

10 · *Invasions by non-indigenous species*

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10.1 Marine invaders: background

Invasions by marine non-indigenous species (NIS, see Box 10.1 for definitions) have long been recognised. For example, Carl Emil Hansen Ostenfeld described the invasion of the planktonic diatom *Biddulphia (Odontella) sinensis* Grev. into the North Sea in 1903, probably transported by ships (Ostenfeld, 1908), and over 50 years ago Charles Elton provided the first overview with narrative accounts of impacts associated with high profile marine invasions by oysters and cordgrass (Elton, 1958). However, marine invasions were first approached with a systematic research effort following J. Carlton's seminal work in San Francisco Bay (Carlton, 1979). Today it is recognised that marine NIS comprise a diverse group of organisms found in most marine systems. In a recent review, Hewitt and Campbell (2010) tallied almost 1800 marine NIS and cryptogenic species (Box 10.1) worldwide, dominated by arthropods (444), molluscs (350), fish (166), red algae (153), annelids (104, mainly polychaetes), cnidarians (100), heterokonts (73), bryozoans (73) and green algae (51). Although marine NIS have been introduced around the world, some bioregions are more invaded than others; the most heavily invaded regions are the Mediterranean Sea (467 NIS), Australia and New Zealand (429), the South Pacific (289), the north-east Pacific (284) and the north-east Atlantic (216) (Hewitt and Campbell, 2010). More locally, estuaries centred around metropolitan areas and with extensive shipping traffic are typically the most invaded systems. For example, *c.* 230, 200 and 100 marine NIS are found in San Francisco Bay, Chesapeake Bay and Port Phillip Bay, respectively (Hewitt *et al.*, 2004; Ruiz *et al.*, 2011). The most

important marine vectors are transportation on ships (mainly hull fouling), inside ships (in ballast water, ballast sediments and sea-chests), with aquaculture (in particular associated with oyster transplantations) and via human-mediated removal of physical barriers (e.g. the Suez Canal which connects biota between the Red and the Mediterranean Seas).

No biological species live in an ecological vacuum (Agosta and Klemens, 2008) and each NIS that establishes a permanent population will therefore impact many local species via direct (e.g. consumer–resource and competitive–facilitative interactions) (Byers, 2000; Eastwood *et al.*, 2007) and indirect (e.g. enemy/facilitation cascades) (Thomsen *et al.*, 2010a) biotic interactions. These interactions will typically also influence local community structures and patterns of biodiversity and ecosystem functioning (BEF, see Chapters 1–5 for overview). For example, early in the invasion phase, local species richness automatically increases by one (the new NIS) and global homogenisation automatically increases simply because the invaded region now contains one more species from the global species pool (Olden and Rooney, 2006). Furthermore, each NIS will, via its demography (e.g. population growth), its interactions (e.g. competition), and its impact on community structures (e.g., adding a new species to the system) also modify ecosystem functioning and therefore the provision of ecosystem services (Crooks, 2002a, 2009).

The most pressing question about marine invasion impact is no longer *if* a NIS has an impact or not, but more precisely:

1. What is the direction of impact (is it positive or negative on local species, ecosystem function and biodiversity – see also Box 10.1)?
2. What is the pathway of impact (are effects direct or mediated via indirect pathways)?
3. What is the magnitude of impact (is it too weak to be detected in a variable world)?
4. How do direction, pathway and magnitude vary over space and time within and between invaders, taxa, life stages, invaded habitats and with co-occurring stressors? (how are impacts context dependent)?
5. Are there rules that can be used to predict context-dependent variability in impact?
6. How do NIS modify ecosystem functioning and its relationship with biodiversity?
7. What can be done – if anything – to minimise the impacts of NIS?

The remainder of this chapter will focus on these questions, summarising findings from reviews and case studies.

Box 10.1 *Definitions*

NIS. Non-indigenous species (= alien, exotic, non-native, introduced) are species living outside their native distributional range, which have arrived there by human activity, either deliberate or accidental (Wikipedia). We do not include new species that have arrived by their own dispersal mechanisms across natural barriers, but only survive due to climate changes, as NIS.

Invasive species. NIS are typically coined invasive if they are highly successful (e.g. rapid spread and high abundance) and/or have a strong impact on local ecosystems. In invasion biology all invaders are NIS, but in biogeographical research invaders can also be native that arrive to new regions by natural dispersal mechanisms or 'natural' breakdown of physical barriers.

Cryptogenic species. Of unknown origin; detailed taxonomic, biogeographical, and molecular analysis is required to determine if the species is a native or NIS.

Transport vectors. Pathway whereby NIS arrive to a new system associated with human activity. In marine systems the most important vectors are hull fouling (outside ships), ballast water and sediments (inside ships) and aquaculture (intentional, escapees, and 'blind passengers').

Invasion impact studies. Studies that focus on how invaders affect a property of an invaded habitat/system. The invader is assumed to be the causal agent of change and is considered the independent variable that, typically, is portrayed graphically on the x -axis (in invasion success studies the invader is considered the dependent variable). Impact can be larger or smaller than a reference value (often defined as 0) and impact is then either positive (>0) or negative (<0). Positive or negative impact is a statistical measure that differs from whether the impact is 'good' or 'bad' (the human interpretation of the statistical measure). Impact can be reported on cultural (economics, health, cultures) or natural properties. Natural properties can be divided into biotic and abiotic properties. Biotic properties can be divided into impact reported on or above the species level (the fundamental unit in biology); negative impact on the species level is simple to interpret whereas negative impact reported above the species level may hide opposing effects (i.e. that certain species benefit whereas others are harmed, by the invader).

Mensurative experiments. The researcher has no control over the abundance of the invader, but compares responses between sample sites and sample periods that (hopefully) reflect different levels of invaders. Mensurative experiments are important because they can be conducted on large and long space–time scales, with a wide range of invasive taxa and are without artefacts associated with cages, tethers or experimental disturbances.

Manipulative experiments. The researcher has control over the abundance (and other attributes) of the invader either adding invaders to uninvaded plots/locations or removing invaders from already invaded plots/locations. Manipulative experiments are important because causality can be inferred between the invader and the responses and because invader densities and the spatio–temporal context can be controlled to form part of advanced hypothesis testing.

Keystone and cascades terminology. ‘Keystone’ and ‘cascade’ describe ‘a disproportionately large ecological effect’ and ‘a proportional large ecological effect effectuated via repeated ecological interactions’, respectively. ‘Cascade’ is the more precise term because the first and second interaction in the chain are the same, and therefore takes precedence over ‘keystone’. Effects on focal species are always positive in three–level cascades, either via ‘a friend of my friend is my friend’ (cascading habitat formation, mutualism) or ‘an enemy of my enemy is my friend’ (cascading consumption, competition). By contrast, effects can be either positive or negative if the cascade contain more than three levels. We differentiate different keystone interactions based on the first interaction in a chain reaction; e.g. keystone consumption and keystone mutualism imply that the first interaction is consumption or mutualism, respectively. The effect on focal organisms from keystone interaction chains with more than three levels can be positive or negative depending on the direction of the two chained interactions (see Figure 10.1 for contrasting examples).

10.2 How do marine invaders impact the local biota?

In this section we exemplify common processes whereby marine NIS impact native organisms, classified according to direction (positive vs.

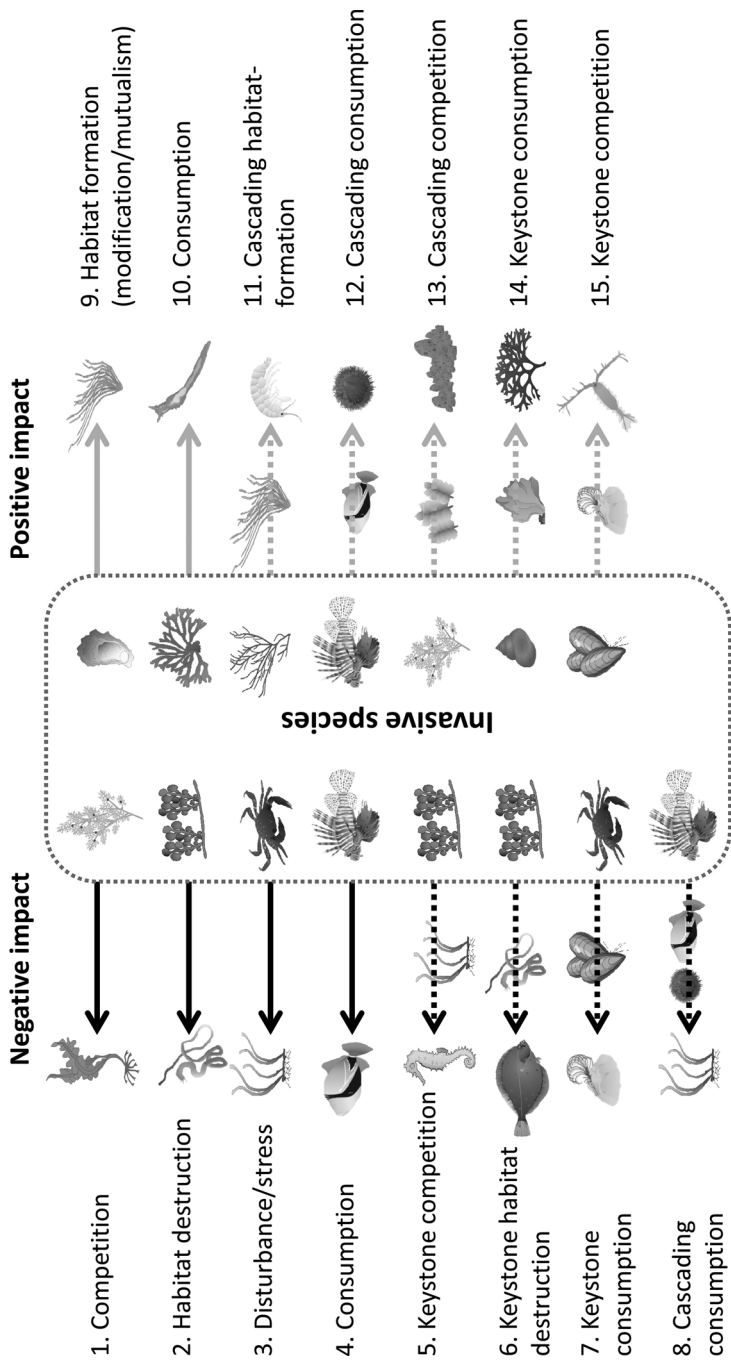


Figure 10.1 Overview of common ecological processes whereby marine NIS (within dashed line) impact local plants and animals.

These processes ultimately cascade up to impacts on communities, patterns of biodiversity (cf. Figure 10.2a and D3 on Figure 10.3) and ecosystem functions (cf. Figure 10.2b and C4 on Figure 10.3). Black and green arrows = negative and positive invasion effects, respectively. Solid and dashed arrows = direct and indirect invasion effects, respectively. See Section 10.2 for examples and details on each process. Images used in the figure courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.

