

Invasive Alien Species and Their Effects on Marine Animal Forests



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Abstract Nonindigenous species are increasingly transported around the world through multiple pathways by a diversity of vectors. Invasive species are a subset of those that are introduced into the receptor community, where they establish and increase their population to a size where they impact the native system. Marine invasive species can therefore interact with and modify native animal forests and/or create novel ones resulting in simple-to-complex changes in material cycling, energy flow, ecosystem structure, and function. Despite the ever increasing number of

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studies dealing with marine invasive species, mostly biological invasions are mentioned generically as one of a number of threats of direct and indirect effects of human activities on animal forests. In order to redress this imbalance, this chapter focuses on invasive species as modifiers and creators of marine animal forests. As well as some theoretical consideration of biological invasion, we consider how pathways and vectors have changed over time and the importance of historical collections. We overview the available information regarding the main taxonomic groups of marine species that are invasive to animal forests, what makes them successful invaders, and how they interact with and effect the receptor community. The establishment of novel animal forests through biological invasion is also reviewed. We identify knowledge gaps and present perspectives and challenges for future research.

Keywords *Carijoa riisei* · Ecosystem engineer · Invasive · *Mytilus galloprovincialis* · Nonindigenous · *Oculina patagonica* · Pathways · Reproduction strategies · *Tubastraea* spp. · Vectors

1 Introduction

Biological invasions, as one of the most detrimental and pervasive impacts of human-induced global change, are one of the biggest conservation concerns. Biological invasions involve unwanted cascade effects altering natural ecosystems, while invasive species have profound impacts in what has become an integrated, globally connected society (Aguin-Pombo 2012; Sánchez 2017). A major consequence of biological invasions is the occurrence of ecological regime shifts, which are dramatic, abrupt changes between states of populations, communities, and/or whole ecosystems that are persistent in time and include key structural species (Conversi et al. 2015). In marine environments, invasive species threaten biodiversity, ecosystem functions and services, the economy (including fisheries and tourism), and human health (Bax et al. 2003; Sorte et al. 2010b). Global maritime traffic is predicted to increase by 240–1209% by 2050 resulting in a 3- to 20-fold increase in global invasion risk (Sardain et al. 2019).

Marine animal forests (MAFs) are megabenthic communities dominated by sessile suspension feeders (such as sponges, corals, and bivalves) which form three-dimensional habitats and provide architectural complexity and shelter for several species (Rossi et al. 2017a). Invasive species may have numerous direct or indirect effects on the structure and ecological functioning of marine animal (and algal) forests. For MAFs these consequences fall into two groups: (1) they form novel marine animal forests where they did not exist before; (2) they change the structure and functioning of existing marine animal forests (Table 1).

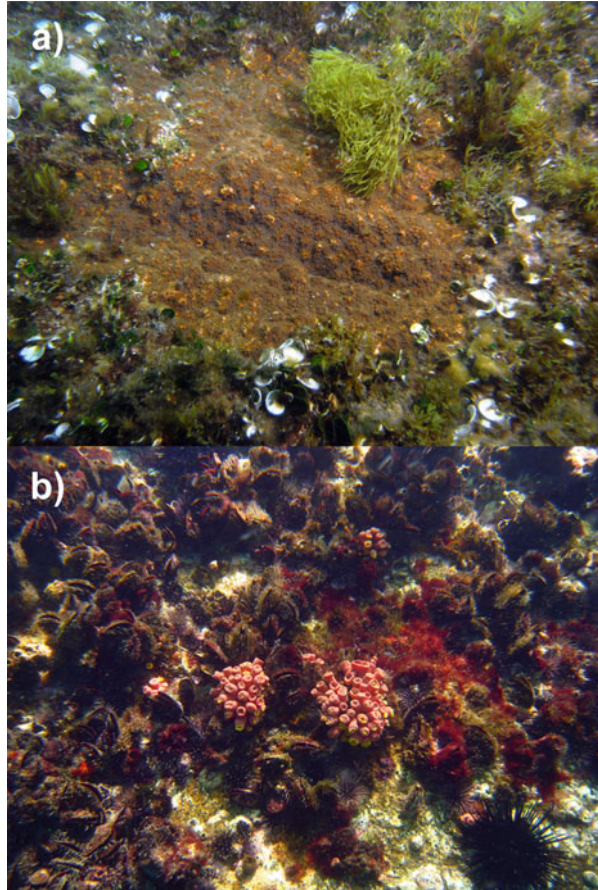
In this chapter we focus on the role that invasive species have and will play in creating or modifying the structure and function of MAFs by considering the theory behind the invasion of MAFs, invasion history and evolution, the vectors and

Table 1 Theoretical transformations which nonindigenous species (NIS) may bring about the following invasions

Mechanism	Direction	Example
Invasion by dominant alga	MAF → Algal forest	<i>Caulerpa racemosa</i> (Forsskål) J. Agardh replacing gorgonian forests (Mediterranean; Cebrian et al. 2012)
Invasion by dominant animal (structural: ecosystem engineer; competitive exclusion)	MAF1 → MAF2	<i>Pyura doppelgangera</i> Rius & Teske, 2013 replacing green-lipped mussel <i>Perna canaliculus</i> (Gmelin, 1791) (New Zealand, Davis et al. 2018)
Invasion by keystone animal with indirect or cascading effects (interactive: predator, parasite, trophic cascade)	MAF1 → MAF2 or MAF → Algal forest	Lionfish <i>Pterois volitans</i> (Linnaeus, 1758) and <i>P. miles</i> (Bennett, 1828) (coral-to-algae trophic cascade, Bahamas; Lesser and Slattery 2011)
Invasion by dominant space occupying animal (structural: ecosystem engineer; competitive exclusion)	Algal forest → MAF	<i>Oculina patagonica</i> de Angelis, 1908 [phase shifts from macroalgal-to coral-dominated state, Mediterranean (Serrano et al. 2012) (Fig. 1a)]
Invasion by herbivore or animal causing trophic cascade	Algal forest → MAF	^a , but see prediction regarding potential rabbitfish [<i>Siganus luridus</i> (Rüppell, 1829) and <i>S. rivulatus</i> Forsskål & Niebuhr, 1775] invasion of the Caribbean Sea (Bellwood and Robert Goatley, 2017)
Substratum modification by invasive species	MAF → Algal forest or Algal forest → MAF	Asian mussel <i>Arcuatula senhousia</i> (Benson, 1842) (= <i>Musculista senhousia</i>) (hard substrate on soft bottoms, Crooks 1998); <i>Didemnum vexillum</i> Kott, 2002 (mat forming on soft bottoms; Mercer et al. 2009) (Algal forest → MAF = ^a)
Multiple invasive species act together (coupled invasion or invasional meltdown)	MAF → Algal forest or Algal forest → MAF	<i>Eucheuma</i> J. Agardh, 1847, <i>Kappaphycus</i> Doty, 1988, <i>Gracilaria salicornia</i> (C. Agardh) E. Y. Dawson, and <i>Acanthophora spicifera</i> (M. Vahl) Børgesen (coral reefs to algal, Kane’ohe Bay (O’ahu, Hawai’i, USA; Conklin and Smith, 2005) <i>Tubastraea coccinea</i> Lesson, 1830 and <i>T. tagusensis</i> Wells, 1982 (algal forest to mussel bed to corals, Brazil; Mantelatto and Creed 2015; Paula et al. 2017) (Fig. 1b)

^aUnknown

Fig. 1 Photographs of invasive species which create novel or modify existing nonindigenous marine animal forests: **(a)** *Oculina patagonica* replacing algal forests on rocky reefs in the Spanish Mediterranean; **(b)** the sun coral *Tubastraea* spp. invading a nonindigenous mussel (*Perna perna*) beds on a tropical rocky reef wall in southeast Brazil. Photo credits: Eduard Serrano Gras **(a)** and Marcelo Mantelatto **(b)**



pathways, and the main invasive taxa. Furthermore we consider the chemical and microbial ecology of invasion, which nonindigenous species (NIS) form novel MAFs, and present some case studies as well as perspectives and challenges for future research.

2 Theoretical Considerations

Invasion ecology theory has been useful for explaining the success of invasive species such as aspects of invasive species attributes, the characteristics of invaded communities, resource availability in invaded systems, or predator-prey interactions (Davis et al. 2000; Keane and Crawley 2002). This centers on a controversial discussion in ecology: are species distributions and abundances more influenced by deterministic or stochastic processes? (Adler et al. 2007). The Niche (Chesson

2000) and Neutral theories (Hubbell 2001; Rosindell et al. 2011; Volkov et al. 2003) have been broadly used to explain species regulation processes which are relevant to invasion ecology theory.

The Niche theory is commonly invoked in studies of invasive species (Shea and Chesson 2002) and suggests that differences in species' ecological traits influence advantage in resource use, ability to establish in new areas, or how invader performance is influenced by the environment (Caswell 1978). Interpretations of this theory suggest that the success of an invader is based on niche differences between it and native species. According to this theory, each species can persist under a limited set of conditions, and coincidence of limiting factors can control whether a new species establishes in the community (MacDougall et al. 2009).

Niche-based mechanisms underpin the diversity-resistance hypothesis, which suggests that the greater the diversity of competitors in a community, the greater the resistance to the establishment of a NIS (Elton 1958). Communities with lower diversity are considered to be more easily invaded (Stachowicz and Tilman 2005), as they are more likely to offer vacant niches and invaders may have biological traits that do not exist in the receptor communities (MacDougall et al. 2009). These arguments can be supported by the enemy escape hypothesis which states that NIS are more likely to establish and become dominant when free from the negative effects of natural enemies such as competitors, predators, and pathogens (Keane and Crawley 2002).

Neutral theory is a more recent and alternative view which assumes that species of the same functional group are ecologically equivalent and that stochastic forces such as drift, limitation of dispersion, extinction, and speciation influence the abundance of these species in a random fashion over time (Hubbell 2001; Daleo et al. 2009; Rosindell et al. 2011). This view suggests that rules of community structuring are grounded in dispersion rather than in the niche. Interpretations of this theory suggest that both high- and low-diversity communities are equally susceptible to invasion and that all species have the same capacity and likelihood to invade and persist, as well as to impact a given environment in a similar and stochastic way (Daleo et al. 2009).

These arguments have gained strength mainly because Niche theory fails to explain empirical evidence of invasions, such as in the case of NIS with niches similar to those of resident species that succeed in invading, which is contrary to that predicted by the theory (MacDougall et al. 2009). However, the Neutral theory also fails to fully explain why some invasive species with different biological characteristics can impact native communities.

