2009), our database is biased toward molluscs, crustaceans and seaweed. Getting taxonomic balance will help us learn whether certain levels of taxonomic organisation show biases in biogeographic comparisons. Also, as most invasion reviews have reported, various regions around the globe are understudied, for example, the tropics (Figure 4). Moreover, Asia, Africa and South America are highly underrepresented (Figure 2). This underrepresentation likely affects biogeographic comparisons heavily because one needs data from two regions of the world to make comparative studies. When half the world is highly understudied (in many cases even with no baseline inventories of what is native vs introduced), that makes these comparisons rare. In particular, many invaders originate from Asia, often where there are no data from the native range. This was a problem that heavily affected Parker et al. (2013), who sought to compare the world's 100 worst invasive species that formed their target list of species in their native and introduced ranges. Many of those 100 species were native to Asia and had to be dropped from the meta-analysis for lack of native range data. Some studies are starting to obtain their own native range data from Asia (Keogh et al. 2017, Krueger-Hadfield et al. 2017, Sotka et al. 2018).

Cross-ecosystem evidence for different hypotheses

Working towards a general biogeographic theory of invasion, one of the key questions is whether the different hypotheses identified in this review receive similar or different support across ecosystems. Except for the ERH, there are too few studies to test for the strength of different hypotheses across ecosystems. Jeschke et al. (2012) showed approximately 75% support for the ERH in marine ecosystems from a small number of papers (13). The level of support was not statistically different from that observed in terrestrial and freshwater ecosystems, suggesting relatively equal support for this hypothesis across ecosystems. With the addition of further studies, we will ideally be able to ascertain the underlying strength of the different hypotheses reviewed here, including their differences across ecosystems.

Conclusions/summary

Biogeographic study of invasions is more than a one-way street. Throughout this article, we have stressed how biogeography may inform invasive species biology through comparative analysis. It is also the case that invasive species may inform biogeography. After all, invasive species are a unique opportunity to inform biogeography because without invasion, you cannot study species in similar climatic regions where they do not already exist. However, through species invasions, one can test biogeographic regions for interchangeability and similarities in biological suitability using the receptivity of the region and the subsequent fitness of the invasive species as proxies for the similarity and substitutability of multiple biogeographic regions.

Despite the huge size of the biological invasion literature, given the difficulties of working at continental scales, it is perhaps understandable that biogeographic comparative studies, especially experimental ones, are lacking. However, as we have shown here, the growing number of comparative studies provides interesting insight and much-needed empirical evidence to address the theoretical biogeographic hypotheses for the success of invasive species. The evidence for and against these hypotheses should improve over time as researchers plug many of the knowledge gaps we have exposed.

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