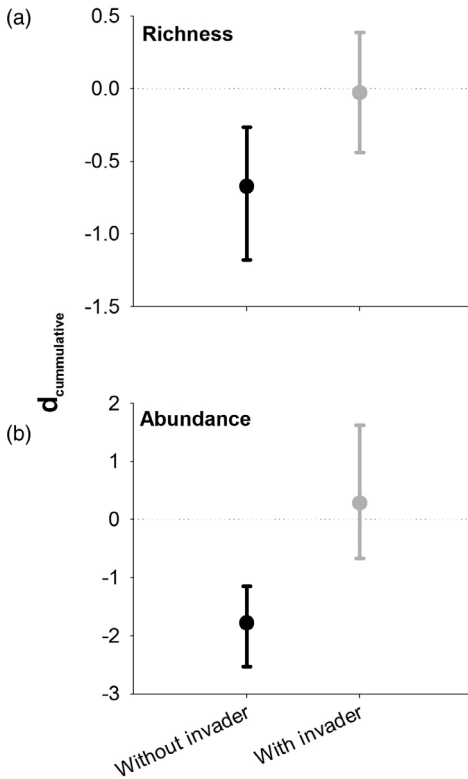


Figure 10.2 Meta-analysis of manipulative field experiments that quantify impact of marine plant invaders on local plant richness (a) and total plant abundance (b). Hedges' effect size ($d_{\text{cumulative}}$) was calculated as a traditional impact analysis, i.e. without inclusion of the invasive species itself (black circles) and contrasted to the same data set where we added the invaders own 'richness' (=1 species more per plot in invasion treatments) and abundance (a relatively high per cent cover or biomass in invasion treatments) (grey circles). Replication for richness = 30 experiments from 11 research papers. Replication for abundance = 23 experiments from eight research papers. The graphs show strong negative impact of marine plant invaders on richness and total abundance from traditional impact analysis, but that net community effects changes to zero (error bars overlap zero) when the taxonomic status and abundance of the invader itself was added to the community data.

negative) and pathway (direct vs. indirect effects). Note that 'direction' simply refers to whether the quantified effect is larger or smaller than a reference value (often defined as 0). Invasion impact is, therefore, here considered a statistical measure that can be either positive (>0) or negative (<0), and this measure gives no direct indication as to whether the

impact should be considered ‘good’ or ‘bad’ (which represents the human interpretation of the statistical measure, see Chapter 1). Understanding the complexity of ecological interactions between invasive and native species is a prerequisite to understanding how biodiversity and ecosystem functioning also are impacted.

10.2.1 Negative impacts

Invasion impact studies have traditionally focused on how native species have been negatively affected by invaders (Rodriguez, 2006) via direct (Figure 10.1, 1–4) and indirect (Figure 10.1, 5–8) mechanisms. Most of these studies have focused on the direct effects (White *et al.*, 2006) although with an increasing number of species in a community the number of possible indirect effects increases exponentially and much faster than the number of direct interactions (Wootton, 1994). In the following sections, we first describe direct effects followed by simple cases of indirect effects that involve 3–4 species interacting in ‘chain of events’, whereby a ‘primary invader’ has an effect on a ‘focal native species’, but mediated by 1–2 ‘intermediate species’.

Competition

Marine invaders often compete with native species for limited resources (reviewed in Byers, 2009). For example, the invasive *Sargassum muticum* competes with native canopy-forming seaweeds for light (Figure 10.1, 1) (Staehr *et al.*, 2000; Britton-Simmons, 2004) – although the impact sometimes is minor, especially in the intertidal zone where light limitation is less important (Sánchez and Fernández, 2005; Olabarria *et al.*, 2009). Similarly, invasive *Caulerpa* species compete with native seagrasses for space, light and nutrients, with some studies suggesting strong negative impacts (de Villele and Verlaque, 1995; Ceccherelli and Cinelli, 1997), whereas others do not (Jaubert *et al.*, 1999; Ceccherelli and Sechi, 2002; Jaubert *et al.*, 2003; Thomsen *et al.*, 2012b). These examples suggest that invasion impact is context dependent, varying from dramatic to negligible, depending on specific invader–habitat interactions (Strayer *et al.*, 2006; Thomsen *et al.*, 2011b). Invasive seaweeds may also compete with sessile animals for limited resources. For example, accumulations of drifting mats of *Gracilaria vermiculophylla* can reduce recruitment of sessile organisms that require hard substrates (including the reef-forming oyster themselves), thereby altering sessile communities probably intercepting propagules from the water column and physical smothering (Thomsen and McGlathery, 2006). In this study, the impact on

community structure was similar across hydrodynamic regimes (non-significant interaction in multivariate analysis), suggesting that at least in some cases impacts can be constant along environmental gradients. Other examples of competitive effects between plants and animals include invasive turf alga that competes with sessile coral animals for space (Linares *et al.*, 2012; Cebrian *et al.*, 2012) or encrusting fouling bryozoa (*Membranipora membranacea*) that live as epiphytes on kelp blades (Levin *et al.*, 2002; Saunders and Metaxas, 2008), thereby shading the kelp and increasing susceptibility to frond breakage (note that the invasive bryozoa is positively affected by the kelp, using the kelp as habitat).

Habitat destruction

Habitat destruction by invaders can be common, particularly where unvegetated sedimentary habitats are converted to vegetated meadows, a process that may result in displacement of obligate infauna and other organisms that depend on sediments. However, there are surprisingly few cases documenting strong negative impacts on infaunal species from invasions by marine plants (Wright *et al.*, 2007; Gribben *et al.*, 2009b; Tsai *et al.*, 2010), perhaps because many infaunal species are facultative mud-flat inhabitants that still survive in the vegetated meadows. Destruction of mud flats has been reported for invasive *Caulerpa* species (Figure 10.1, 2) (Gribben and Wright, 2006; McKinnon *et al.*, 2009; Byers *et al.*, 2010; Klein and Verlaque, 2011; Pacciardi *et al.*, 2011), *Gracilaria vermiculophylla* (Thomsen *et al.*, 2007, 2010a; Byers *et al.*, 2012), *Sargassum muticum* (Strong *et al.*, 2006), invasive seagrasses (Posey, 1988; Baldwin and Lovvorn, 1994; Berkenbusch *et al.*, 2007; Willette and Ambrose, 2009; Ruesink *et al.*, 2010; Willette and Ambrose, 2012), invasive salt marshes and mangroves (Neira *et al.*, 2007; Thomsen *et al.*, 2009a; Wu *et al.*, 2009; Demopoulos and Smith, 2010) and several invasive sessile animals, such as oysters and mussels (Kochmann *et al.*, 2008). Furthermore, habitat destruction could also occur if invasive consumers wipe out a habitat-former, as has been observed following outbreaks of native consumers (e.g. urchins converting kelps to barrens). However, we are not aware of examples documenting this process with invasive consumers (although disease outbreaks on habitat-formers may involve human-mediated introductions).

Disturbances

Marine invaders can cause negative impacts by physical disturbances. For example, native seagrasses (*Zostera marina* and *Halophila ovalis*) can be uprooted and their seeds buried by invasive crabs (*Carcinus maenas*)

(Figure 10.1, 3) (Davis *et al.*, 1998), snails (*Batillaria australis*) (Hoeffle *et al.*, 2012) and polychaetes (*Marenzelleria viridis*) (Kristensen *et al.*, 2011). These disturbances are probably most important in sparse seagrasses, at seagrass edges, on individual seedlings and around newly established small patches where interconnected rhizomes are few and physical integration low. Furthermore marine invaders may also, via their activities, make the habitat more hostile for native species. For example, the invasive polychaete *Marenzelleria viridis* can decrease the oxic zone in sediments (Kristensen *et al.*, 2011; Norkko *et al.*, 2012), potentially having a negative impact on native seagrasses.

Consumption (by the invader)

Marine invasive animals can have a direct negative impact on native species via consumptive processes (reviewed in Rilov, 2009). For example, invasive lionfish exert strong top-down control in invaded Caribbean reefs, particularly on juvenile tropical reef fish, in part because the native prey appear to be naive to this new enemy (Figure 10.1, 4) (Albins and Hixon, 2008; Albins, 2013). Similarly, invasive crabs, such as *Carcinus maenas* or *Hemigrapsus sanguineus*, consume large quantities of native mussels (DeGraaf and Tyrrell, 2004) and the jellyfish *Mnemiopsis leidyi* has, via its predation on fish larvae, been implicated in the collapse of the anchovy fishery in the Black Sea (Kideys, 2002) (but see also Bilio and Niermann, 2004)). Another well-documented example is how the invasive snail *Littorina littorea* causes dramatic grazing effects on rocky intertidal shores and tidepools, denuding *Fucus* recruits (Lubchenco, 1983) and ephemeral algae from rocky tidepools (Lubchenco and Menge, 1978). Still, such top-down effects that are evaluated from manipulative experiments, may be overestimated, because invader-driven niche shifts or local reductions/extinctions of functionally similar native species, can be extremely difficult to detect. For example, *Littorina littorea* may have displaced the native sibling *Littorina saxatilis* (Eastwood *et al.*, 2007) that otherwise can carry out similar ecosystem functioning in the absence of the invasive grazer. This highlights an important problem when evaluating impact from experiments conducted in already invaded locations.

Keystone competition

When invasive plants have negative impacts on native plants, this can lead to indirect negative impact on animals that prefer to forage around and inhabit the native plant. For example, syngnathid and monacanthid fish

have been found to be more abundant around native seagrass compared to invasive *Caulerpa* species (Figure 10.1, 5) (York *et al.*, 2006), juvenile fish can be more abundant in native seagrass beds compared to invasive *Halophila stipulacea* (Willette and Ambrose, 2012) and gastropods and seastars are typically more common on native kelp compared to invasive *Codium fragile* (Schmidt and Scheibling, 2006). Still, many of these indirect effects appear to be relatively minor, probably because marine animals are often generalists that can survive on different vegetation (Bell, 1991), a finding supported by many ‘epibiota comparisons’ that typically find larger spatio-temporal differences in epibiota community structures, compared to between an invasive and native plant competitor (Viejo, 1999; Wernberg *et al.*, 2004; Guerra-García *et al.*, 2012; Janiak and Whitlatch, 2012).

Keystone habitat destruction

Indirect negative effects associated with keystone habitat destruction is conceptually similar to keystone competition; i.e. if invasive plants destroy habitats (e.g. converting mudflats to meadows), this can lead to indirect negative impact on animals that prefer to inhabit and forage in sediments (Figure 10.1, 6). Organisms that are likely to be indirectly negatively influenced by mudflat–vegetation conversions include burying fish such as flounders and stargazers, as well as many wading birds that feed on mudflats, particularly during migrations (although few studies have documented this for invasive marine plants; Parks, 2006). Whether these types of negative effects arise through direct interactions with the invader or indirect effects, for example, mediated through the disappearance of a food source, may be difficult to evaluate, but can be important to know, particularly from a conservation perspective, to ensure that management action works according to intentions. For example, if a management objective is to conserve a species whose decline is possibly caused by habitat destruction by an invader, then ‘encouraging’ the establishment of alternative resources (in habitat and/or food) for the declining native species could be an alternative to control or eradication of the invader.

Keystone consumption

Consumers may also have large indirect effects on native organisms via keystone consumption (see Box 10.1), in particular where a consumer preys on important habitat-formers. For example, invasive crabs, such as *Carcinus maenas* or *Hemigrapsus sanguineus*, consume large quantities of sessile animals, in particular mussels (Grosholz and Ruiz, 1996; DeGraaf

and Tyrrell, 2004) that are important biogenic habitat-formers for sessile animals and plants (Figure 10.1, 7) (Altieri *et al.*, 2007; Lang and Buschbaum, 2010). Keystone consumption is likely to be particularly important in estuarine soft-sediment systems where biogenic habitat formation is particularly important (Buschbaum *et al.*, 2009; Thomsen *et al.*, 2010a).