From the point of view of scale, studies that evaluate the relationship between the biodiversity of the receptor community and its susceptibility to invasion have found different answers according to the scale of observation, a phenomenon that has been called the "invasion paradigm" (Fridley et al. 2004). Work carried out from observations at broad scales usually find positive relationships between the success of biological invaders and native biodiversity (Fridley et al. 2007), supporting the neutral view that the biodiversity of the resident community does not change susceptibility to invasion. In contrast, studies at smaller scales have found negative

correlations between the diversity of native biota and the invasion by NIS (Fridley et al. 2007), corroborating the view associated with the niche, in which a more biodiverse community would reduce susceptibility to invasion (Daleo et al. 2009).

Despite controversy surrounding the two theories, several more recent studies have proposed their unification (Adler et al. 2007; MacDougall et al. 2009). These studies highlight the importance of the observational scale and the context of the investigated process, which can be explained by niche-based mechanisms and complementary neutrality. MAFs are widespread throughout the world's oceans (Rossi et al. 2017b) but locally dominated by specific sessile suspension feeders (such as sponges, corals, and bivalves) that are capable of generating three-dimensional frameworks, with high structural complexity that give shelter to other species (Rossi et al. 2017a). As such, they are useful and interesting systems where hypotheses and theories regarding invasion processes and mechanisms may be tested over different spatial scales.

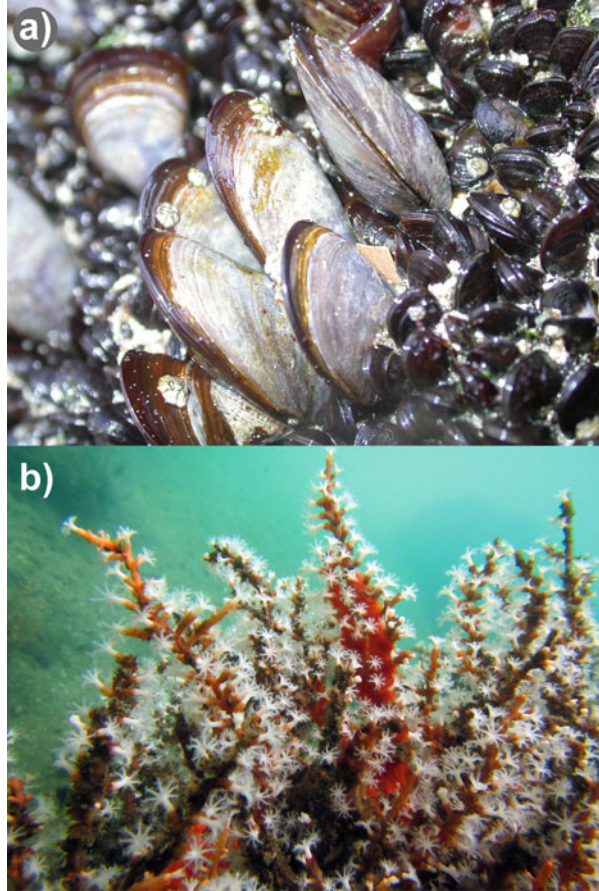
Latitudinal patterns of richness in NIS indicate that the number of invasions relative to tropical regions is low when compared to the temperate regions (Wells 2019), maybe because of a greater biotic resistance (Cheng et al. 2019) in the tropics. Evolutionary theory predicts that interactions between species are stronger and more specialized in the tropics, resulting in higher rates of diversification and greater species richness, thus decreasing the success of colonization, establishment, abundance, and dispersion of invasive species (Sax 2001).

On the other hand, there is a second hypothesis that predicts that many tropical areas may be under-sampled, causing an underestimation of the number of non-native species (Freestone et al. 2013). We may have insufficient taxonomic knowledge when it comes to MAFs such as tropical reefs, which may prevent the recognition of invasive species in most groups (Hewitt 2002). The question of the disparity, in taxonomic terms, between tropical and temperate systems was not supported by the results of research on the coast of Australia (Hewitt 2002). In the Pilbara region on the western coast of Australia, both hypotheses have been tested, and the relatively low number of invasive species in the region is not due to lack of knowledge or lack of sampling but because of biological factors (Wells 2019).

3 Historical and Evolutionary Considerations

It is probable that marine species were being carried around in the sea by human activity before the Common Era, maybe as much as 9000 years BP (Bednarik 1997). The introduction of marine species to new areas has occurred over most of the last millennium (Ojaveer et al. 2018). This has led to an appreciation of a number of historical difficulties in recognizing NIS today (reviewed by Carlton 2009) as well as important advances regarding historical overviews of marine biological invasions which have confirmed these "deep invasions" (Carlton 2009). A good example is the brown mussel *Perna perna* (Linnaeus, 1758), native to Africa and likely introduced into the Americas during the slave trade (Hicks and Tunnell 1993) (Fig. 2a).

Fig. 2 Photographs of two species which have a deep history of invasion and which create novel nonindigenous marine animal forests. **(a)** the brown mussel *Perna perna* competing for space with native mussels [*Mytilaster solisianus* (d’Orbigny, 1842)] and barnacles; **(b)** the snowflake coral *Carijoa riisei* which has a stoloniferous growth form (note the associated commensal sponge on the central erect portion). Photo credits: Joel C. Creed



However, it has also been recognized that our perception of the history of marine biological invasions is tainted by the “shifting baseline” syndrome, leading to underestimation of change (Ojaveer et al. 2018).

It is clear that the history of biological invasions in the sea is compatible with timescales over which evolution may occur, especially in MAFs mainly composed of sessile invertebrate suspension feeders (Rossi et al. 2017a). For example, there is a systematic increase in body size in receptor communities compared to origin in a number of invasive marine invertebrates (Grosholz and Ruiz 2003) which may be explained by escape from natural enemies allowing NIS to reallocate resources from defense to growth and competitive ability via evolutionary mechanisms (Chan and Briski 2017).

Today, coastal environments comprise the most invaded ecosystems in the world, yet research on the long-term ecological and evolutionary consequences is lagged with respect to continental systems (Grosholz 2002). Invasive species induce two-fold evolutionary changes (Lee 2002). Both NIS and species in invaded

communities are subject to new selective pressures. In part, success during an invasion depends on invaders adapting rapidly to new environments, and there are always effects on native species in receptor communities including competitive displacement, predation, or even extinction (Mooney and Cleland 2001). Sometimes the movement of species across biogeographic boundaries provides new opportunities and habitats for NIS. This is the case in the invasive snowflake coral *Carijoa riisei* (Duchassaing & Michelotti, 1860) (Fig. 2b; Sect. 10.5), which occurs at relatively low abundances within its donor range in the western Atlantic, except on shipwrecks (Barbosa et al. 2014), but dominates the landscape and outperforms local octocorals in invaded Eastern Pacific animal forests (Sánchez and Ballesteros 2014; Sánchez 2017).

Ultimately, the success of an invasive species depends on evolution, mainly with regard to abiotic conditions acting on traits responding successfully to clines (Hodgins et al. 2018). In the case of *C. riisei*, one such trait could be the facultative presence of the mutualistic sponge, *Desmapsamma anchorata* (Carter, 1882), conferring the coral cytotoxic activity on contact with other corals (Calcinai et al. 2004) (Sect. 10.5). MAFs offer a natural laboratory for studying the evolutionary effects on invasions in the marine realm.

4 Role of Reproduction Strategies

Owing to their large and dense populations, MAFs need successive, overlapping generations of its member species for construction (Potts 1983, 1984), which is easiest to achieve if recruits are of local origin, coupling high reproductive capacity with rapid growth, as seen in cloning species that employ fragmentation (Hoeksema et al. 2018). The latter may appear to show short generation times, but in fact the ongoing cloning results in long-lasting generations. Hence, the species composition of MAFs largely depends on the reproduction strategies of its component species. The role of asexual reproduction is usually not considered but may be particularly important for sessile benthic invertebrates as a strategy also facilitating biological invasion (Capel et al. 2017). Studies of the life histories of free-living corals (Fig. 3) suggest that mixed species assemblages are likely generated by sexual reproduction, as shown in French Polynesia (Hoeksema and Benzoni 2013), whereas monospecific aggregations appear to be produced by asexual reproduction, either budding or fragmentation, as seen in Indonesia (Hoeksema 2004; Hoeksema and Gittenberger 2010; Hoeksema et al. 2019), and only rarely by a combination of sexual and asexual reproduction, as observed in New Caledonia (Heintz and Laboute 2020). After autotomy (self-fragmentation), the clones are free-living and, depending on the species, can colonize sandy and/or hard bottoms (Walker and Bull 1983; Hoeksema 2012). Some cnidarians and sponges show reattachment after accidental damage (Wulff 2010; Coppari et al. 2019). Reattachment can also occur in invertebrates that have colonies with a tendency to multiply by fission, such as ascidians and octocorals (McFadden 1997; Muñoz et al. 2015). Some benthic invertebrates use

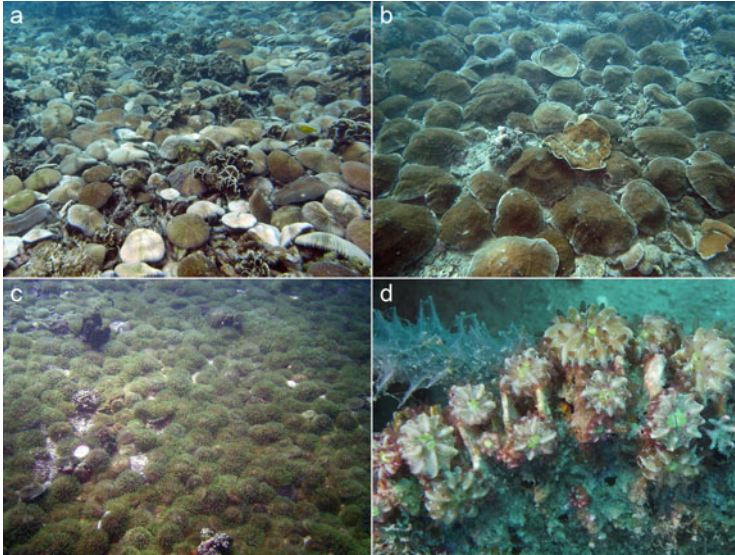


Fig. 3 Photographs of mushroom coral fields: (a) Mixed assemblage of free-living species at Koh Tao (Thailand); (b) Monospecific aggregation of fragmenting corals (*Zoopilus echinatus*) with multiple mouths at NW Lombok (Indonesia); (c) Monospecific aggregation of budding corals with a single mouth (*Heliofungia fralinae*) at East Kalimantan (Indonesia); (d) Buds (asexually derived propagules) sprouting from the margin of a dying *H. fralinae* at NW Lombok (Indonesia). Photo credits: Bert Hoeksema/Naturalis

stolons to expand rapidly, such as octocorals, scleractinians, and bryozoans (Kahng and Grigg 2005; Quintanilla et al. 2017; Schack et al. 2019).