Cascading consumption

Possibly the best studied indirect interaction is cascading consumption (= ‘trophic cascades’) (Hairston *et al.*, 1960; for a review of multitrophic effects and marine invaders, see Grosholz and Ruiz, 2009). It is well established that second order consumers have positive indirect effects on plants (Shurin *et al.*, 2005), and we can therefore extend this insight to speculate that third order consumers have negative impacts on plants (Daskalov *et al.*, 2007; Casini *et al.*, 2008). However, we are unaware of studies that have documented four-level cascading consumption involving marine invasive top predators (but see Tronstad *et al.*, 2010, for an example with a freshwater invader). Still, a hypothetical case can illustrate the process. For example, it has been documented that invasive lionfish *Pterois volitans* consume trigger fish (Albins, 2013), and that triggerfish consume urchins (McClanahan *et al.*, 1996; O’Leary and McClanahan, 2010) and that urchins can denude tropical seaweeds (McClanahan *et al.*, 1996; O’Leary and McClanahan, 2010) and seagrasses (Alcoverro and Mariani, 2004). Hence, we speculate that lionfish could have indirect negative impact on tropical seaweeds via four-level cascading consumption (Figure 10.1, 8).

10.2.2 Positive impacts

Although there has been a traditional research focus on negative effects of invasions, positive effects have gained increasing scientific interest (Rodriguez, 2006) and more and more examples are documented, both from direct (Figure 10.1, 9–10) and indirect (Figure 10.1, 11–15) mechanisms, which we describe below.

Habitat formation, modification and mutualism

Many marine invaders can have direct positive effects on native species by creating and modifying habitats. Thus, many invaders create three-dimensional structures that are inhabited by native species, including invasive oysters (Figure 10.1, 9) (Lang and Buschbaum, 2010; Markert

et al., 2010; Padilla, 2010), mussels (Sousa *et al.*, 2009), snails (Wonham *et al.*, 2005; Thomsen *et al.*, 2010b), tunicates (Castilla *et al.*, 2004), bryozoa (Wilson, 2011), seaweeds (Thomsen *et al.*, 2006b; Nyberg *et al.*, 2009; Thomsen *et al.*, 2010a; Klein and Verlaque, 2011; Byers *et al.*, 2012), and seagrasses (Posey, 1988; Berkenbusch and Rowden, 2007; Willette and Ambrose, 2012). Of these examples, oyster invasions are particularly important, because they have affected enormous areas of soft-bottom estuaries worldwide (Padilla, 2010), thereby creating hard substratum (a limiting resource for many sessile organisms in sedimentary systems) for native sessile organisms. Many of these direct positive effects are rather obvious as physical structures provide a place to escape enemies and abiotic stress and find 'friends' and resources, processes that are particularly important for interstitial organisms (Huston 1994). Positive invasion effects may not only occur on barren sediments, but may also occur in already vegetated habitats, as invaders can still 'add' structure (Roscher *et al.*, 2005) to support 'more' native species. For example, the invasion of *Sargassum muticum* in Denmark has probably resulted in a system-wide increase in macroscopic plant biomass and thereby (additional) habitat for epiphytic plants (Thomsen *et al.*, 2006c) and invertebrates (Wernberg *et al.*, 2004). Positive effects are, like negative effects, typically context dependent. For example, experimental data suggest that positive habitat formation effects of the invasive seaweed *Gracilaria vermiculophylla* can vary between depth levels, invader density, native taxa and life stage of native taxa (e.g. threshold vs. continuous positive impact on snails vs. bivalves; Thomsen, 2010; Thomsen *et al.*, 2013). Density-dependent thresholds have also been documented experimentally with invasive *Sargassum muticum*, where positive habitat-formation effects changed to negative competitive effects at high densities (White and Shurin, 2011). In addition to creating habitat (autogenic engineering) for sessile plants and animals and mobile interstitial invertebrates, many invaders can also modify the environment (habitat modification; allogenic engineering) to make it more benign for native species. For examples, invasive seaweeds, oysters, mussels and tunicates may reduce desiccation stress on native species (Castilla *et al.*, 2004; Bulleri *et al.*, 2006), increase sediment organic matter via faecal production and increase water clarity by filtering out plankton thereby increasing light levels for native benthic plants (Petersen *et al.*, 2008; Thomsen *et al.*, 2010b). Invasive bioturbators may also increase sediment oxygen levels and potentially thereby reduce stress on native seagrass and infauna. In contrast to common studies documenting direct positive effects from invasive habitat-formers, there has

been less emphasis on how impacted native species also can influence the invader. It is possible that many reciprocal interactions can be classified as mutualisms, for example, if native grazers consume epiphytes on invasive plants, thereby increasing light levels, or if native animal excretions provide nutrients to invasive plants.

Consumption (of the invader)

The second common type of direct positive effect is through consumption, i.e. where the invader is a food source for native species. Thus, if invasive plant and animals increase system-wide standing stocks there should be more food available to native grazers and higher order consumers. For example, siphonalian invaders (*Codium* and *Caulerpa* spp.) can have positive impacts on specialist saccoglossan grazers (Figure 10.1, 10) (Trowbridge and Todd, 2001; Trowbridge, 2002; Harris and Jones, 2005). Similarly, juvenile invasive seaweeds (Thornber *et al.*, 2004; Sjutun *et al.*, 2007) and seagrass (Reynolds *et al.*, 2012) can provide an important seasonal food supply for grazers, and invasive *Codium fragile* and seagrass can be an important food source for periwinkles (Scheibling *et al.*, 2008) and waterfowl. Still, positive effects associated with consumption are probably less important than effects due to habitat formation, as many invasive plants are relatively poor food sources (Scheibling and Anthony, 2001; Britton-Simmons, 2004; Thomsen and McGlathery, 2007; Monteiro *et al.*, 2009; Nejrup and Pedersen, 2010; Cebrian *et al.*, 2011; Engelen *et al.*, 2011; Tomas *et al.*, 2011; Nejrup *et al.*, 2012), some of them having deterring toxins (Boudouresque *et al.*, 1996; Gollan and Wright, 2006; Nylund *et al.*, 2011). Invasive animals can also provide new food sources (Rilov, 2009). For example, invasive *Littorina littorea* snails are consumed by crabs (Trussell *et al.*, 2002, 2004; Eastwood *et al.*, 2007), invasive *Carcinus maenas* crabs are consumed by blue crabs (*Callinectes sapidus*) (DeRivera *et al.*, 2005), the invasive clam *Nuttallia obscurata* is consumed by native crabs (Byers, 2002), invasive copepods are consumed by native fish (Bollens *et al.*, 2002), and invasive lionfish may be consumed by groupers (Maljković *et al.*, 2008). Note, however, as shown for invasive seaweeds, many animal invaders are also relatively resistant to enemies, e.g. invasive *Batillaria australis* snails are rarely consumed by fish or crabs (Thomsen *et al.*, 2010b) and invasive lionfish are toxic to many native species (Whitfield *et al.*, 2002).

Cascading habitat formation and modification

Marine invaders can have many types of indirect positive effects. A common indirect facilitation mechanism is cascading habitat formation. For

example, the invasive snail *Batillaria australis* provides habitats for sessile plants and animals (in particular native seaweeds) (Thrring *et al.*, 2014), that again provide additional habitat for many smaller hydrozoa, bryozoa and mobile invertebrates (Figure 10.1, 11) (Thomsen *et al.*, 2010a). Therefore *Batillaria australis* has indirect positive impacts on invertebrates mediated through its epiphytes. Similar forms of cascading indirect effects may occur following all the direct positive habitat formation processes described above. That is, invasive habitat-formers like oysters, mussels, snails, seaweeds and angiosperms may have indirect positive effects on native organisms by being the ‘primary habitat-former’ that provides habitat for ‘intermediate habitat-formers’. These types of indirect positive effects can also occur through cascading habitat modification. For example, invasive seaweeds may reduce sediment oxygen levels thereby forcing native bivalves to move to the sediment surface and be exposed to fouling by sessile species (Gribben *et al.*, 2009a; Hoeffle *et al.*, 2012). The invasive seaweed thereby has indirect positive effects on fouling species by modifying the environment for bivalves.

Cascading consumption

The most frequently studied indirect positive interaction involves three-level consumption cascades (Hairston *et al.*, 1960; Estes and Palmisano, 1974) (for a review of multitrophic effects and marine invaders, see Grosholz and Ruiz, 2009). For example (as also outlined in Figure 10.1, 8), invasive lionfish can consume trigger fish (Albins, 2013) and herbivorous fish, thereby releasing predation pressure on urchins (Figure 10.1, 12) (McClanahan *et al.*, 1996; O’Leary and McClanahan, 2010) and seaweeds (Lesser and Slattery, 2011), respectively. Another example is when invasive crabs consume or alter the behaviours of grazing snails (Trussell *et al.*, 2002, 2004; Eastwood *et al.*, 2007), thereby indirectly facilitating seaweeds in a three-level density or trait-mediated consumption cascade.

Cascading competition

Positive indirect effects can also occur via cascading competition, in particular when the basal and intermediate competitors compete for a different resource compared to the intermediate and focal competitors (Levine, 1999). We are not familiar with examples documenting cascading competition from marine invasive basal competitors, but we suggest that invasive canopy-forming *Sargassum muticum* mainly compete with smaller understory algae for light, whereas understory algae likely compete with encrusting plants and sessile animals for space (Figure 10.1, 13)

(Staehr *et al.*, 2000; Thomsen *et al.*, 2006c) (for an example of cascading competition, but with native canopy-formers, turfs and crusts, see Wernberg *et al.*, 2012b). Thus, a marine invader may have an indirect positive impact on a con-trophic species by reducing the abundance of another con-trophic (strong) competitor.

Keystone consumption

Consumers can have indirect positive effects on lower trophic levels by preferentially consuming a competitively dominant species (Paine, 1966). A classic example is invasive *Littorina* snails that consume fast growing seaweeds like *Ulva* species thereby reducing competition for slower-growing less palatable species like *Chondrus crispus* (Lubchenco, 1978, 1983). Thus, in this case the consumer provides a similar function as the canopy former in Figure 10.1, 14, or a physical disturbance that opens up space, in each case indirectly facilitating a competitively inferior native species.

Keystone competition

Our final example involves indirect positive effects associated with keystone competition, such as when a basal competitor has a negative impact on an intermediate competitor, but the two competitors use different resources. On rocky shores, invasive mussels compete with native limpets and barnacles for space (Steffani and Branch, 2005), but whereas the mussels consume phytoplankton, the limpets and barnacles consume seaweeds and zooplankton, respectively. The mussel can therefore have indirect positive effects on seaweeds and zooplankton by outcompeting limpets and barnacles (Figure 10.1, 15). Similarly, invasive crabs compete with native crustaceans (Rossong *et al.*, 2006; Williams *et al.*, 2006; MacDonald *et al.*, 2007), but consume slightly different prey, and invasive oysters compete with native mussels (Kochmann *et al.*, 2008), but filter slightly different plankton components. In these examples, the native prey that is preferentially consumed by the native competitor may be indirectly facilitated by the invasive consumer.

The examples above represent common mechanisms whereby marine invaders affect local species and functional groups. These different types of effects eventually scale up to the entire community, as different species in the community are influenced by positive and/or negative impacts, to modify local patterns of biodiversity and ecosystem functioning. In the next sections we describe common processes whereby invaders modify

the abiotic environment, and review studies of marine invasions and their impacts on biodiversity.

10.3 How do marine invaders affect the local abiotic environment?

All NIS modify abiotic conditions and elemental cycling, either directly by their metabolic and behavioural activities and/or indirectly by modifying the invaded biotic community. Invasion impacts on the abiotic environment can be classified as effects on *abiotic conditions* that are not utilised by the invader, such as temperature or salinity, and *abiotic resources* that are utilised by invader. Resources can become *depleted* (e.g. macronutrients) or *not* (calcium carbonate, used in shells). Impacts on resource levels can be quantified in terms of compartment themselves (e.g. total nitrogen in sediments) or as fluxes between compartments (e.g. the flux of nitrogen between water and sediment).