Reproduction strategies can play a crucial role in invasion of existing MAFs or by forming a new substrate for a MAF when composed of itself. Well-known examples of negatively impacted MAFs usually concern cultivated animals that live at shallow depths. In these cases, harmful invasive species usually overgrow native ones, such as the common slipper limpet [*Crepidula fornicata* (Linnaeus, 1758)], Japanese oysters [*Magallana gigas* (Thunberg, 1793) (= *Crassostrea gigas*)], and stalked sea squirts (*Styela clava* Herdman, 1881) outcompeting mussels and flat oysters in Western Europe (Lützen 1999) and sun corals (*Tubastraea* spp.) overgrowing mussel beds in Brazil (Mantelatto and Creed 2015) (Fig. 1b). Except for the sun corals (see below), there are no signs of asexual reproduction playing a role here, since the attackers arrive as sexually derived offspring that settle on the shells, which eventually may lead to MAFs becoming overgrown by the intruders. Overgrowth and smothering have also been employed by invasive octocoral species (*Xenia* sp. in Venezuela, *C. riisei* in Hawaii) that have been observed to overgrow native coral species (Sects. 10.2 and 10.5).

Invasives can also affect native species by competitive exclusion, such as *Tubastraea* spp. causing damage to native corals and aggregations of zoantharians (Creed 2006; Miranda et al. 2016; Luz and Kitahara 2017; Fig. 4). Sexual

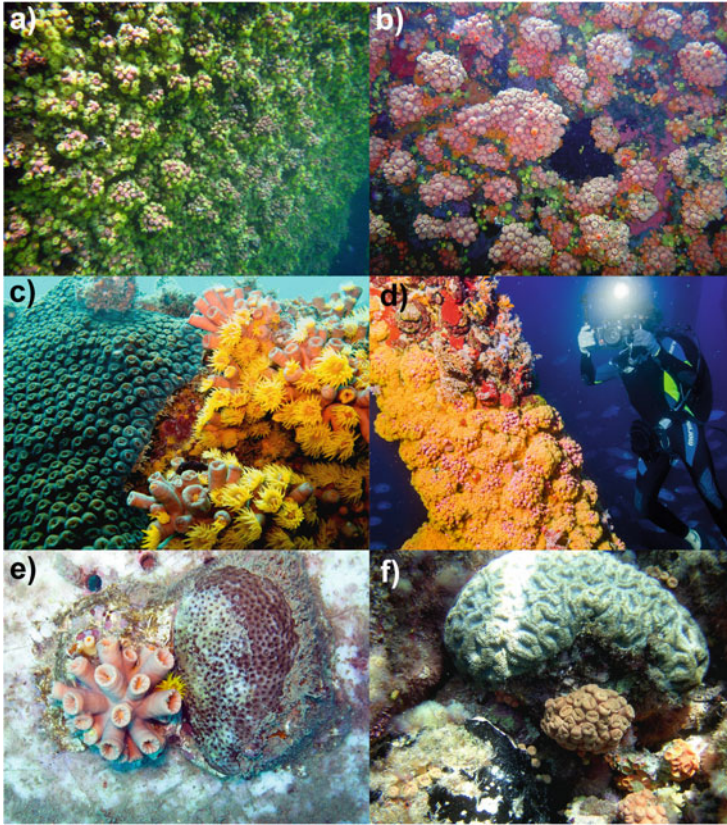


Fig. 4 Photographs of the invasive sun corals *Tubastraea* spp. in Brazil. (a) a marine animal forest dominated by *T. tagusensis*; (b) a subtidal rock reef dominated by *T. coccinea*; (c) a coral reef being invaded by *T. tagusensis*; (d) an offshore natural gas platform covered with sun corals; (e) experimental transplant of *T. tagusensis* beside the native coral *Siderastrea stellata*, showing lighter necrosing area; (f) natural contact between *T. coccinea* and the native coral *Mussismilia hispida*, showing deformed growth. Photo credits: Ricardo J. Miranda (c, e), Leonardo Schlögel Bueno (d) and Joel C. Creed (a, b, f)

reproduction in *Tubastraea* spp. appears to be continuous but of minor importance as Brazilian populations are highly clonal (Capel et al. 2017) and their reproduction success and dispersal are due to both sexually and asexually produced larvae which settle near the parent colonies (Paula et al. 2014). *Tubastraea* spp. are also well able to regenerate damaged polyps (Luz et al. 2018) and “bail out” polyps under stressful environmental conditions (Capel et al. 2014). This is probably the reason why their populations are able to dominate large, rocky surfaces.

5 Vectors and Pathways

Marine traffic is the principal pathway for the introduction of marine NIS (Carlton 1985; Hewitt et al. 2009). For example, ship sub-vectors include the fouling of hull and niche areas, the boring of organisms into the vessel structure and uptake of organisms associated with ballast, heavy material, such as gravel, sand, iron, lead, or water placed low in a vessel to improve its stability (Hewitt et al. 2009). The early ships had wooden hulls and solid ballast, so hull fouling, the boring of shipworms and gribbles, and marine derived solid ballast were important sub-vectors. Solid ballast was replaced by bulk seawater around 1880, and solid ballast was phased out by 1950 (Hewitt et al. 2009), which resulted in a new suite of different, mainly pelagic, species being transported. The use of steel resulted in very little opportunity for boring organisms, and, due to improved antifouling biocide paints (Qian et al. 2013), hull fouling was perceived to be a less important vector. Thus, ballast water became the most important shipping vector for marine NIS (Carlton 1985), and due to environmental concerns about further species introductions, the “International Convention on the Control and Management of Ship’s Ballast Water and Sediments” was adopted. Unfortunately the highly efficient tributyltin antifouling paints caused toxicity to organisms in nontarget habitats (Antizar-Ladislao 2008) and with the restricted use/ban of tributyltin in antifouling paint concern focused once again on biofouling (Minchin et al. 2009).

There is no doubt that shipping has transported NIS that have impacted MAFs. For example, the sun corals *Tubastraea* spp. have been transported around the world on oil platforms (Creed et al. 2017; Fig. 4d) on which they are usually the dominant organism (Friedlander et al. 2014). In fact, oil platforms may transport entire virtually intact reef communities (Hopkins and Forrest 2010; Wanless et al. 2010).

Other marine vectors are also important. Sea canals have allowed the transference of a large number of organisms across biogeographical barriers, either by their own means (swimming, crawling, or drifting) or on shipping (Gollasch et al. 2006). For example, more than half of the NIS in the Mediterranean Sea have been introduced through the Suez Canal (Galil et al. 2018). Other invasive species that create or impact MAFs have been introduced intentionally or unintentionally through aquaculture. Non-native oysters have been introduced around the world (Ruesink et al. 2005), and as they are ecosystem engineers, they can have substantial impact because of their influence on habitat quantity and quality. In most cases oyster introductions have created new MAFs as biotic reef structure is enhanced, as was the case for the Pacific oyster *M. gigas* introduced into northern Patagonia, Argentina (Escapa et al. 2004). However, introduced oysters may also modify the structure of MAFs by outcompeting native species, as did the oyster *Magallana ariakensis* (Fujita, 1913) (= *Crassostrea ariakensis*) with the native *Crassostrea virginica* (Gmelin, 1791) in North Carolina, USA (Grabowski et al. 2004).

Ornamental species are imported in the aquaria trade and because keeping animals or algae alive in aquaria is challenging; the industry probably passively filters hardy, fast growing, and widely tolerant species. When released accidentally

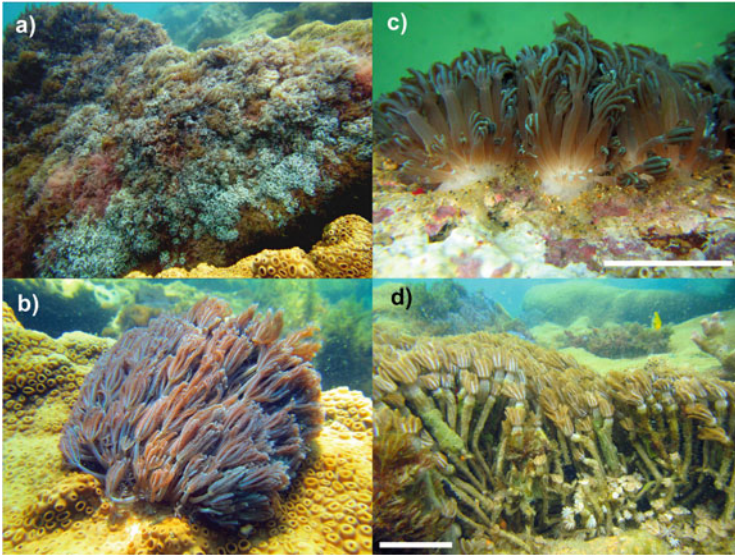


Fig. 5 Photographs of the two nonindigenous soft corals of aquarium origin invading animal forests in the southwestern Atlantic, Brazil. (a) tropical shallow subtidal rocky reef covered with *Sansibia* sp.; (b) detail of a colony of *Sansibia* sp. surrounded by native zoantharian *Palythoa caribaeorum* Forrest; (c) *Sansibia* sp.; (d) *Clavularia* cf. *viridis*; scale bar = 2 cm. Photo credits: Joel C. Creed

or on purpose into the environment, species with these characteristics may be most likely to survive and/or become highly invasive. The tropical red lionfish (*P. volitans*) and devil firefish (*P. miles*) and the “Xenia blue” and “Green Star Polyp” soft coral (*Sansibia* sp. and *Clavularia viridis* (Quoy & Gaimard, 1833) cf. *viridis*, respectively) are examples of released aquarium species which have impacted MAFs (Lesser and Slattery 2011; Mantelatto et al. 2018; Fig. 5). Furthermore, entire communities can be imported, such as those on “live rock” sold in aquarium stores, which may harbor dozens of species (Padilla and Williams 2004).

An increasing quantity of marine anthropogenic debris spread across the planet via drifting along coastlines and across oceans and which may support, maintain, and transport living organisms (Carlton and Fowler 2018). Because of this phenomenon, rafting on floating debris is becoming an increasingly important vector of invasion (Carlton et al. 2017), particularly for the kinds of invertebrate species which are major invaders for MAFs.

6 Overview of Marine Invasive Groups

6.1 Sponges

Sponges are an important component of benthos in all habitats (Wulff 2012; Pawlik et al. 2018), playing a diversity of roles in the structure and functioning of marine environments (Bell 2008; de Goeij et al. 2013). Sponge invasions are still poorly reported (Carlton 2009), but the number of studies reporting new NIS of sponges has increased over the last decade (van Soest et al. 2007; Longo et al. 2007), despite little information on their effects on the invaded ecosystem. All the cases reported are of fouling species (Ávila and Carballo 2009), given that sponge larvae usually have very short life spans in the water column (Guardiola et al. 2012). Such fouling may be on ships' hulls (Ávila and Carballo 2009) or aquaculture systems (Longo et al. 2007).