In marine systems, abiotic conditions like temperature, salinity or waves can in rare cases be modified by NIS. For example, invasive species dominating the intertidal zone can, at low tides, reduce *temperature* fluctuations and *evaporation* and thereby increase *moisture* levels within and beneath the NIS (Thomsen, unpubl.; Critchley *et al.*, 1990). Similarly, structurally dominant NIS can reduce *hydrodynamic forces*, such as *Spartina* marshes reducing flows compared to unvegetated mudflats (Neira *et al.*, 2006). However, a counter-example is that in a small-scale removal experiment *Sargassum muticum* did not affect flow rate (Britton-Simmons, 2004). Flow reductions are most likely to occur when the invader is structurally large and covers large areas. These types of invasion effects are probably of relatively minor importance in marine habitats.

Of greater ecological importance are invasion impacts on resource levels, particularly those that occasionally become depleted or where 'by-products' can be toxic. The most important abiotic resources impacted by marine NIS involve elemental fluxes of *nutrients such as nitrogen and phosphorous*. For example, invasive plant invaders can take up nitrogen and phosphorous from the water column and sometimes also sediments from soft-bottom systems (Tyler *et al.*, 2005; Tyler and McGlathery, 2006), store it in live tissue, which can be transported to adjacent ecosystems (Thomsen *et al.*, 2009b), and the nutrients released again through decomposition (Thomsen *et al.*, 2009b; Byers *et al.*, 2012). Fluxes and storage of nitrogen and phosphorous can be controlled by invaders, particularly when NIS dominate in habitats with low abundances of

native structural species, e.g. *Crassostrea gigas*, *Gracilaria vermiculophylla* and *Caulerpa* species invading mudflats. However, nutrient fluxes can also change if a NIS replaces a native species that appears to be 'similar'. For example, invasive *Sargassum muticum* is morphologically similar to, and phylogenetic related to, the native *Halidrys siliquosa*, but has significantly faster nutrient uptake rate, growth and decomposition and only the invader sheds its laterals, a mechanism that locally can remove nutrients stored in tissue (Wernberg *et al.*, 2001; Pedersen *et al.*, 2005). Partial replacement of *Halidrys* with *Sargassum* (Staehr *et al.*, 2000) may therefore have relatively low impact on the general physiognomy of the invaded system, but a larger 'hidden' impact on elemental cycling and nutrient transfer. Sessile animals also modify fluxes of nutrients, for example by increasing pore-water ammonia in sediments as done by the invasive bivalves *Musculista senhousia* (Reusch and Williams, 1998) and *Crassostrea gigas* (Green *et al.*, 2013).

Another important abiotic resource that can be locally depleted is light. Large species that produce dense canopies intercept light (often >90% of incident light) and shade understory species. Such shading is typical for canopy-forming invasive macrophytes such as *Eucheuma denticulatum* in seagrass beds (Ekloef *et al.*, 2006), *Sargassum muticum* on rocky reefs (Critchley *et al.*, 1990; Britton-Simmons, 2004) and *Gracilaria vermiculophylla* morphologies on mudflats. By contrast, many invasive filter feeders (oysters, mussels, polychaetes) can potentially increase light levels by removing large amounts of organic materials from the water column (Davies *et al.*, 1989; Padilla, 2010).

Marine invaders can modify oxygen levels through photosynthesis, respiration and indirectly by bacterial oxygen consumption of decaying/lost organic material (Green *et al.*, 2012). For example, *Caulerpa taxifolia* reduced oxygen in the water column compared to unvegetated sandflats (often to hypoxic levels) (Wright *et al.*, 2010) and the invasive snail *Batillaria australis* reduced the depth to sulfide horizon (i.e. increased anoxia) (Hoeffle *et al.*, 2012). The latter result appears counterintuitive because the snail is a bioturbator that moves sediments. However, Hoeffle *et al.* hypothesised that the snail deposits organic matter within sediment and that bacterial decomposition caused reduced oxygen levels. Indeed, sediments are often reported to be modified by marine invaders, including organic matter content, grain size, sedimentation rates, and sediment stability/erosion rates. Thus, several studies have shown increases in sediment organic matter when unvegetated mudflats are invaded by NIS, such as saltmarsh plants (*Spartina alterniflora*) (Neira *et al.*, 2006) and sessile

bivalves (*Musculista senhousia* and *Crassostrea gigas*) (Reusch and Williams, 1998; Kochmann *et al.*, 2008). Note, however, that if oysters invaded systems already dominated by native bivalves, sediment organic matter was of similar magnitude (= a 'substitution' process, see Section 10.5 for meta-analytical example) (Kochmann *et al.*, 2008). Increased organic matter in sediment comes from organic material deposited by the invader itself and because the NIS reduces hydrodynamic forces, which increases deposition and reduces resuspension. Still, not all studies have found increases in organic matter; there were no increases in organic matter on sand flats invaded by *Caulerpa racemosa* (Pacciardi *et al.*, 2011) or in seagrass beds invaded by *Euchema denticulatum* (Ekloef *et al.*, 2006). Marine NIS can also change the *inorganic sediment texture*. For example, mudflats invaded by *Spartina alterniflora* had a higher proportion of fine particles (Neira *et al.*, 2006), whereas *Caulerpa* had the opposite impact, with a higher gravel content and less sand at invaded than non-invaded sites (but only for one of two invaded areas) (Pacciardi *et al.*, 2011). Related to texture and organics are *sedimentation rates*, which also have been shown to be modified by invaders. For example, *Undaria pinnatifida* increased sedimentation rates but only in the absence of bulldozing urchins (Valentine and Johnson, 2005), as did *Spartina alterniflora* compared to adjacent mudflats (Neira *et al.*, 2006). By contrast, invasive drift mats of *Gracilaria vermiculophylla* reduced sedimentation on oyster reefs (Thomsen and McGlathery, 2006) whereas *Sargassum muticum* had no detectable impact on shallow subtidal reefs (Britton-Simmons, 2004). Finally, mobile invaders can change *sediment stability and erosion rates*, such as through bioturbation and burrowing. For example, the Chinese mitten crab *Eriocheir sinensis* and the isopod *Sphaeroma quoyanum* make burrows in banks, potentially causing bank erosion or converting marsh to mud (Rudnick *et al.*, 2005; Davidson and de Rivera, 2010), and at the same time changing invertebrate communities living in and around the holes (Davidson *et al.*, 2010).

Finally, we present a case study to illustrate how a single invasive species (the mollusc *Batillaria australis*) could impact abiotic conditions in an entire ecosystem. A primary assumption is that the behaviour and activity of *Batillaria* can be scaled up from individuals to the entire population in the system (Parker *et al.*, 1999; Ruesink *et al.*, 2006). A secondary assumption is that *Batillaria* has not dramatically altered populations of native molluscs. This assumption is supported by circumstantial evidence; correlative survey data and field experiments suggest low impact of *Batillaria* on native molluscs because the invader can be found

in extreme high densities together with native molluscs, and because few shell deposits have been found in sediment cores suggesting that no 'bivalve mass extinction' has occurred (Thomsen *et al.*, 2010b, 2012a; Hoeffle *et al.*, 2012). *Batillaria* was introduced to the Swan River in Perth with imported oysters about 50 years ago. It has been conservatively estimated that 3.6 billion *Batillaria* exist in the Swan River today (Thomsen *et al.*, 2010b). Except for a minor population outside of the mouth of Swan River, the nearest population is more than 3000 km away. *Batillaria* is the dominant gastropod in the estuary, occupying most habitats and depth strata. It is on average 2.4 cm long and typically lives 3–4 years.

Here we restate the impact questions to 'what do these 3.6 billion snails do?' Most importantly, *Batillaria* produces hard substratum within the estuarine 'sea of soft sediments', corresponding to *c.* 1.7 km² of *Batillaria* substratum or 3 111 243 kg ash free dry weight (primarily CaCO₃) that move around on a daily basis in the Swan River. Assuming the population is not growing anymore and that the majority of empty shells eventually are buried in sediments, >3000 tonnes CaCO₃ are buried over a 3–4 year period in this single estuary. *Batillaria* moves around on the sediment surface or just below and we calculated that up to 450 000 m³ sediments could be in physical contact, and thus potentially moved, with the snail daily in the estuary. An unknown proportion of this sediment will be ingested and oxygenated, and diatoms, bacteria, organic material and invertebrate eggs and larvae possibly consumed. Similarly, *Batillaria* can affect sediment properties through faecal production and re-mineralisation of nitrogen. We calculated that more than 2 kg nitrogen may be released daily in the system by this single snail. Finally, if *Batillaria* is a dual feeder like its sibling species *Batillaria zonalis* and *Batillaria flectosiphonata*, then, in addition to deposit feeding on sediments it may also filter the water column for particulate organic matter. Assuming that *B. australis* has similar traits to its native congeners, then, theoretically, up to 3 billion litres of Swan River water could be cleared of suspended particles each day. More specifically, assuming a mixed water column, *Batillaria* in a seagrass bed at 1 m depth could potentially clear the entire water column every few hours. Similar simple ballpark estimates could be made for most marine invaders to provide first-order approximation of which species influence specific biogeochemical cycles the most (for analogous ballpark calculations that emphasise productivity changes, see Ruesink *et al.*, 2006). Ultimately, all of the above types of impact on

local abiotic conditions and resources will interact with effects on local species and on BEF relationships.

10.4 How do invaders impact local communities?

The previous sections exemplified how marine invaders affect local abiotic conditions and biota, but with little consideration of how entire communities and patterns of biodiversity might be altered. Here we review and analyse the effects of marine invaders on entire communities.

10.4.1 Review of reviews

Several authors have already reviewed impacts of invasive marine seaweeds using vote-counting (counting studies that find a particular type of effect, Schaffelke and Hewitt, 2007; Williams and Smith, 2007) and quantitative meta-analysis (calculate average impact and confidence limits, Thomsen *et al.*, 2009c). Schaffelke and Hewitt (SH) and Williams and Smith (WS) reviewed 69 and 68 impact papers, respectively, including both mensurative and manipulative experiments (Box 10.1). We revisited these studies to evaluate what impacts have been reported on local communities, as measured by univariate diversity metrics and/or multivariate community structures. For each reviewed study (Table 1 in both SH and WS) we tallied impact direction (positive, negative, zero, non-directional), experimental method (mensurative vs. manipulative), and impacted organisms (plant or animal diversity, multivariate community structure) (Table 10.1). This table highlights that little is known about marine plant invasion impacts; for example, there were only one (SH) or three (WS) examples of documented negative or zero impacts on local plant diversity from manipulative experiments, and not a single experimental study documented positive effects of marine plant invaders on local plant diversity. Evidence was only slightly stronger for mensurative data; SW reported mostly negative impacts on plant diversity, whereas WS reported almost equal numbers of negative, positive or zero impacts. There were even fewer studies reporting impacts on local animal diversity than those on plant diversity; not a single manipulative experiment was identified, whereas a few mensurative experiments documented both positive and negative effects. Finally, no manipulative studies were found to alter multivariate community structures significantly (WS; 1 reviewed study with no effect).

Table 10.1 *Community impacts from invasive seaweeds tallied from Table 1 in Schaffelke and Hewitt (2007; SH) and Table 1 in Williams and Smith (2007; WS).*

| Impact on → | Plant diversity | | | | Animal diversity | | | | Community structure | | | |
|-------------|-----------------|----|------|----|------------------|----|------|----|---------------------|----|------|----|
| | Man. | | Men. | | Man. | | Men. | | Man. | | Men. | |
| Method → | SH | WS | SB | WS | SB | WS | SH | WS | SH | WS | SH | WS |
| Reviewer → | SH | WS | SB | WS | SB | WS | SH | WS | SH | WS | SH | WS |
| Effect ↓ | | | | | | | | | | | | |
| Negative | 1 | 2 | 11 | 4 | 0 | 0 | 5 | 5 | 0 | 0 | 4 | 10 |
| Zero | 0 | 1 | 1 | 3 | 0 | 0 | 0 | 4 | 0 | 1 | 5 | 2 |
| Positive | 0 | 0 | 1 | 3 | 0 | 0 | 4 | 2 | NA | NA | NA | NA |

Some studies documented both negative, positive and zero impact from the same single experiment (e.g. on plants, animals, and community structure, respectively). Impact on community structure was classified as ‘negative’ or ‘zero’ if the multivariate tests were significant or non-significant, respectively. The majority of studies reviewed by SH and WS documented negative impact of invasive seaweeds on diversity. Man. and Men. = Manipulative and Mensurative experiments (see Box 10.1). Diversity = univariate diversity metrics; Community structure = multivariate metric.

The meta-analytical review (Thomsen *et al.*, 2009c) tested more specifically if marine plants have different effects within versus across trophic levels and on different levels in the ecological hierarchy. Evaluated from manipulative experiments only, it was shown that impact on plant abundances and plant diversity was negative, probably caused by competition processes. However, a net positive impact was reported on the diversity of animals, probably because the invasive plants created habitat and food for the animals (but this result was calculated from only two primary studies).

Several other reviews have evaluated invasion impacts in marine systems, focusing on ecological – not taxonomic – comparison, including competition, predator/prey, ecosystem-engineering and multitrophic effects (qualitative reviews/vote-counting; Byers, 2009; Crooks, 2009; Grosholz and Ruiz, 2009; Rilov, 2009) and how density, identity or origin of the invader may modify impact (quantitative meta-analysis; Thomsen *et al.*, 2011a, 2011b, 2012b). However, none of these reviews emphasised impacts on local communities or biodiversity; a keyword search for ‘diversity’ or ‘richness’ in these seven papers resulted in only 10 hits and several of these hits used ‘diversity’ in a different context.

More telling, only two specific diversity-impact examples were provided in these reviews; *Phragmites australis* and *Spartina alterniflora* (intertidal marsh plants) can reduce resident plant richness, probably via competition for space, light and nutrients (reviewed in Byers, 2009), and infaunal invertebrate richness and diversity, probably by converting mud habitat to vegetated habitat (reviewed in Grosholz and Ruiz, 2009). Overall, our examination of invasion impact reviews found that only a few case studies reported ‘large’ impacts on community metrics, and that major research gaps exist concerning community impacts. These reviews also emphasise that the mechanisms that cause large or small community impacts are poorly known, but that there is a tendency for negative impacts to occur via plant–plant competition, and positive impacts to occur via habitat formation (on sessile epibiota and mobile animals), and food provision (on local grazers).

10.4.2 New meta-analysis

As indicated in the previous section, little is known about how marine invaders affect local community structures and ecosystem functions, a knowledge gap also highlighted for terrestrial plant invaders (Levine *et al.*, 2003; Powell *et al.*, 2011; Vilà *et al.*, 2011; Pyšek *et al.*, 2012), and more generally in invasion biology (Parker *et al.*, 1999; Byers *et al.*, 2002; Thomsen *et al.*, 2011a). Importantly, invasion impacts on community metrics are traditionally analysed separately from the invader itself (because it is the independent test variable) – but the invader itself is at the same time an integral part of the new community. To better understand BEF relationships, we suggest evaluating invasion impacts on communities using both the traditional type of analysis, but also by adding the invader to the community/ecosystem variable that is quantified. We therefore conducted a meta-analysis that compared community effects with versus without inclusion of the invader (i.e. by adding the independent invader to the dependent community data set). More specifically, we tested if invasion impact, on *species richness* and *total standing stock* would differ if the invader itself was included as part of the total community. We focused on these two metrics because they are most commonly reported; far fewer field impact experiments have quantified impacts on ecosystem functions (but total plant abundance can be interpreted as a surrogate, as abundance often correlates with function).

We used seaweed invaders as model organisms because this literature has been summarised in detail (see previous section), and focus on

experimental studies to be able to infer causality. We reviewed experimental studies that report impacts on local plant communities to ensure commensurability in units between the invader and response community (typically biomass or percentage cover of both the invasive seaweed and impacted local plants). Thus, studies that reported invader abundance as biomass, but impacted plant community as per cent cover, could not be included (Thomsen and McGlathery, 2006). Tests were evaluated from published replicated field experiments that compared invaded and non-invaded plots using invader-addition or -removal manipulations. Literature search, data extraction and meta-analyses generally followed methods described in recent reviews (Thomsen *et al.*, 2009c; Thomsen *et al.*, 2011a, 2011b). We found eight papers (describing 23 experiments) that reported both the abundance of the invader and total abundance of all local plant species, and 11 papers (describing 30 experiments) that reported impacts on local plant richness (Table 10.2).

More specifically, we extracted the last data-point from repeated-measure experiments and compared controls to the highest invader density from multi-density experiments. Nested, orthogonal and repeated experiments and different experiments within a paper were treated as 'independent' experiments. We calculated Hedges' effect size d , corrected for small sample sizes ($= d_{\text{individual}}$), where $d_{\text{individual}}$ is <0 if the invader reduces biodiversity or total abundance. We subsequently calculated 'combined- $d_{\text{individual}}$ ' values to represent invasion effects on the entire community that included the invader itself (as it is part of the 'new' plant community).

It is straightforward to compare richness effects with versus without inclusion of the invader, simply by adding '1' to the mean effect per plot (there is on average one more species in each invaded plot when the invader itself is included). Adding a constant ($= '1'$) to all samples does not influence the standard deviation. We calculated the new total plant abundance in invasion treatments by adding the abundance of the invader to the total abundance of all the local species (see Table 10.2 for details). The new total standard deviations were averaged from individual SD-values. Multiple $d_{\text{individual}}$ from individual experiments were averaged into a single effect size using equal weighting (Borenstein *et al.*, 2009). We calculated unweighted cumulative effect sizes and 95% bias-corrected CL in Metawin 2.1 from the independent $d_{\text{experiment}}$ values (Rosenberg *et al.*, 2000; Thomsen *et al.*, 2009c). Finally, we evaluated if a test-factor was significantly different from zero or another test-factor if 95% CL did not overlap zero or each other, respectively.

Table 10.2 List of manipulative field experiments reporting impacts of invasive seaweeds on local plant richness and total plant abundances (and also reporting the abundance of the invader). Total community richness was calculated by adding one species (the invader itself) to reported impact on 'local species richness'. Total community abundance was calculated by adding the abundance of the invader itself to reported abundances of all local species combined (see footnotes for details).

| Reference | Invader | Impact on plant . . . |
|--------------------------------|---------------------------------------|----------------------------------|
| Britton-Simmons (2004) | <i>Sargassum muticum</i> | Richness |
| Bulleri <i>et al.</i> (2010) | <i>Caulerpa racemosa</i> | Richness, Abundance ⁷ |
| Casas <i>et al.</i> (2004) | <i>Undaria pinnatifida</i> | Richness, Abundance ³ |
| Gennaro and Piazzzi (2011) | <i>Caulerpa racemosa</i> | Richness |
| Gribben <i>et al.</i> (2009a) | <i>Caulerpa taxifolia</i> | Richness |
| Klein and Verlaque (2011) | <i>Caulerpa racemosa</i> | Richness, Abundance ⁶ |
| Olabarria <i>et al.</i> (2009) | <i>Sargassum muticum</i> | Richness |
| Piazzzi and Ceccherelli (2006) | <i>Caulerpa racemosa</i> | Richness |
| Piazzzi <i>et al.</i> (2005) | <i>Caulerpa racemosa</i> | Richness, Abundance ⁵ |
| Sánchez and Fernández (2005) | <i>Sargassum muticum</i> | Richness, Abundance ¹ |
| Thomsen and McGlathery (2006) | <i>Gracilaria vermiculophylla</i> | Richness |
| Valentine <i>et al.</i> (2007) | <i>Undaria pinnatifida</i> | Abundance ⁸ |
| Viejo (1997) | <i>Sargassum muticum</i> | Abundance ⁴ |
| White and Shurin (2011) | <i>Sargassum muticum</i> | Richness, Abundance ² |

Superscript numbers in the column 'Impact on plant . . .' refer to how total community abundance was calculated – by adding . . .

¹ Cover values for *Sargassum muticum* to cover values of *Bifurcaria bifurcata*, *Gelidium spinosum* and 'rest of species' (extracted from their Figure 1).

² Biomass of *Sargassum muticum* (high density treatment) to biomass of native seaweed (extracted from their Figure 4).

³ Biomass of *Undaria pinnatifida* to biomass of all species (extracted from their Table 1).

⁴ Cover of *Sargassum muticum* to total cover of native species (extracted from their Figure 2).

⁵ Cover of *Caulerpa racemosa* to total cover of native species (extracted from their text and Figure 1).

⁶ Biomass of *Caulerpa racemosa* to total biomass of local taxa (extracted from their Figures 1 and 2).

⁷ Biomass of *Caulerpa racemosa* to biomass of canopy, erect, turf and encrusting alga (extracted from their Figure 2 and Appendix Figure 1).

⁸ Biomass of *Undaria pinnatifida* to total abundance of canopy, erect, turf and encrusting alga (extracted from their Figure 3).

Our analysis revealed that marine plant invaders have significant negative impacts on both local plant abundance ($d = -1.78$, 95% CL from -2.53 to -1.14 , Figure 10.2a) and plant community richness ($d = -0.67$, 95% CL from -1.18 to -0.26 , Figure 10.2b). These negative effects suggest that competition dominates interactions between invaders and natives within a trophic level. Importantly, the negative effects were cancelled out when the contribution of the invader itself was included in the estimates of total standing stock ($d = 0.28$, 95% CL from -0.67 to 1.63) and total community richness ($d = -0.03$, 95% CL from -0.44 to 0.39). Thus, at least for abundance and richness, marine plant invaders appear on average across studies, species and invaded systems, to substitute, rather than increase or decrease, total biodiversity and standing stocks. However, clearly more impact studies are needed, especially on functional community responses, such as total system productivity, respiration, decomposition rates and nutrient uptake to test if ecosystem functioning is typically unaffected, enhanced or reduced following invasions. For a few rare examples, see Altieri *et al.* (2009), Cacabelos *et al.* (2012) and Green *et al.* (2012, 2013).

10.5 A simple framework to discuss BEF and marine invasions

It is essential to understand how biodiversity affects ecosystem functioning (Chapters 1, 5) because ecosystem functions relate to provision of ecosystem services for humans (Hooper *et al.*, 2005; Barbier *et al.*, 2011; Hooper *et al.*, 2012; Chapters 1, 2). The first BEF studies originated in terrestrial grasslands, but in the last decade marine systems have also been studied in detail (reviewed in Chapter 5). Currently, the functioning of marine ecosystems is being strongly affected by impacts on patterns of biodiversity by human stressors, in particular climate change (Petchev *et al.*, 1999; Schmitz *et al.*, 2003; Wrona *et al.*, 2006; Wernberg *et al.*, 2012a), fisheries (Chapter 6), habitat alterations (Chapter 7), pollution (Chapters 8, 9) and species invasions (this chapter).