A common strategy of sponges to better compete for space with corals on reefs is by overgrowth (Wulff 2012; Mclean et al. 2015), and for invasive sponges, this is a particularly important strategy for the consolidation and expansion in the receptor community. The presence of chemical compounds toxic to corals has been described in several species of sponges, used in order to outcompete surrounding benthic invertebrates (Wulff 2012). In Hawaii, two introduced species of the genus *Mycale* Gray, 1867, *M. grandis* Gray, 1867 and *M. armata* Thiele, 1903, have been reported overgrowing and killing the coral *Porites compressa* Dana, 1846 (Coles and Bolick 2007). Similarly, in the Mexican Pacific, the invasive sponge *Chalinula nematifera* showed a very high specificity for living on live corals of the genus *Pocillopora* Lamarck, 1816 (94% vs. 6% on rocks), overgrowing coral tissue, and killing the polyps underneath (Ávila and Carballo 2009). Additionally, *Terpios hoshinota* Rützler & Muzik, 1993 is commonly described as an invasive sponge on Pacific coral reefs, overgrowing and killing mainly Poritidae, Acroporidae, and Merulinidae (Ashok et al. 2019).

Paraleucilla magna Klautau, Monteiro & Borojevic, 2004, a sponge which has invaded the Mediterranean Sea and has been widely studied (Longo et al. 2007; Guardiola et al. 2012), adopts an *r*-strategy that allows it to successfully establish for long periods (at least 10 years) (Longo et al. 2007). This sponge is able to grow on the native algae *Halopteris* spp. and *Corallina* spp. (Guardiola et al. 2012) and has been reported to negatively impact mollusk farming (Longo et al. 2007).

As feeders on suspended particles, sponges may filter up to 24,000 L of seawater per day per kilogram of sponge, leaving the expelled water pretty sterile (Hentschel et al. 2002). They also capture large quantities of phytoplankton, thus regulating primary and, consequently, secondary production (Kimmerer et al. 1994). Filtering by *Hymeniacidon sinapium* de Laubenfels, 1930, which has invaded California, is thought to influence the composition of the soft bottom habitat community there (Wasson et al. 2001).

6.2 Cnidarians

The phylum Cnidaria Verrill, 1865, contains about 11,000 species which occur in aquatic habitats. The state of knowledge regarding NIS cnidarians has been recently reviewed (González-Duarte et al. 2016), so here we provide an overview emphasizing groups or species which may be particularly important in creating or modifying MAFs.

A number of (stony) hexacorals (Scleractinia) have been introduced around the world. The mushroom coral *Lobactis scutaria* (Lamarck, 1801) (= *Fungia scutaria*) endemic to the Indo-Pacific was purposefully introduced onto coral reefs at Discovery Bay, Jamaica, in the 1960s (LaJeunesse et al. 2005). Three species of the now notoriously invasive azooxanthellate coral genus *Tubastraea* Lesson, 1830 (Scleractinia: Dendrophylliidae): *T. coccinea*, *T. tagusensis*, and *T. micranthus* (Ehrenberg, 1834), have also been introduced from the Pacific to the tropical and subtropical Atlantic (Brazil, Caribbean Sea, Gulf of Mexico, Canary Islands, as well as on oil platforms off Africa, Brazil, and in the Gulf of Mexico; Fig. 4) (Creed et al. 2017; López et al. 2019).

Oulastrea crispata (Lamarck, 1816) is a zooxanthellate scleractinian native to nearshore coral reefs in the central Indo-Pacific which has been found in shallow waters of Corsica and Catalonia (western Mediterranean Sea) since 2012 and is a native of nearshore coral reefs of the central Indo-Pacific. Also in the Mediterranean, a large colony of the zooxanthellate coral *O. patagonica* was found in 1966 near Savona harbour (Gulf of Genoa, Italy) and was found “prosperous and spreading” when surveyed again in 1971 and 1972 (Zibrowius 1974) (Fig. 6). During the last decades, *O. patagonica* has spread throughout the Mediterranean and colonized new

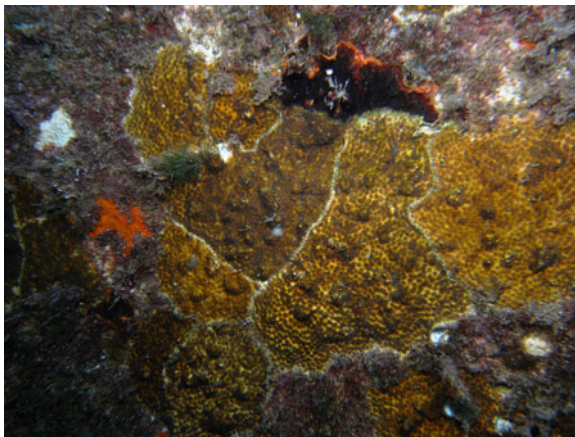
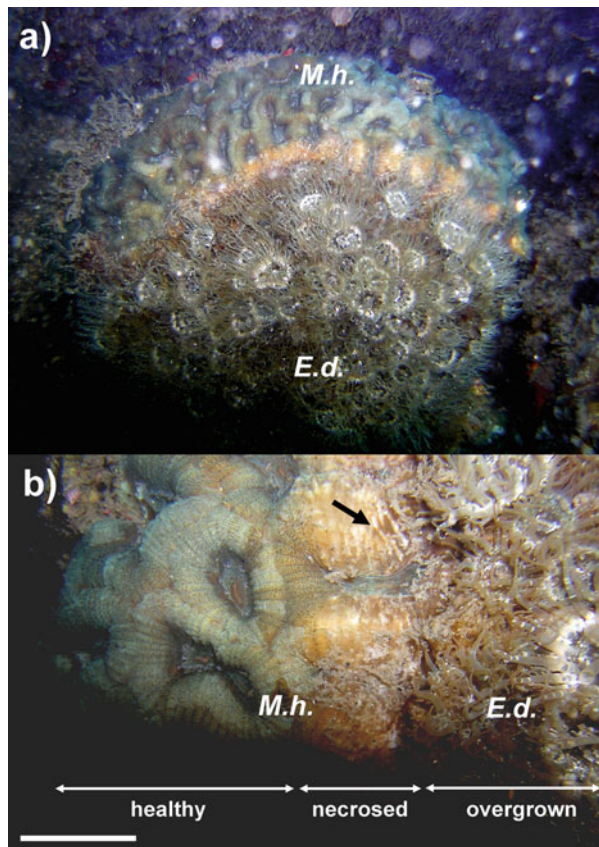


Fig. 6 Photograph of novel marine animal forests formed by invasive incrusting stony coral *Oculina patagonica* in a rocky reef community in the Spanish Mediterranean. Photo credit: Eduard Serrano Gras

areas from the subtropical eastern Atlantic and tropical western Atlantic (Fine et al. 2001; Colín García et al. 2018; Serrano et al. 2018; López et al. 2019; see Sect. 9).

A number of sea anemones (Actiniaria) have also been reported as NIS around the world. For example, four *Diadumene* Stephenson, 1920 species [(*D. cincta* Stephenson, 1925, *D. franciscana* Hand, 1956, *D. leucolena* (Verrill, 1866), and *D. lineata* (Verrill, 1869)] are members of the widespread fouling community, despite being ephemeral in nature (reviewed by González-Duarte et al. 2016). *D. lineata* is particularly widespread, originated from the Asian Pacific, but now found in Western Europe, the Mediterranean Sea, the east coast of North America, the Gulf of Mexico, Brazil, and Argentina, as well as Malaysia, Hawaii, Chile, and additional sites in the Pacific Ocean (Häussermann et al. 2015). *Aiptasiomorpha minima* (Stephenson, 1918) has been reported as a NIS to Japan (Mito and Uesugi 2004). González-Duarte et al. (2016) attribute two NIS of the genus *Aiptasia* [*A. pulchella* Carlgren, 1943 and *A. cf. insignis*] to *A. pallida* [now *Exaiptasia diaphana* (Rapp, 1829), a notoriously weedy invasive which overgrows corals and is a pest in aquaria] (Fig. 7). Other NIS of sea anemones are listed and discussed by González-Duarte et al. (2016).

Fig. 7 Photographs of invasive *Exaiptasia diaphana* (*E.p.*) overgrowing a whole colony of the stony coral *Mussismilia hispida* (*M.h.*); (b) detail of the healthy, necrosed and overgrown zones. Note the septa becoming visible in the necrosing zones (arrow). Scale bar = 1 cm. Photo credits: Joel C. Creed



Seven NIS of octocorals [Clavulariidae (three species), Xenidiidae (two), Melithaeidae (one), and Nephtheidae (one)] are known. All three clavulariids are NIS to the southwest Atlantic (Brazil), but while *Carijoa riisei* is a widespread invasive fouling species (see Sect. 10.5; Fig. 2b), *Clavularia viridis* cf. *viridis* has only been reported from one location as an aquarium release (Mantelatto et al. 2018; Fig. 5c, d). The third species, *Stragulum bicolor* van Ofwegen & Haddad, 2011, has recently spread along the Brazilian coastline, was described for the first time from Brazil, but is not native to the Atlantic and of unknown origin (Van Ofwegen and Haddad 2011).

Similarly, the nephtheid *Chromonephthea braziliensis* van Ofwegen, 2005 was introduced in southeastern Brazil from the Indo-Pacific on oil platforms and was also described for the first time from Brazil, of unknown origin (van Ofwegen 2005; Ferreira et al. 2009; Mantelatto et al. 2018).

The gorgonian *Melithaea erythraea* (Ehrenberg, 1834) (= *Acabaria erythraea*) which is native to the Red Sea has invaded the Mediterranean through Lessepsian migration and was first reported in the harbor of the Hadera power station, Israel in 1999 (Fine et al. 2005). In 2015 specimens were found on a natural substrate about 23 km north, so it is restricted but expanding its distribution (Grossowicz et al. 2020).

A single colony of an invasive xeniid soft coral with close genetic affinities to *Xenia membranacea* Schenk 1896 native from Indonesia was first found in 2007 on a reef in the Venezuelan Caribbean and has increased in abundance, dominated substrates, and extended its range several kilometers away to other sites after a few years, overgrowing native corals (Ruiz Allais et al. 2014). In 2017 another xeniid, *Sansibia* sp., was detected in communities on shallow subtidal tropical rocky reefs in southeast Brazil (Mantelatto et al. 2018; Fig. 5a, b). *Sansibia* sp. has now dominated deeper communities, associated positively with some macroalgae and negatively with the zoantharian *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860), which probably provided greater initial biotic resistance to invasion (Mantelatto et al. 2018; Fig. 5a, b). As *Sansibia* Alderslade, 2000, is a newly described genus, its origin is unknown but as this species and *C. viridis* (see above; Fig. 5) were both found at the same site and time and are typical ornamental species, they were probably derived from the same aquarium release.

Regarding the Hydrozoa Owen, 1843 which comprise about 3500 valid species (Daly et al. 2007), those which occur in the benthos (hydroids) can be highly conspicuous and/or dominant and play an important role in shallow coastal assemblages. They may be especially abundant on artificial substrates such as those associated with ports, docks, and floating vectors which may act as primary receptor hubs. Furthermore they may access multiple vectors of invasion such as ballast water and fouling.

González-Duarte et al. (2016) reviewed six NIS of hydrozoans whose negative effects have been studied or that have a high invasive potential: *Blackfordia virginica* Mayer, 1910; *Clytia hummelincki* (Leloup, 1935); *Cordylophora caspia* (Pallas, 1771); *Eudendrium carneum* Clarke, 1882; *Garveia franciscana* (Torrey, 1902); and *Macrorhynchia philippina* Kirchenpauer, 1872. However, while these

species are known to impact plankton and potentially fish stocks by predating eggs and larvae, as well as cause economic impacts by fouling boats and other artificial substrates, there is little information available about how they impact native MAFs or contribute to the creation of novel MAFs, as hydroids are a neglected component of MAFs in general (Di Camillo et al. 2017). However, *C. hummelincki* represents one case of an invasive hydroid that forms meadows (Gravili et al. 2008; Di Camillo et al. 2017). This introduced species is particularly abundant in the central Mediterranean at 0.5–2 m depth in sea urchin barrens, mainly in full light, on bare substrates covered by encrusting coralline algae, being absent on sandy and muddy ones (Gravili et al. 2008).

As a response to ocean warming, several cnidarian species are expanding their native distribution range poleward (Vergés et al. 2014; Canning-Clode and Carlton 2017). However it is not yet clear whether novel animal forests will emerge as a result (Vergés et al. 2014). When large-scale change in communities occurs as a result of range expansion, phase shifts can occur (Lonhart 2009). One example is the corallimorpharian *Rhodactis howesii* Saville-Kent, 1893, which was discovered smothering coral reefs at Palmyra in 2007. Its distribution around a shipwreck and mooring buoys fastened by iron chains suggested that substances leaching from metals might have been driving the spread of the infestation on the reef (Work et al. 2008, 2018). Similarly phase shift from corals to the zoantharian *Palythoa* cf. *variabilis* on reefs in the southwest Atlantic is thought to be mediated by human-induced environmental impacts (Cruz et al. 2015).

6.3 Bryozoans

The phylum Bryozoa contains about 6400 species which form encrusting, arborescent, or stolonial colonies. Around 80 species have been reported as introduced (Ahyong et al. 2019). Fouling species have been introduced in many regions, among which *Bugula neritina* (Linnaeus, 1758), *B. stolonifera* (Ryland, 1960), and *Amathia verticillata* (delle Chiaje, 1822) have wide distributions but no evidence of impact on MAFs.

The bryozoan *Tricellaria inopinata* d'Hondt & Occhipinti-Ambrogi, 1985, is among the fouling species typically found in European ports and marinas. Considered to be of Pacific origin, it was first reported in Italy in 1982 and has since then established itself in many regions in the Mediterranean and Atlantic Europe (Occhipinti-Ambrogi and Savini 2003; Streftaris and Zenetos 2006). In 2010 it was reported in the USA, where it outcompeted previously established bryozoans (Johnson et al. 2012). Not only does this species overgrow algae, ascidians, sponges, mussels, and other calcareous organisms, but it also creates a novel MAF because of its erect and complex architecture. A study in Cadiz, Spain (Gavira-O'Neill et al. 2018), revealed three introduced crustaceans associated with this bryozoan: the amphipods *Caprella scaura* Templeton, 1836 and *Monocorophium sextonae* (Crawford, 1937) and the isopod *Paracerceis sculpta* (Holmes, 1904), comprising

52.5% of all individual crustaceans found. The creation of this new MAF thus may facilitate the establishment of other invaders, a process so-called invasion meltdown [by which the negative impacts induced on native ecosystems by one invading NIS are exacerbated by interactions with another exotic species, posing further threat to native biodiversity (Simberloff and Von Holle 1999)].

Bryozoans of the genus *Watersipora* Neviani, 1896, grow as a single encrusting layer or as a complex structure of erected folded sheets that provide abundant settlement substrate for sessile epifauna and potential refuge for mobile epifauna (Sellheim et al. 2010a). The identity of species in this genus has been confused, but a recent taxonomic review indicates that three species have been transported worldwide: *W. subtorquata* (d'Orbigny, 1852), *W. subatra* (Ortmann, 1890), and *W. arcuata* Banta, 1969 (Vieira et al. 2014).

Watersipora (probably *W. subatra*) has invaded California, USA, modifying MAFs composed of a native ascidian that forms aggregations on artificial substrates; in experiments a different community composition was evident after 2 or 6 months (Sellheim et al. 2010b). In a longer-term study, historical data revealed an apparent shift in foundation species from mussels (*Mytilus californianus* Conrad, 1837 and the mussel complex *Mytilus trossulus* Gould, 1850/*Mytilus galloprovincialis* Lamarck, 1819) to *Watersipora*. The mussels were dominating pier pilings and floating docks in ~1976 but were scarce or absent by 2004 (Needles and Wendt 2013). The mechanism of change has not been determined, but an increase in sea otter predation of mussels or climate change may have enhanced *Watersipora*, given that it is very resistant to water warming (Sorte et al. 2010a). Whichever, the dominance of *Watersipora* resulted in the reduction of several native species and the establishment of an alternative stable state. Recently the bryozoan has been documented on natural substrates in Central California (Zabin et al. 2018) which raises concerns about community shifts to this novel type of MAF.

6.4 Polychaetes

A recent review listed 292 polychaete species as introduced in at least 1 site with Families Sabellidae, Serpulidae, and Spionidae being most invasive worldwide (Çinar 2013). Many species of Serpulidae and Sabellidae are notorious foulers that produce large aggregations that modify communities and ecosystem dynamics through competition for space and food, change in water circulation, deplete plankton, and increase deposition of feces. Examples include the serpulid *Hydroides elegans* (Haswell, 1883) that invaded harbor environments worldwide but is absent in natural communities (Schwan et al. 2016). *Sabella spallanzanii* (Gmelin, 1791) is originally from the Mediterranean and invaded Western Australia in the 1960s. It is found in the shallow subtidal, preferring sheltered harbors and embayments where it influences recruitment of other sessile taxa (Holloway and Keough 2002). More recently it has spread its distribution to the southern coast of Australia (Murray and Keable 2013) and New Zealand (Read et al. 2011). *Branchiomma* Kölliker, 1858 is

another sabellid genus with at least five species with a history of invasion (Keppel et al. 2015). Three of these species have been reported in the Mediterranean Sea, *B. bairdi* (McIntosh, 1885), *B. luctuosum* Grube, 1870, and *B. boholense* (Grube, 1878), where they have spread to many harbor areas. Their aggregation behavior, high densities, and high filtration capacities suggest they may modify the environment. *B. luctuosum* has reduced the abundance of the native *S. spallanzanii*, and the differences in size, density, and clearance rates of those species suggest that further ecosystem changes will occur (Mastrototaro et al. 2015).

Ficopomatus enigmaticus (Fauvel, 1923) is another iconic example of a NIS able to create novel MAFs. It is distributed in most brackish waters in temperate zones throughout the world, being abundant in low-current, turbid eutrophic waters where it builds reefs as high as 40 cm on vertical stone walls (Le Havre, France; Charles et al. 2018) or forms circular reefs up to 7 m in diameter by 0.5 m in height on soft bottoms (Mar Chiquita coastal lagoon, Argentina; Schwindt et al. 2004) (Fig. 8a). Apart of these ecosystem-level effects, the invasive polychaete reefs also interfere at the local scale by accumulating more diverse infauna than the sediment around them and modifying the native benthic community structure creating refuges for the macrofauna (Schwindt et al. 2001; McQuaid and Griffiths 2014). MAFs formed

Fig. 8 Photographs of aggregations of the Australian tubeworm *Ficopomatus enigmaticus* in Argentina. (a) banks on soft bottoms; (b) the polychaete profiting from new construction in estuaries. Photo credits: Alejandro Bortolus



by *F. enigmaticus* are increasing in area and biomass, profiting from new construction in estuaries as well as garbage accumulation that provide hard substrate for larval initial attachment (Schwindt et al. 2004; McQuaid and Griffiths 2014; Fig. 8b). For example, in the Zandvlei Estuary, South Africa, over 25 years, mass per unit area has tripled, and 25% of the total area is now covered (McQuaid and Griffiths 2014), while in the Mar Chiquita coastal lagoon, Argentina, the reef covers about 40 km², representing 86% of the lagoon (Schwindt et al. 2001).

Spionidae includes invasive boring species belonging to the genera *Boccardia* Carazzi, 1893, *Dipolydora* Verrill, 1881, and *Polydora* Bosc, 1802 that can cause severe damage to shells of commercially grown oysters and mussels (Çinar 2013). In the 1880s an invasion of a mudworm (*Polydora* sp.) supposedly from New Zealand to Australia caused a catastrophic disappearance of native MAFs formed by beds of subtidal oysters that have never recovered since (Ogburn et al. 2007). A century later, another group of three spionid species of the genus *Marenzelleria* Mesnil, 1896 have invaded soft bottoms in the Baltic Sea and appear to have established abundances as high as 16,955 individuals m⁻² in the region in less than 30 years (Kauppi et al. 2015). Despite the high density, taxa richness did not decrease, and turnover and number of traits actually increased at one study site (Hewitt et al. 2016). However, the polychaete significantly enhanced all bioturbation metrics examined, with implications for ecosystem functioning, especially in deeper, hypoxia-affected areas, where *Marenzelleria* spp. are sometimes the only macrofaunal taxon present (Kauppi et al. 2018).

6.5 Barnacles

As conspicuous ship-fouling organisms, it is expected that many barnacle species have their modern distribution explained by human-mediated translocations (Carlton et al. 2011). Out of a total of 185 Balanidae species known, 128 (69%) have been reported as NIS at some location around the world (Torres et al. 2012). The gregarious behavior of these intertidal and shallow subtidal species creates well-known MAFs in horizontal zones dominated by barnacles that, in many cases, ameliorate conditions for associated species. Prior to the invasion of *Amphibalanus improvisus* (Darwin, 1854) in the northern Baltic Sea, there were no other benthic suspension-feeding species. *A. improvisus* altered the habitat through the construction of dense crusts on hard surfaces, and those dense populations facilitated the arrival of associated species, such as chironomid larvae, ostracods, copepods, and juvenile bivalves (Leppäkoski and Olenin 2000).