Recent reviews highlight that surprisingly little is known about how invaders influence ecosystem functioning (Vilà *et al.*, 2010; Simberloff, 2011; Strayer, 2012). Still, two aspects of invasions and BEF have received scrutiny. First, many studies have tested how biodiversity modifies community ‘invasibility’ (typically considered an ecosystem function) within the ‘biotic resistance hypothesis’ framework (Elton, 1958; Levine *et al.*, 2004; Parker and Hay, 2005). This theory suggests that high taxonomic

richness correlates with functional diversity and efficient resource utilisation and less opportunity for new species to become established. Many marine studies have tested this theory, although often with opposing results (Stachowicz *et al.*, 1999; Byers, 2002; Stachowicz *et al.*, 2002a; Stachowicz and Byrnes, 2006; Ruesink, 2007). Today, it is acknowledged that there is no simple relationship between biodiversity and how easy it is for invasive species to invade a community, because numerous co-varying factors (e.g., trophic positions of species, potential presence of facilitator-species, spatio-temporal heterogeneity and scale) influence establishment (Fridley *et al.*, 2007; Stachowicz *et al.*, 2007; Catford *et al.*, 2009). Our focus here is primarily on how invasive species modify ecosystem functioning via changes to biodiversity (i.e. we treat the invader as the independent variable), not how biodiversity and ecosystem processes modify invasions (i.e. where the invader is the dependent variable). For details on the latter see the literature listed above.

Second, there is an extensive literature documenting impacts of invasive ‘ecologically important species’ (e.g. ecosystem engineers, habitat-formers, foundation species, keystone consumers) on various ecosystem functions (Crooks, 1998, 2002a, 2009; Pedersen *et al.*, 2005; Wallentinus and Nyberg, 2007; Thomsen, 2010; Thomsen *et al.*, 2010a; Green *et al.*, 2013). Typically, however, these studies do not frame invasion impacts within the context of BEF relationships. A first impression suggests that these and many other invasion impact studies are at odds with traditional BEF studies. Many BEF relationships follow saturation curves where the addition of species to communities with low diversity often results in large positive effects on ecosystem functioning as new ‘functions’ are added by keystone species and ecosystem engineers. However, addition of species to a high diversity community typically result only in *small positive effects*, as niches are increasingly ‘filled out’ by species that can substitute for each other (insurance/redundancy type hypotheses). In contrast, most invasion studies emphasise that addition of a single (invasive) species, also in a highly diverse community, has *dramatic, typically negative, effects*. However, several mechanisms may explain this difference (Ruesink *et al.*, 2006). For example, invasion studies selectively target ‘high profile’ invaders, with ‘easy-to-identify’ high impacts, sometimes adding or destroying entire functional groups. By contrast, BEF studies typically document that addition of a ‘randomly selected’ species, within a functional group, has a low net effect (Scherer-Lorenzen, 2005). Furthermore, trophic position sometimes differs between invasion impact and BEF studies; large documented invasion impacts are often associated

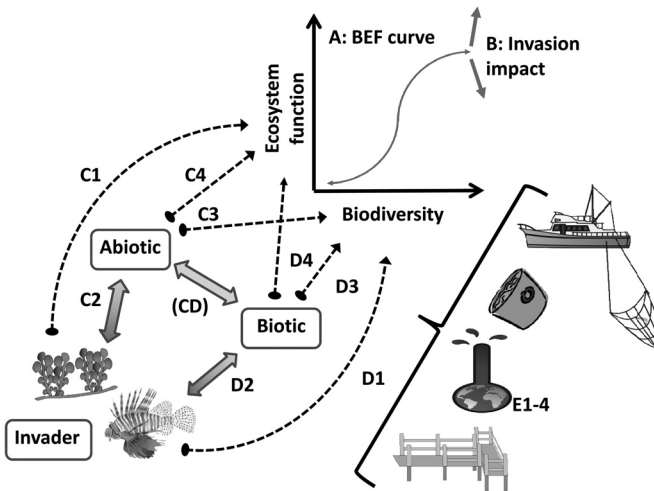


Figure 10.3 Interface between biodiversity–ecosystem functioning (A) and invasion impact (B). Marine invasive species (e.g. *Caulerpa* seaweeds or the Indo-Pacific lionfish, *Pterois volitans*) impact ecosystem function and local biodiversity (arrows) directly by its mere presence and metabolic activity (C1, D1) and indirectly by modifying the local abiotic and biotic environment (C2, D2). These interaction pathways are modified by human stressors such as fisheries, pollution, climate changes and habitat alterations (E1–4). Note that (a) invasion impact differ from the other human stressors by directly modifying BEF curves (C1, D1) and (b) local ecosystem functions and patterns of biodiversity also modify how successful the invader is (reversed arrows). See Section 10.5 for detail. Images used in the figure courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

with consumer effects across trophic and/or functional levels, whereas many BEF studies that document saturation effects focus on plant–plant interactions within trophic and/or functional levels. Finally, it is of course also possible that a lack of co–evolution between invaders and native species creates fundamentally different interactions and thereby also different BEF effects, compared to relationships only involving co–evolved native species. Most importantly, none of the speculations above have been tested systematically or in any detail.

As well as affecting ecosystem functioning via changes in the abiotic environment (Section 10.3), species interactions (Section 10.2) and biodiversity (Section 10.4), marine NIS may also affect the relationship between biodiversity and functioning, further complicating prediction of their effects. Given that little is known about how invasive species modify BEF relationships, we here provide a simple schematic overview (Figure 10.3; capital letters in brackets correspond to the linkages on

the figure). There are many studies that have quantified different BEF curve-shapes depending on specific operating mechanisms within an experimental context (Schulze, 1994; Hooper *et al.*, 2005, 2012; Cardinale *et al.*, 2006, 2011). A typical scenario involves a rapid initial increase in EF as keystone/dominant species are added from a random species pool, but approaching a saturating EF level as niches are slowly filled and resources used more efficiently (A). Superimposed on this pattern, and as discussed in the previous sections, invasion impacts are often documented as large negative or large positive effects even in rich and well-established communities, following the addition (or removal) of a single NIS (B). The invader itself (in Figure 10.3 exemplified by two high profile invaders, the green seaweed *Caulerpa racemosa* and the Indo-Pacific lionfish *Pterois volitans*) has direct impacts on ecosystem functioning (C1) and local biodiversity (D1) (arrows) by its mere presence and metabolic activity, for example by adding one species to the total species richness and adding its nutrient uptake to the system-wide nutrient uptake rates. Examples of how the addition of the invaders themselves modify biodiversity and ecosystem function were examined in Section 10.4 where we tested if invasion impact on plant richness and total standing stock changed depending on whether the invader itself was added to the community dataset. More importantly, invasive species can also have numerous impacts on the local abiotic (C2) and biotic (D2) environment, causing indirect and cascading impacts on the BEF curves (C3–4, D3–4). For example, *Pterois volitans* is a voracious consumer of herbivores on coral reefs (Albins and Hixon, 2008), which potentially could lead to extinctions of local populations and reduced biodiversity (D3) as well as expansive seaweed growth, followed by coral dieback and reduced calcification rates (D4). The processes whereby invaders affect local biota (D2) were reviewed in detail in Section 10.3, because only by understanding the breadth and scope of these processes are we able to understand the more complex cascading effects on BEF (and because these processes are much better studied than invasion vs. BEF curves). Invasive species also modify the local abiotic environment. For example, invasive *Caulerpa* seaweeds alter elemental fluxes in the sediment (C2), typically decreasing oxygen levels and redox potential (Wright *et al.*, 2007; Gribben *et al.*, 2009a). Reduced oxygen levels can then have a cascading impact on biodiversity, for example by killing off infauna that are susceptible to anoxia (C3) or by altering iron-precipitation rates (C4). Effects of invaders on abiotic conditions and biogeochemical fluxes (C2) were discussed in Section 10.4. More complex indirect interactions can also be envisioned between the invader and the invaded abiotic

environment and biotic communities (CD), but are beyond the scope of this chapter.

Our emphasis has been on how marine NIS impact abiotic and biotic conditions and the invasive species was therefore representing an ‘independent test variable’. The ‘arrow’ on Figure 10.3 therefore points towards the BEF curve (= ‘invasion impact studies’). However, we emphasise that the invader itself is controlled by abiotic and biotic ‘filters’ (Richardson *et al.*, 2000); that is, the invasive species is often considered the dependent response variable (= ‘invasion success’ studies). To fully understand the relationship between invasive species and BEF curves, reciprocal interactions between the invader, and the invaded abiotic and biotic environment also need to be considered (see Chapter 5).

10.6 Do invasion impacts co-occur with other human stressors?

Importantly, invasion impact does not operate in isolation from other human-induced stress and disturbances (for brevity here ‘stressors’, Figure 10.3, E1–4). Indeed, all pathways shown in Figure 10.3 are constantly modified by climate change (a global stressor), fisheries, pollution and habitat alterations (local stressors). In this section, we provide examples of possible interactions between invasive impacts, and other human stressors. We note that invasion impacts differ from the other human stressors by being of ‘biological/taxonomic nature’ and therefore (1) have a direct effect on BEF relationships (cf. arrow D1; irrelevant for abiotic stressors) and (2) experience strong reciprocal effects from the abiotic and biotic environment (by contrast, biodiversity has little reciprocal impact on how humans contribute to climate change or habitat alteration). If, where and when these stressors facilitate the survival, establishment and population expansions of marine NIS, impacts will also increase because effect sizes co-vary with invader abundance (Thomsen *et al.*, 2011b). There are three fundamental ways these stressors can facilitate marine invaders: by (1) improving abiotic conditions and resource levels; (2) ‘favouring friends’ of the invader (Simberloff and Von Holle, 1999; Thomsen *et al.*, 2010a); or (3) ‘disfavouring enemies’ of the invader. For example, eutrophication can increase resource availability for invasive plants (Davis *et al.*, 2000), pollution with heavy metals can kill native competitors, and fisheries can reduce top-down control mechanism of native top predators. In these examples, space and other resources become more available and the biotic

resistance of the system decreases, after which NIS can more readily establish new populations (Byers, 2002). A few studies have reviewed interactions between multiple human stressors (Crain *et al.*, 2008; Darling and Cote, 2008), but with virtually no emphasis on marine NIS (only one marine invasion study was listed by Crain *et al.*, 2008). Below we describe a few examples that suggest marine NIS impacts can increase when co-occurring with other human stressors.

Overfishing is a pressing conservation problem (Lotze *et al.*, 2006) as food webs are fished down around the world, first reducing populations of apex predators and subsequently lower trophic levels. Large-scale reduction of predatory fish is likely to open up opportunities for marine invaders that typically are top-down controlled – a process that probably is more relevant for invasive animals than plants. For example, large groupers have been fished down in tropical systems potentially facilitating establishment of lionfish (Maljković *et al.*, 2008) which then reduce abundances and diversity of native species (Albins and Hixon, 2008). Similarly, cod populations in the Baltic Sea have been severely reduced by fishing, thereby removing enemies for invasive round goby, that also can modify biodiversity (Almqvist *et al.*, 2010; Kornis *et al.*, 2012). Finally, it is possible that overfishing of California flounder, *Paralichthys californicus* and other fish in California has led to reduced predation on invasive bivalves (Crooks, 2002b), which also can have wide-ranging cascading impacts on biodiversity (Crooks, 1998; Crooks and Khim, 1999).