Besides creating new MAPs, NIS of barnacle can interact with native species and other invasive MAFs. *Balanus glandula* Darwin, 1854 invaded Japan 30–50 years ago and is becoming a dominant species in the upper littoral fringe, especially in embayments, largely at the expense of the tropical endemic barnacle *Fistulobalanus albicostatus* (Pilsbry, 1916) (Kado 2003). In Hawaii, *Chthamalus proteus* Dando & Southward, 1980 arrived ~40 year ago and is now the most abundant and widespread

non-native barnacle in the intertidal zone on the island of Oahu, where the abundance of an earlier invader, the larger and faster growing barnacle *Amphibalanus reticulatus* Utinomi, 1967, is reduced via substrate preemption in the zone of overlap between the two barnacle species (Zabin 2009).

6.6 Bivalves

Bivalves are among the most successful MAF invaders in marine systems. Mussel and oyster invasions have been documented throughout the world (e.g., Ruiz et al. 1997). An iconic example is the mussel *M. galloprovincialis*—a widespread species forming dense beds—originally from Europe (mostly in the Mediterranean, the Black Sea, and the eastern Atlantic). This mussel species is among the 100 of the World's Worst Invasive Aliens (Lowe et al. 2000), having being introduced by human activities and aquaculture. It has overgrown and replaced other intertidal benthic taxa both on natural and man-made hard substrata. Similar colonization patterns have been recorded for the brown mussel *P. perna*, native to Africa, likely introduced during the slave trade in the eighteenth century into North and South America and now considered a well-established and commercially exploited species (Hicks and Tunnell 1993; Ferreira et al. 2009) (Figs. 1b and 2a).

A classic example of the impact on resident communities is the Asian mussel *A. senhousia* (= *Musculista senhousia*), which became a pest on mudflats in the Eastern Pacific, by altering sediment properties and the resident native benthic assemblages, forming complex byssal mats (Crooks 1998) (Fig. 9a, b).

The Indo-Pacific mussel *Brachidontes pharaonis* (P. Fischer, 1870) in the Mediterranean Sea (Rilov et al. 2004) and the purse oyster *Isognomon bicolor* (C. B. Adams, 1845) (Fig. 9c, d) in the western Atlantic are two examples of invasive bivalves that form novel MAFs leading to monospecific beds that exclude native species (Domaneschi and Martins 2002). *B. pharaonis* entered into the Mediterranean from the Red Sea just after the opening of the Suez Canal in 1869 but remained rare until the 1990s. During the few last decades, anthropogenic impacts along the Eastern Mediterranean rocky shores likely facilitated the outbreak of *B. pharaonis* populations and the subsequent high pressure of invasive propagules resulted in exclusion of the native mussel beds of *Mytilaster minimus* (Poli, 1795) (Safriel and Sasson-Frosting 1988; Rilov et al. 2004; Didham et al. 2007). Similarly, *I. bicolor*—likely introduced by oil platforms—has caused dramatic changes in the receptor communities, leading to a competitive displacement of native MAFs composed of barnacle populations on rocky shores along the Brazilian coast (Breves-Ramos et al. 2010) (Fig. 9c, d).

The establishment of an invasive MAF may also ameliorate stressful conditions which a native MAF may undergo, thus ultimately leading to coexistence rather than a dominance shift. This kind of facilitation process has been demonstrated between the blue mussel *Mytilus edulis* Linnaeus, 1758 and the Pacific oyster *M. gigas* (= *Crassostrea gigas*) in the Wadden Sea (North Sea) (Reise et al. 2017). About

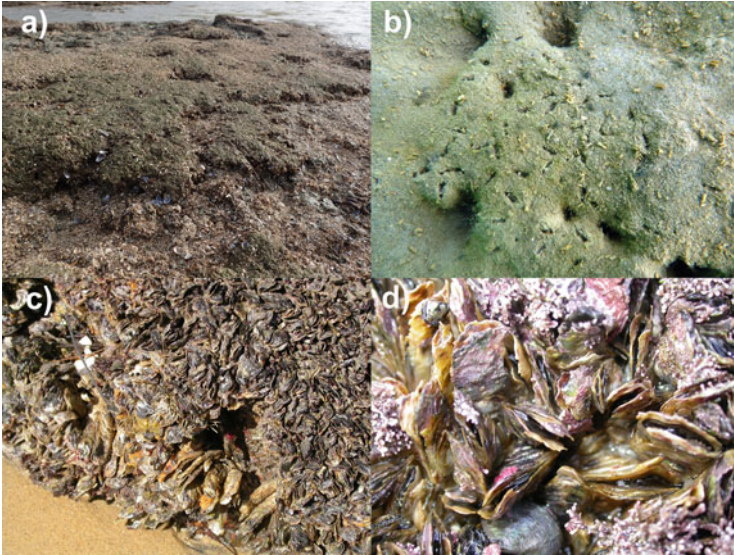


Fig. 9 Photographs of invasive bivalves that form novel marine animal forests. **(a)** bank of, and, **(b)** detail of the Asian date mussel *Arcuatula senhousia* (= *Musculista senhousia*) in Kiapara Harbour, New Zealand; **(c)** bed of the purse oyster *Isognomon bicolor* competing with barnacles on a tropical rocky reef in Brazil, **(d)** creating new habitat. Photo credits: Chris Woods **(a, b)**; Joel C. Creed **(c, d)**

25 years after the introduction of Pacific oysters for aquaculture purposes, the community effect of the invaders shifted from a competitive displacement to a co-dominance, with layers of resident mussel beds receiving shelter from physical and natural disturbances by upper-level invasive oyster reefs (Reise et al. 2017).

6.7 Ascidians

Ascidians are sessile filter-feeding animals considered models in studies of invasion success because of the significant ecological and economic damage to invaded habitats (Zhan et al. 2015). Among the 3000 currently described species, Shenkar and Swalla (2011) recognized 64 species that had been introduced in at least 1 site, with 27 records in tropical regions and 50 in temperate environments. A few species, such as *Botrylloides violaceus* Oka, 1927, *B. schlosseri* (Pallas, 1766), *Ciona intestinalis* (Linnaeus, 1767), *C. robusta* Hoshino & Tokioka, 1967, *D. vexillum* Kott, 2002, *Microcosmus squamiger* Michaelsen, 1927, *S. clava*, and *Styela plicata* (Lesueur, 1823) (Zhan et al. 2015), have received most of the attention because of their negative impact on the bivalve industry, but most of this does not concern natural MAFs.



Fig. 10 Photographs of a bed of the invasive cunjevoi *Pyura praeputialis* in the intertidal zone at Antofagasta, Chile. Photo credits: Patricio Manriquez

Solitary ascidians of the *Pyura stolonifera* (Heller, 1878) complex, of which three are invasive species, are engineering species capable of dominating the space in the intertidal and shallow subtidal zones (Rius et al. 2017). *Pyura praeputialis* (Heller, 1878) has been introduced in the Bay of Antofagasta, Central Chile, probably at the beginning of the twentieth century (Castilla et al. 2002) (Fig. 10). This species is originally from Australia where it mainly occurs on horizontal wave exposed, rocky substrates where it forms dense aggregates (Rius and Teske 2011). *P. praeputialis* dominates the mid-to-low intertidal rocky shore fringe replacing the former MAF dominated by the mussel *Perumytilus purpuratus* (Lamarck, 1819) (Caro et al. 2011). A consequence of this new MAF was a dramatic increase in local rocky shore biodiversity: whereas over 110 species of macroinvertebrates and algae coexist on and within the *P. praeputialis* bed, only 28 species live along adjacent coastlines (Cerdeira and Castilla 2002), suggesting unoccupied niche space is being exploited.

Pyura doppelgangera, originally from the southern shores of Bass Strait, invaded the northern tip of New Zealand in the beginning of this century and has now been recorded at more than 22 locations where it is replacing the MAF formed by the green-lipped mussel *P. canaliculus* (Davis et al. 2018). While gastropod mollusks and crustaceans dominated the assemblage within mussels, tubicolous polychaetes dominate the fauna associated with the ascidian. Furthermore, sessile filter-feeding epifauna, notably barnacles and calcareous tube-dwelling polychaetes which were common on mussels, are never found in the ascidian forest.

Styela is another genus of solitary ascidians which can be invasive. In contrast to *Pyura*, *Styela* is more common in fouling communities associated with artificial, rather than natural, substrates. However, recent reports of *S. clava* in Northern Patagonia, Argentina, show that although the invasion occurred after 2012, the species has already spread onto natural substrates, both in intertidal and subtidal zones down to 20 m, reaching densities of 84 ind. m⁻² (Pereyra et al. 2015). Specific impacts on local communities are unknown, but *Styela* is one of the main substrates



Fig. 11 Photograph of a marine animal forest invaded by the colonial ascidian *Eudistoma carolinense* (gray, lobed colony in the foreground) at Guaratuba, Brazil. Photo credit: Rosana M. Rocha

for the recruitment of another introduced species, the alga *Undaria pinnatifida* (Harvey), facilitating the introduction of this species. As both ascidia and alga are bioengineers, local communities are expected to be substantially transformed. In northwest Europe, *S. clava* grows on various substrates, including shells of living mussels [*M. edulis*, *Modiolus modiolus* (Linnaeus, 1758)], oysters, and barnacles (Lützen 1999), but the impacts to those MAFs have not been studied.

As well as aggregations of solitary NIS of ascidians, some colonial species can also form three-dimensional habitats, as it is the case of *Eudistoma carolinense* Van Name, 1945 which was first observed forming a horizontal belt along the sublittoral fringe in south Brazilian rocky shores in 1996 (Moreno and Rocha 2006) (Fig. 11). The invader has occupied space originally used by *P. perna* (also nonindigenous, see Sects. 2 and 6.6 and Figs. 1b and 2a) and created a new MAF providing habitat for 128 different taxa, including vagile polychaetes, crustaceans, mollusks, among others, as well as providing substrate for sessile bryozoans, hydrozoans, ascidians, and sponges (Moreno and Rocha 2006).

Colonial invaders can also impact MAFs, usually by competing for space and smothering competitors. Three years after its introduction in Long Island Sound—USA around 2002, the temperate didemnid *D. vexillum* had colonized at least 230 km² of the soft bottom, overgrowing sea scallops, mussels, sponges, bryozoa, hydrozoa, calcareous tube worms, and other native colonial ascidians (Valentine et al. 2007). The species also acts as an ecosystem engineer, forming a mat on soft bottoms, altering benthic-pelagic coupling and influencing the biogeochemical

cycling of many nutrients and elements. It does so by creating a physical barrier between the underlying seafloor and the water column above, resulting in subtle shifts in community structure and functional group dominance (Mercer et al. 2009).

6.8 Algae

Macroalgae are one of the most successful invasive groups (Chapman et al. 2006). Invasive algae, such as *Womersleyella setacea* (Hollenberg) R. E. Norris, *Kappaphycus alvarezii* (Doty) Doty ex P. C. Silva, and *Dictyosphaeria cavernosa* (Forsskål) Børgesen have altered gorgonian (Cebrian et al. 2012), sponge (de Caralt and Cebrian 2013), and coral populations (Stimson et al. 2001; Chandrasekaran et al. 2008) on Indian and Hawaiian coral reefs. Furthermore, on Mediterranean reefs, the alga *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon has induced changes in coral microbial communities (Greff et al. 2017), and on Hawaiian reefs, the alga *Gracilaria salicornia* (C. Agardh) E. Y. Dawson has modified physical habitat quality by reducing irradiance, increasing sedimentation, and brought about greater variation in dissolved oxygen and pH in the water negatively impacting reef corals (Martinez et al. 2012).

Ramsay-Newton et al. (2016) presented rare empirical data showing effects of the invasive red alga *Dasysiphonia japonica* (Yendo) H.-S. Kim on native species, community, and ecosystem-level responses in the western North Atlantic Ocean. The effects included decreases in biodiversity, changes in nutrient uptake of algal assemblages over time, and changes in the functional characteristics of invaded communities, with implications for ecosystem-level processes such as nutrient fluxes.

Species of the genus *Caulerpa* J. V. Lamouroux have also received attention due to their negative impacts on MAFs in reef systems. Invasive traits, such as thallus size and density, levels of asexual reproduction (fragmentation), and total biomass are important to their invasion success in some areas such as in Australia (Wright 2005) (Fig. 12). *Caulerpa taxifolia* (M. Vahl) C. Agardh has strong negative effects on the reproductive traits (timing of reproductive development and spawning; follicle and gamete production) of the native bivalve *Anadara trapezia* (Deshayes, 1839), even though the invader has positive effects on recruitment (Gribben and Wright 2006; Gribben et al. 2009). *C. taxifolia* biomass is positively associated with the composition and abundance of the epifaunal community but negatively correlated with the abundance of infauna (Gribben et al. 2013).

Bulleri et al. (2010) demonstrated that *C. racemosa*, once established, can enhance sediment accumulation, favoring algal turfs persistence over erect algal forms, and enables them to monopolize space. Additionally, this invasive alga impacted survival, necrosis rates, and population biomass of the gorgonian forests of *Paramuricea clavata* (Risso, 1826) on Mediterranean rocky reefs (Cebrian et al. 2012). Some authors comment that *Caulerpa* species that rely on disturbance to

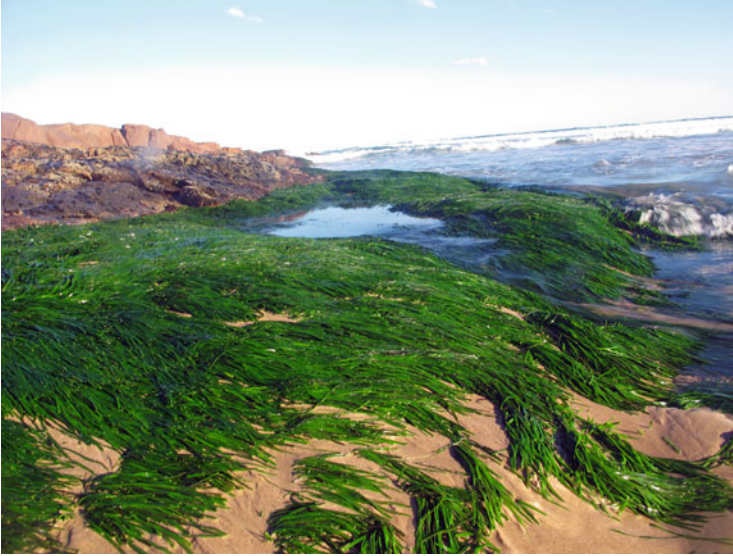


Fig. 12 Photograph of the invasive green alga *Caulerpa filiformis* dominating and transforming the substratum at Anna Bay, Port Stephens, New South Wales, Australia. Photo credit: Ricardo J. Miranda

establish can subsequently become the main drivers of ecological change (Bulleri et al. 2010).

More recently, studies have evaluated combined effects of invasive algae and sea warming on native species and ecological processes (Kersting et al. 2015; Miranda et al. 2019). The results can be complex involving direct negative or indirect positive effects. For example, the invasive algae *Caulerpa cylindracea* Sonder and *Lophocladia lallemandii* (Montagne) F.Schmitz combined with warming increased tissue necrosis and reduced photosynthetic efficiency of native coral *Cladocora caespitosa* (Linnaeus, 1767) (Kersting et al. 2015). *C. filiformis* presence can indirectly influence reduction of gastropod herbivory intensity on native kelp *Ecklonia radiata* (C. Agardh) J. Agardh under future warming scenarios (Miranda et al. 2019) (Fig. 12).

6.9 Fish

The Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) are among the most invasive marine predators of recent years (reviewed by Andradi-Brown 2019). They have spread rapidly across the western Atlantic, increasing in abundance dramatically between 2004 and 2010 to a level where they represent nearly 40% of the total predator biomass in the ecosystem. The increase in lionfish abundance has been paralleled with a 65% decline in the biomass of the lionfish's 42 Atlantic prey fish

species in just 2 years (Green et al. 2012). These invaders are now also becoming abundant on eastern Mediterranean rocky reefs (Azzurro et al. 2017), with currently unknown impacts on the local communities.

Given that their prey include parrotfishes (Albins and Hixon 2008; Morris and Akins 2009), Albins and Hixon (2013) pointed out that predation by invasive lionfish may have indirect effects on Atlantic and Caribbean reef-building corals, a major MAF group. On mesophotic coral reefs in the Bahamas, the lionfish invasion has caused a phase shift to increased algal cover from 31% to 94% at 46 m and from 8% to 92% at 61 m over 4 years (Lesser and Slattery 2011; Andradi-Brown 2019). Coral cover at 46 m changed from 19% in 2005 to less than 2% over the same period, an indication that phase shift to algal dominance may have been caused by the abovementioned trophic cascade, resulting in algae competitively excluding corals and other benthos (Lesser and Slattery 2011; Andradi-Brown 2019).

Numerous studies of coral reefs have shown that overfishing of herbivores reduces the health of reef corals by reducing herbivory allowing seaweeds from outcompeting corals and/or restricting coral recruitment (Mumby and Steneck 2008). So when lionfish effectively “overfish” juvenile parrotfish and other small herbivores, they can have devastating indirect effects. In areas where trophic cascades already occur [where top predators such as large groupers that prey on mesopredators that feed on herbivores are already overfished—a phenomenon called “mesopredator release” (Prugh et al. 2009)]—lionfish can increase the stress on herbivores even further and lead to a total domination of algae on the reef.

7 Chemical Ecology

The study of chemically mediated interactions among members of biological communities is a recent approach to understanding ecosystems. Chemical signals emitted by marine organisms (natural products or secondary metabolites) act as a language for communication between members of sea life. However, the impact of these signals is still very poorly understood. These substances strongly affect the populations and communities’ structures and the function of ecosystems (Hay 2009). Several theoretical models on resource allocation have been developed to explain the pattern of the secondary metabolites in marine organisms in response to chemical, physical, and biological stresses (Cronin 2001). The ecological and evolutionary consequences of secondary metabolites and their effects on marine biodiversity are increasingly recognized (Hay and Fenical 1996). However, there is little evidence of the adaptive response of marine invasive species under selective pressure from a new environment.

Some marine organisms are prolific in providing unique bioactive chemicals, such as terpenes, steroids, fatty acids, polyketides, and alkaloids, with ecological functions, such as defense against predators, competitors, and fouling organisms. For some invasive species, their chemical defenses may enhance their invasion success. Regarding MAFs the invasive Porifera *T. hoshinota* (Demospongiae)

(Pacific Ocean to Central Pacific Reef) aggressively competes for space by killing and overgrowing living corals (Rützler and Muzik 1993). This coral-killing sponge is known to produce the bioactive compounds terpiodiene, nakitriol, nakiterpiosin, and nakiterpiosinone that are toxic to corals (Teruya et al. 2002; Uemura et al. 2009). Wang et al. (2012) showed that endosymbiotic cyanobacteria are engulfed by *Terpios* cells and may be responsible for the “black disease” that results from outbreaks of this cyanobacteria-sponge holobiont and cause death of stony corals (Yang et al. 2018).

Cup corals *T. coccinea* and *T. tagusensis* (Scleractinia), which have invaded the Caribbean, Gulf of Mexico, and the Brazilian coast from the Indo-Pacific Ocean (Paula and Creed 2004; Creed et al. 2017; Figueroa et al. 2019; Figs. 1 and 4), produce chemical defenses that influence interactions with predators (generalist fish), foulers, and competitors. Their methanolic crude extracts exclude and decrease the settlement and survival of the fouling organisms such as crustose algae *Lithophyllum* sp. and the green alga *Cladophora* sp., respectively (Lages et al. 2010). In a competition interaction experiment, necrosis has been detected on the tissues of the coral *Mussismilia hispida* (Verrill, 1902), and this species induced variation in sterol, alkaloid, and fatty acid production in *Tubastraea* tissues. In this way, they are able to affect community structure and ecosystem dynamics (Lages et al. 2011, 2012; Paula et al. 2017).

Field experimental assays with the NIS (Indo-Pacific Ocean) soft coral *C. braziliensis* (Alcyonacea), also invasive on the Brazilian coast, showed that chemicals from this coral have an allelopathic effect causing large necrotic patches on tissues of the endemic gorgonian *Phyllogorgia dilatata* (Esper, 1806). Bioassay-guided experiments with fractions from the unpalatable hexane extract from this coral revealed a new steroid, 23-ketocladiellin-A, which exhibited potent feeding deterrence against fish, suggesting a reason for the observed success of the invasion by this NIS coral (Lages et al. 2006; Fleury et al. 2008).

Cebrian et al. (2012) reported the strong and consistently negative effects on different components of fitness of the Mediterranean gorgonian *Paramuricea clavata* by the invasive algae *C. racemosa* and *W. setacea*. Although secondary metabolites of *W. setacea* are unknown and the caulerpenyne concentration in *C. racemosa* is low (Jung et al. 2002), they did not rule out possible allelopathic activity (Cebrian et al. 2012). The alkaloids and crude extracts from invasive ascidian *Didemnum* spp. (Ascidiacea) also inhibit predators and foulers (Pisut and Pawlik 2002).

8 Microbial Ecology

As seen above, a holobiont-approach is often needed to assess if the associated microbiota confer invasive species advantages over native species in MAFs. Competitive exclusion by the invader can be enhanced by carrying pathogens that act as biological weapons (Vilcinskis 2015). Disease-mediated invasions include cases as

diverse as grasses, salt marshes plants, ladybirds, squirrels, and crawfish carrying parasites such as fungi and viruses that infect native competitors successfully decimating their populations (Li et al. 2014; Young et al. 2017).