Pollution, in particular with excessive nutrients, also facilitates some marine invaders. Plant invaders with high nutrient uptake capacity and an ability to transform nutrients into rapid growth are likely to be facilitated by eutrophication. These types of invaders are typically ephemeral sheet-forming and filamentous seaweeds (often small epiphytic weedy species) that, when nutrients are abundant, gain a competitive advantage over slow-growing, large canopy-forming (native) seaweeds (Sand-Jensen and Borum, 1991). These fast-growing ephemerals are typically hull-fouling species that can be transported between ports and harbours on commercial and recreational vessels. We therefore expect a positive correlation between nutrient pollution, boat traffic and invasions, potentially leading to reduced local plant diversity if slow-growing native canopy species are outcompeted. Interestingly, decreased plant biodiversity and degradation of seagrass beds are often attributed to nutrient fuelled blooms of ‘native’ ephemeral seaweeds. However, many of these ‘native’ species could indeed be NIS, as they often are difficult to identify (simply being assumed to be native) and because these species have

been translocated on ships between regions for centuries (i.e. they may have been introduced to new regions prior to scientific investigations). Thus, perhaps many impacts associated with 'weedy seaweeds' ultimately are driven by a combination of invasions and eutrophication, although detailed taxonomic, biogeographical and molecular studies are needed to test this hypothesis (Carlton, 1996; Thomsen *et al.*, 2006a; Blakeslee *et al.*, 2008). Other types of pollution, such as with metals and hydrocarbons, might also indirectly favour stress-resistant invasive sessile species, such as tunicates, bryozoa and hydrozoa. For example, many sessile fouling invaders are highly resistant to the toxins found in marine harbours, thereby indirectly facilitating them over less stress-resistant native species (Piola and Johnston, 2006, 2008; Dafforn *et al.*, 2009).

Destruction and alteration of habitats modify invasion impacts; coastal forests have been destroyed around the world as they are converted to agricultural landscapes and urban centres. This process accelerates nutrient (see above) and sediment loadings (Syvitski *et al.*, 2005), often with detrimental impacts on marine organisms (Airolidi, 2003; Fabricius, 2005). Heavy sediment load is likely to favour opportunistic invaders. Several invaders appear to be resistant to sediment stress, including certain bivalves (*Theora lubrica*), tunicates (*Styela clava*, *Ciona intestinalis*, *Ascediella adspersa*), bryozoa (*Watersipora subtorquata*) and polychaetes (*Sabella spallanzanii*). These species are typically associated with hull fouling and ballast water transport and are (as for weedy seaweeds) difficult to identify and may therefore have been mistaken for native species (Kremer and Rocha, 2011). Thus, as for nutrient pollution, habitat alteration may have large but potentially underestimated impacts on community structure and biodiversity by disadvantaging slower-growing native species. A more direct mechanism whereby habitat alteration modifies invasion impacts is by creation of hard substrates from wind farms, oil rigs, jetties and seawalls. These structures provide space for sessile species, and are often found in areas of intensive boat traffic and nutrient and sediment pollution, further favouring the establishment of invasive opportunistic species (Connell, 2001; Bulleri and Chapman, 2010; Chapter 7). Hard structures typically support a diverse flora and fauna, occasionally dominated by invaders, and can function as stepping stones for newly arrived NIS, facilitating a rapid secondary spread to nearby locations.

Finally, *global climate change* can modify invasion impacts, because climate change can reduce the resilience of communities to invasions and simultaneously increase the potency of invaders (Stachowicz *et al.*, 2002b; Thuiller *et al.*, 2007; Walther *et al.*, 2009; Raitos *et al.*, 2010; Sorte *et al.*,

2012). Climate change modifies marine ecosystems through altered wave regimes (in some areas storm frequencies have increased), rising sea levels, and increasing acidification and temperature. Increased temperature will likely lower resistance to invasions as some native species become thermally stressed and, at the same time, facilitate survival and establishment of warm-tolerant invaders. For example, invasive lionfish are expected to 'perform' better and extend their invaded range pole-ward in the Atlantic with increasing temperatures (Cheung *et al.*, 2009; Cote and Green, 2012). Invasion impacts might also become more severe under increased temperatures. For example, *Gracilaria vermiculophylla* had little impact on native seagrass under cold temperatures (under both low and high invasion densities), but had a strong negative impact under high temperatures in high densities, suggesting increased negative impacts in a future warmer world (Hoeffle *et al.*, 2011). This strong context-dependent impact happened in part because the seagrass became less resistant to stress near its upper temperature tolerance level, in part because the effects of the invader became more severe as respiratory processes (leading to localised toxic anoxia) become increasingly important at high densities and high temperatures. An important large-scale, long-term effect of warming on species distributions is equatorial range-contraction and pole-ward range expansion (Raitsos *et al.*, 2010; Wernberg *et al.*, 2011; Wernberg *et al.*, 2012b). However, in some cases species may not move fast enough and pole-ward movements can be interrupted by natural or human-created barriers. The interface between NIS invasion and climate change stress creates several conundrums for conservation biologists. First, biologists face a definition issue; are species that spread pole-ward by natural dispersal mechanisms, but only establish reproducing populations due to warming, actually NIS that need to be managed and perhaps even eradicated, or are they simply 'new natives'? Furthermore, as many native species become increasingly heat stressed the local communities are likely to become less resistant to invasions (Stachowicz *et al.*, 2002b; Wernberg *et al.*, 2010). From a practical perspective it can be difficult to distinguish if a new species has arrived by its own dispersal mechanisms and now survives due to warming or if it has arrived with human transport vectors and needs to be managed. Finally, if local species become heat stressed but are prohibited from moving pole-ward because of dispersal limitation, it has been argued that these species should be intentionally introduced to lower latitudes to save them from extinction. However, such 'assisted translocation' is resisted by invasion ecologists because adverse side-effects associated with intentional introductions can be expected (Ricciardi and

Simberloff, 2009; Sandler, 2010; Seddon, 2010; Seddon *et al.*, 2011; Chauvenet *et al.*, 2012).

Finally, we highlight that invasions typically co-occur not only with one but many human stressors, and more studies should aim to address invasion impacts in a multi-stressor framework. For example, it is likely that the infamous anchovy collapse in the Black Sea resulted as a combination of overfishing, eutrophication and climate-induced facilitation of the invasive comb jelly *Mnemiopsis leidyi* (Oguz *et al.*, 2008). The similarly infamous invasion in the Mediterranean Sea of *Caulerpa* species – with potentially dramatic negative impacts on native seagrasses (Meinesz, 1999) – co-occurred with climate changes and increased temperature stress (Díaz-Almela *et al.*, 2007), eutrophication and pollution with metals and hydrocarbons (Danovaro, 2003), excessive sediment loadings (Airoldi, 2003) and overfishing (Lejeusne *et al.*, 2010). Importantly, these co-occurring processes all stress local seagrasses and likely caused them to be susceptible to *Caulerpa* invasions. The above examples of interactions between multiple human stressors and invasions also exemplify the difficulty of distinguishing whether the invader is a main cause (driver) of ecosystem change, mainly following another stressor (passenger) that causes ecosystem change, or interacting with the other stressor to cause ecosystem change (back-seat driver) (MacDougall and Turkington, 2005; Bulleri *et al.*, 2010; Bauer, 2012). This distinction is vital from a conservation perspective because if the invader drives changes, the invaded ecosystem can be restored by controlling the invader, whereas if the invader is a passenger or back-seat driver, other management schemes (e.g. nutrient reduction) need to be implemented as well.

10.7 Invisible invasions: invasion impact is so much more than leaves and legs

Our review has overwhelmingly focused on invasion impacts associated with macroscopic plant and animal NIS – i.e. NIS with ‘leaves and legs’ (Cowan *et al.*, 2013). We have done this because this is our area of expertise, but also because the vast majority of research focus has been on macroscopic NIS. However, there are potentially vast ‘invisible’ invasions associated with microbes (unicellular algae, protists, fungi, bacteria, viruses; Litchman, 2010) and parasites (Torchin *et al.*, 2002) that should not be forgotten in future NIS research programs. Invasive terrestrial (e.g. chestnut blight, caused by the fungus *Cryphonectria parasitica*) and freshwater (e.g. crayfish plague caused by the water mold *Aphanomyces astaci*)

microbial pathogens have long been recognised (Elton, 1958). However, even though one of the first documented examples of a marine invasion involved microbes (Ostenfeld, 1908), only recently have microbial marine NIS been appreciated for their ubiquity and importance (Cowan *et al.*, 2013). A lack of appreciation of microbial invasion impacts may partly stem from the outdated ‘everything is everywhere – but the environment selects’ paradigm (De Wit and Bouvier, 2006). However, today it is well established that marine microbes also have specific biogeographical distributions with endemic genotypes, and therefore may be susceptible to invasions (Litchman, 2010). The most important transport vector for marine microbes is via shipping activities, and an increasing number of studies have quantified microbes in ballast water, ballast sediments, ship cavities and biofilms, suggesting that ballast water is the single most important vector (Ruiz *et al.*, 2000; Drake *et al.*, 2002, 2005, 2007). It has been suggested that up to 12 billion tons of ballast water is moved across the oceans annually (Ibrahim and El-Naggar, 2012), providing a potentially enormous microbial transport mechanism. Indeed, microbes associated with shipping may be particularly successful (and have dramatic impacts) due to microbial traits of high abundances, multiple modes of reproduction, high growth rates, ability to form resting stages, efficient resource utilisation, and potential toxicity (Hallegraeff, 1993; Ruiz *et al.*, 2000; Drake *et al.*, 2002, 2005, 2007; Litchman, 2010). For example, bacterial densities in ballast water can vary from 10^7 – 10^{10} cells per litre (Ruiz *et al.*, 2000; Drake *et al.*, 2002, 2005) and detailed sampling in the Chesapeake Bay region suggest that up to 10^{20} bacteria and viruses are discharged annually from ballast waters (Ruiz *et al.*, 2000; Drake *et al.*, 2007), of which more than half survive the discharge into the new habitat. Of these, massive amounts of released microbes, pathogens and microbes that can cause ‘harmful algal blooms’ are of obvious concern (Hallegraeff, 1993, 2010; Landsberg, 2002; Butrón *et al.*, 2011). For example, faecal streptococci, *Escherichia coli*, *Salmonella* spp., *Clostridium perfringens* and *Vibrio cholera* have all been detected in ballast water (McCarthy and Khambaty, 1994; Altug *et al.*, 2012; Emami *et al.*, 2012; Morris, 2013) and Ruiz *et al.* (2000) detected pathogenic strains of *V. cholerae* – the agents of human cholera – from >90% of the ships entering Chesapeake Bay. Taken in concert, these studies provide strong indications that invisible NIS may have dramatic impacts on marine biodiversity and ecosystem functioning. However, it will be up to future researchers to provide strong and novel data that link detected microbial and parasitic NIS associated with human vectors to actual effects in the invaded environment.

10.8 Discussion

Our review provides examples of the many ways that invaders modify the biotic and abiotic environment, and at first look, impacts appear to be idiosyncratic and almost impossible to predict. Still, many recent studies aim to see through this context dependency to establish first-order rules that can, at least partially, predict impact magnitude and direction. For example, it has been suggested that the ‘history’ of invasion impact can be a useful predictor of future impact (Kulhanek *et al.*, 2011), but this rule has no inherent mechanisms associated with impacts and cannot predict impacts for species with no published impact data. A most obvious rule is that impacts increase with invaded range and invader density (Parker *et al.*, 1999). Density-dependent impacts have subsequently been verified in meta-analyses across invasive species and invaded systems, although these also showed that impacts associated with species identity (also between ecologically similar invaders) are equally important (Thomsen *et al.*, 2011a; Thomsen *et al.*, 2011b). The density rule can be extended to include other attributes of the invader that relate to its ‘fitness’, such as that impacts increase with invader size and ‘fitness’. Another commonly cited rule suggests that impacts are high when invaders are functionally different from native taxa (Ricciardi and Atkinson, 2004), although it appears that certain types of impacts instead may decrease with increasing differences (e.g. hybridisation effects and some types of interspecific competition). The functional dissimilarity rule has been confirmed by many studies that document strong impacts associated with large structural sessile NIS (plants and sessile invertebrates) invading unstructured environments (e.g. sedimentary ecosystems). We suggest that impact rules should be clear about whether they are ‘universal’ or apply within a specific context, such as between trophic groups (Thomsen *et al.*, 2009c) or within or between function groups embedded within a trophic level (Thomsen *et al.*, 2014). For example, within a trophic level, *Sargassum muticum* typically has negative impacts on functionally similar canopy-forming seaweeds that require hard substratum (Staehr *et al.*, 2000), but positive impacts on functionally different epiphytic seaweed that use the invader as habitat (Thomsen *et al.*, 2006c).

A key take-home message of our review is that, from a BEF perspective, invasion impact studies are few and theoretical linkages underexplored. Interestingly, we are not aware of field experiments that have documented ‘massive’ negative impacts on local patterns of diversity, such as through habitat destruction mechanisms (by contrast, it is relatively easy

to demonstrate large positive impact through habitat formation) (Thomsen *et al.*, 2010a). We suggest that abundant NIS that are known to consume habitat-formers from areas where habitat-formers already are few (e.g. in estuaries) would be good candidates on which to conduct field studies searching for strong negative impacts on diversity. Clearly, many more studies are needed to test how invaders modify BEF relationships. Importantly, none of the studies listed in our review compare NIS impacts of the same species from both its invaded and native region. Therefore, we simply do not know if NIS do something ‘unusual’ or just do what would be predicted from studies from its native region (Hierro *et al.*, 2005). More studies are also needed that clearly address marine invasion impacts on a whole array of ecosystem functions, such as testing for multivariate complementarity effects (Stachowicz and Byrnes, 2006). It is vital that these studies always report the abundance of the invaders to allow for meaningful interpretations of impacts, a prerequisite that unfortunately sometimes is ‘forgotten’ (Thomsen *et al.*, 2009c). Our review focused on invasion impacts on macrobiota because these organisms are typically targeted for study. However, it is likely that there is a world of hidden biotic impacts associated with how invaders modify microscopic bacterial (Green *et al.*, 2012) and parasitic communities (Thieltges *et al.*, 2009), probably with complex indirect impacts on the macrobiotic and abiotic environment. Clearly, more studies should address impacts on these microscopic communities and the linkages to better described macroscopic communities. It is also important that new studies report non-significant effects as well as effects from non-pooled treatments (e.g. in online appendixes and with associated data variability), because failing to do this limits synthetic advancement by biasing meta-analyses towards high impact invaders only, thereby making it difficult to identify NIS and environmental contexts that result in true weak impacts. In short, our ability to extrapolate impact assessments across space, time and taxa will increase significantly if above research gaps are targeted.

Our review has highlighted a few take-home messages for managers. For example, some invader are ‘drivers’ of ecological changes (e.g. *Gracilaria vermiculophylla*; Thomsen *et al.*, 2010a), whereas others more often are ‘passengers’ (Jaubert *et al.*, 2003) or ‘back-seat drivers’ (Bulleri *et al.*, 2010). This distinction is important because if the invader drives changes, the invaded ecosystem can be restored by controlling the invader, whereas if the invader is a passenger or back-seat driver, other management schemes need to be implemented as well to control the invader (e.g. nutrient reductions). Second, it is clear that invasions result in both

‘winners’ and ‘losers’ – negative impacts on one group of native species often lead to positive impacts (quantified or not) on another group of native species. Note that these scientific insights do not equate to whether invasions are ‘good’ or ‘bad’, simply that managers and politicians need clear conservation goals. Such goals could be that invaders need to be eradicated irrespective of costs if they have well-documented negative impacts on a highly valued habitat, or that invaders may be preserved if they facilitate a threatened native species (Schlaepfer *et al.*, 2011; Thomsen *et al.*, 2012a). Managers also need to be aware that ecosystem functions may decrease if successful eradication occurs. For example, if *Gracilaria vermiculophylla* or *Spartina alterniflora* are removed from invaded mudflats, nutrient filtering would be reduced. Managers also need to acknowledge that impacts reported in the scientific literature typically focus on mean effects on aggregated responses, cancelling out potentially dramatic negative and positive effects reported on sub-aggregate entities. Perhaps more scientific studies need to analyse and report maximum (or quartile) impacts, so that managers can address invasions more conservatively. Managers should also note whether impacts have been evaluated from mensurative or manipulative experiments (see Box 10.1). For example, strong negative impacts observed in small experimental plots do not necessarily translate into regional scales if larger-scale refuge habitats exist. Similarly, positive effects observed on regional scales from mensurative data are no safeguard against neighbourhood-scale impacts by invaders, because positive impacts reported on large scales typically reflect a complex array of co-varying factors, such as increased habitat complexity, area and sampling effect (Fridley *et al.*, 2007; Powell *et al.*, 2011).

Managers have several options to control invaders. For example, where eradication is impossible or not merited, impacts may be reduced by (1) eliminating other stressors to strengthen the ‘biotic resistance’ of local communities; (2) controlling vectors (i.e. not allowing establishment in the first place or minimising the chance for multiple entries); (3) establishing continuous control actions, such as constant removals (as done for marine nuisance weeds); or (4) facilitating enemies, such as grazers or predators of the invaders (e.g. sea urchins are being trialled to control *Undaria pinnatifida* in Fjordland, New Zealand (<http://www.biosecurity.govt.nz/media/08-07-11/working-together-in-fiordland>)). Finally, there is, in rare cases, the option of eradication. Many eradication attempts on marine invaders have failed, particularly where invaders have been well established or are abundant in nearby locations. Failed eradication on abundant NIS have been documented for *Sargassum muticum* (Critchley *et al.*, 1986), *Undaria pinnatifida* (Hewitt

et al., 2005; Hunt, 2009) and *Pterois volitans* (Barbour *et al.*, 2011). In addition, intensive eradication campaigns on a very rare NIS that did not have nearby populations have also failed (Read *et al.*, 2011). Still, a growing number of studies suggest that eradication is possible in marine systems, in particular if the NIS exists in low population sizes, with no nearby populations, and near its environmental tolerance limits. Such successful (so far) eradications include NIS like *Ascophyllum nodosum* (Miller *et al.*, 2004), *Terebrasabella heterouncinata* (Culver and Kuris, 2000), *Caulerpa taxifolia* (Neverauskas, 2005), *Perna perna* (Hopkins *et al.*, 2011) and *Undaria pinnatifida* (Wotton *et al.*, 2004).

We finally note that a conservative ‘warning’ regarding marine NIS impact is merited. We have previously stated that we are not familiar with global extinctions associated with marine invasion (Briggs, 2010) and we have listed many examples of how local species can be facilitated by NIS. Politicians, managers and the public are therefore likely to ask ‘why worry?’ However, there are several reasons to support a precautionary conservation principle to marine invasion impacts:

1. Any invasion can cause negative impacts on some local species, simply because all invasions have both winners and losers.
2. With each new invasion, global homogenisation increases, as new species are added locally from the global species pool, i.e. the local biota slowly become more similar across biogeographical realms.
3. Scientists know little about possible local extinctions following invasions because distributions of rare species from open subtidal marine ecosystems are notoriously difficult to monitor.
4. Many studies report mean impacts on aggregated responses, implying that stronger negative impacts almost always go unreported as they are averaged out from positive effects.
5. Even if invaders, in isolation, do not cause extinctions, invasions co-occur with other human stressors and the combined multiple-stress effects may be the ‘nail in the coffin’ for local species.
6. In contrast to many other stress effects, marine invaders typically cause irreversible effects, i.e. whereas managers may be able to clean up pollution and rebuild destroyed habitats, marine NIS are difficult to eradicate and even if successfully removed there is no guarantee that local species will bounce back (Klein and Verlaque, 2011).
7. Ecological interactions are not in equilibrium, causing effects to have time lags, and invasion-driven extinction ‘debts’ could occur (i.e. small invasion effects occurring today may accumulate to dramatic effects over long time scales) (Tilman *et al.*, 1994; Kuussaari *et al.*, 2009).

10.9 Key findings and recommendations

- More than 1800 marine NIS exist, being particularly common in the Mediterranean Sea, Australia and New Zealand, the South Pacific, the north-east Pacific and the north-east Atlantic, and in estuaries centred around metropolitan areas.
- Marine NIS can impact local biota negatively directly through competition, habitat destruction, disturbance and consumption, and indirectly through keystone competition, keystone habitat destruction, keystone consumption and cascading consumption.
- Marine NIS can impact local biota positively directly through habitat formation, habitat modification and mutualism, and indirectly through cascading habitat formation, cascading consumption, cascading competition, keystone consumption and keystone competition.
- Marine NIS also modify abiotic conditions, resource levels and elemental cycling, directly by their metabolic and behavioural activities and indirectly by interacting with local species, e.g. by altering pools and fluxes of macro nutrients, light and oxygen levels, the organic matter, texture and erosion rates of sediments, and temperature and moisture levels in the intertidal zone.
- Invasion impacts co-occur with other human stressors, such as pollution, eutrophication, habitat destruction and climate changes. These stressors can increase NIS abundances and, at the same time, stress local communities, thereby making the local biota more susceptible to invasion effects.
- Several reviews of marine invasion impacts exist but none has emphasised impacts on biodiversity. In a meta-analysis of field experiments, we documented that marine plant invaders have negative effects on total plant abundance and plant richness but that these effects were nullified when the invaders' own abundance and taxonomic identity was added to the community data. This suggests that marine invasive plants generally substitute standing stocks and richness.
- Two aspects of invasions and ecosystem functioning have received some scrutiny: (1) how biodiversity modifies community invasibility, often finding opposing results, and (2) how invasive ecologically important species (e.g. ecosystem engineers) impact different ecosystem functions – although these studies have rarely been explicitly framed in a BEF context. Thus, BEF-related invasion impact studies are very few and theoretical linkages under-explored.
- More studies are needed to address how invaders modify BEF relationships, and, if possible, compare impacts from the same species in the

invaded versus native region, impacts on a whole array of ecosystem functions, as well as impacts on microscopic communities and linkages to better described macroscopic communities.

- It is important to know if invaders are drivers or passengers of ecological change; in the first case, ecosystems can be restored by controlling the invader, whereas in the latter additional management schemes also need to be implemented.
- Every invasion results in winners and losers in local communities, but this does not equate to whether invasions are ‘good’ or ‘bad’. Given the complex ways that invaders impact communities, managers need clearly defined goals.
- Managers have several options to control NIS. For example, (1) eliminating other stressors to strengthen the resistance of local communities, (2) controlling vectors, (3) establishing continuous control actions, such as constant removals, (4) facilitating enemies, such as consumers of the invaders, (5) attempting eradication, in particular if the NIS exists in low population sizes with no nearby populations and near its environmental tolerance limits.
- We are not aware of any global extinctions driven by marine NIS but the precautionary conservation principle remains important because (1) any invasion causes negative impacts on some species, (2) global homogenisation increases, (3) negative effects on inconspicuous/rare species may go unreported (including local extinctions), (4) invasions co-occur with other human stressors and the combined effects may be dramatic and difficult to predict, (5) impacts are typically irreversible, and (6) effects may follow time lags, i.e. present-day small local effects may accumulate to dramatic effects over long and large spatio-temporal scales.

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