In octocoral animal forests on rocky reefs in the Eastern Pacific, fungal diseases and bacterial dysbiosis have been consistently observed in gorgonian coral populations where the invasive snowflake coral *C. riisei* is present (Barrero-Canosa et al. 2012; Sánchez and Ballesteros 2014; Sánchez et al. 2014; Quintanilla et al. 2018). However, further research is needed to study the microbiota and pull out which potential pathogens are carried by the snowflake coral.

Invasive species can also disrupt mutualistic symbiotic interactions. In general, continental case studies have preliminarily concluded that symbionts do not comprise as serious threat to natives, given the facultative nature of mutualism (Aslan et al. 2015). Similar cases have been found in MAFs, coral reefs, with zooxanthellae (Symbiodiniaceae) (LaJeunesse et al. 2018). *Durusdinium trenchii* (LaJeunesse) from the Indo-Pacific, previously known as clade D, is considered a recent invader in the western Atlantic, where corals engage in symbiosis with this opportunistic zooxanthella after bleaching, but rarely keep it due to their unfit mutualism (Pettay et al. 2015). A similar case could be zooxanthellae of the genus *Gerakladium* LaJeunesse, which are exclusively found in the sponge genus *Cliona* Grant, 1826 (Granados et al. 2008). They show very little divergence between Indo-Pacific and western Atlantic species, whereas the sponges can also associate with algae of the genera *Zooxanthella* K. Brandt (= *Symbiodinium*) and *Cladocopium* LaJeunesse and H. J. Jeong (Granados et al. 2008; Hill et al. 2011; Ramsby et al. 2017). Although it may not be a recent invasion, it is a case showing that the most recent mutualistic arrival in the region is still facultative among several species. Further research is needed of other mutualistic coral symbionts, such as apicomplexan corallicollicids (Kwong et al. 2019), euendolithic algae (Gonzalez-Zapata et al. 2018b), and endosymbiotic prokaryotes (Gonzalez-Zapata et al. 2018a).

9 Formers of Novel MAFs

Invasive ecosystem engineers (IEE) are potentially one of the most influential types of biological invaders, and some can be formers of new MAFs. They are expected to have extensive ecological impacts by altering the physical-chemical structure of ecosystems, thereby changing the rules of existence for a broad range of resident biota. A recent review and meta-analysis have shown that most studied IEE are macrophytes, but some are also animals, most notably bivalves, colonial worms, and corals (Guy-Haim et al. 2018). IEE were shown to cause dramatic shifts in local biodiversity (both increasing or decreasing taxa richness) and have strong impacts on ecosystem functions in the invaded areas, but there are very few studies that examined the interaction between both impacts. One well-known example is the tubeworm *F. enigmaticus*. This polychaete forms massive reefs within invaded lagoons including mudflats without hard substrate, dramatically modifying the

physical properties and processes in the area as well as strongly impacting the resident biota (Schwindt et al. 2001, 2004) (Fig. 8). The worm has great potential for transferring pelagic production to the benthos: changes water quality and light penetration by filtering large volumes of water (Davies et al. 1989), reduces phytoplankton biomass (Bruschetti et al. 2008), increases carbonate sediments through the accumulation of calcareous tubes (Schwindt et al. 2001), and produces feces and pseudo-feces with organic matter content 20× normal sediment with a C/N ratio of biodeposits of 8 (Bruschetti et al. 2011).

Another example extensively studied and discussed by Crooks (2009) is the soft-sediment dwelling invasive mussel *A. senhousia* (= *Musculista senhousia*). *A. senhousia* forms dense byssus bound mats on intertidal and subtidal soft sediments (Crooks 1998) (Fig. 9). At small spatial scales, the mussel appears to benefit many small organisms that occur in higher abundances within the complex mat matrix when compared to nearby, mat-free areas (Crooks 1998) by offering physical structure (Crooks and Khim 1999). However, it has a detrimental effect on larger organisms such as other bivalves and eelgrass (Reusch and Williams 1998; Crooks 2001).

The encrusting zooxanthellate scleractinian *O. patagonica* was first recorded in the Mediterranean Sea in 1966, with an original description based on ~10,000 years old fossils from the western Atlantic (Zibrowius 1974). However, the origin and taxonomic identification of *O. patagonica* in its present range is uncertain because it is cryptogenic (Zenetos et al. 2017). *O. patagonica*'s range has expanded in multiple directions and established abundant populations over a broad geographical scale, including both western and eastern Mediterranean basins, the subtropical eastern Atlantic (Canary Islands harbor area), and tropical Caribbean Sea (on coral reefs nearby the Veracruz Port, Mexico) (Fine et al. 2001; Serrano et al. 2013; Colín García et al. 2018; López et al. 2019). It exhibits an invasive behavior at both geographical distribution range and population outbreak levels, being able to form novel MAFs in shallow waters and drive phase shifts from macroalgal- to coral-dominated states across the Mediterranean (Serrano et al. 2012, 2018; Salomidi et al. 2013) (Figs. 1a and 6).

The successful proliferation of *O. patagonica* resembles that of the azooxanthellate scleractinians *Tubastraea* spp. (Figs. 1b and 4). Native to the tropical Indo-Pacific, *T. coccinea* was first recorded in some Caribbean islands in the 1930s, probably introduced by fouling floating platforms (Creed et al. 2017). They are increasing their range on rocky and coral reefs throughout the tropical-subtropical Atlantic from the Canary Islands to Southern Brazil, Caribbean Sea, and Gulf of Mexico (Creed et al. 2017; Figueroa et al. 2019; López et al. 2019). The capacity of *T. tagusensis* (Fig. 4a) and *T. coccinea* (Fig. 4b) to reproduce both sexually and asexually (Capel et al. 2014; Paula et al. 2017) and exploit man-made substrates (oil and gas platforms, buoys, and ships; Fig. 4d) has assisted their wide geographic dispersal (Creed et al. 2017).

They have life-history traits similar to those documented for *O. patagonica* (Kramarsky-Winter et al. 1997; Fine et al. 2001). Both invasive *Tubastraea* and *Oculina* have broad tolerance to environmental parameters, are opportunistic high

fecundity colonizers and generalists in terms of substratum utilization, and benefit from current human-related impacts (e.g., their population growth is enhanced in artificial habitats, which likely act as corridors for successful dispersal (e.g., Fine et al. 2001; Serrano et al. 2013, 2018; Mantelatto and Creed 2015; Creed et al. 2017; López et al. 2019).

10 Case Studies

10.1 *Vermetid Reefs*

Vermetids are gastropod mollusks, some of which can form reefs as biogenic MAFs with the help of encrusting coralline algae (Safriel 1975; Fine et al. 2017). They are important in intertidal and shallow subtidal habitats in subtropical and temperate waters. They have a key role as habitat engineers, hosting high biodiversity levels and providing ecosystem services such as coastal protection and regulation of sediment transport and deposition (Milazzo et al. 2017). Likely, the most well-studied vermetid reefs are those from the temperate Mediterranean Sea (Ingrosso et al. 2018), the main reef-building genus being *Dendropoma* Mörch, 1861. In the southeastern Mediterranean (Levant Sea), this ecosystem has experienced a massive population explosion of a Red Sea mussel, *B. pharaonis* that formed extensive mussel beds during the 1980–1990s (Rilov et al. 2004). During the 1990s and the 2000s, the endemic reef-building species *Dendropoma anguliferum* (Monterosato, 1878), itself went ecologically extinct on the Israeli coast for unknown reasons, along with many other native species (Rilov 2016). Similarly, along the Lebanese coast, only a single remnant small population of *D. anguliferum* was found (Badreddine et al. 2019). These findings attest to the potential domination of vermetid MAFs by invasive species and other human disturbances, but the link between the invasion and the MAF loss is not clearcut.

10.2 *Coral Reefs*

Reef corals are MAFs that form calcified skeletons that can act as substrate and form habitats for other kinds of benthic invertebrates on rocky benthic assemblages (Sheppard et al. 2009). Loose coral boulders and free-living reef corals can move downslope and tumble onto soft bottoms underneath, where they can act as solid substrate for attached benthos and thus assist in reef expansion (Sheppard 1981). Most reefs occur in tropical shallow coastal waters, where reef-building corals grow rapidly owing to their symbiosis with light-dependent unicellular algae (zooxanthellae) inside their soft tissue (Muller-Parker et al. 2015). These MAFs have been invaded in Hawaii and India by macroalgae (Stimson et al. 2001; Chandrasekaran et al. 2008), in the western Atlantic by the azooxanthellate coral *Tubastraea*

(Miranda et al. 2016; Fig. 4c), in the tropical Atlantic by lionfish (Andradi-Brown 2019), and in the Venezuelan Caribbean by a xeniid soft coral (Ruiz Allais et al. 2014).

In the last decade, there has been an increase in research attention toward the mesophotic zone (30–150 m depth), where tropical coral communities might be more sheltered from negative human impacts but receive less sunlight than at shallower depths (Laverick et al. 2018). Mesophotic reef MAFs have been transformed by trophic cascades caused by invasive lionfish (Lesser and Slattery 2011; Andradi-Brown 2019). Nothing is known about the biological invasion of the deepest coral reefs, so-called cold-water reefs, where corals live in permanent darkness and without zooxanthellae but still can form extensive frameworks over long periods of time (Roberts and Cairns 2014; Hebbeln et al. 2019).

10.3 Temperate Reefs

Invasive animal species can profoundly transform native ecosystems, particularly when they impact native engineer species. A striking example of marine regime shifts is found on shallow-water temperate reefs where global change has first led to widespread phase shifts from canopy-forming macroalgae- to barren-dominance (Harley et al. 2012). More recently, sea warming-enhanced poleward shifts of subtropical and tropical zooxanthellate corals have led to tropicalization of temperate ecosystems by coral-dominated assemblages (Vergés et al. 2014).

Tosa Bay, in southern Japan, provides one of the most well-known examples where the healthy temperate macroalgae-dominated ecosystem of the 1980s was first replaced by barrens in the 2000s and now by zooxanthellate scleractinian corals such as reef-building *Acropora* species, resulting in a novel coral-dominated ecosystem (Serisawa et al. 2004; Takao et al. 2015). Marginal habitats for coral reefs are predicted to expand poleward under future climate scenarios (Burrows et al. 2011), and small increases in sea temperature in the past have resulted in the appearance of coral reefs at higher latitudes (Greenstein and Pandolfi 2008), which is consistent with the hypothesis and evidence that algal forests in temperate regions are being transformed into coral-dominated forests in an era of global warming.

10.4 Mediterranean Coralligenous Ecosystem

The Mediterranean coralligenous ecosystems are calcareous formations of biogenic origin that are mainly produced by the accumulation of calcareous encrusting algae growing in dim light conditions (Ballesteros 2006). Cavities and crevices within the coralligenous structure sustain a complex community dominated by forests of suspension feeders. The high biodiversity of animal builders contributes to the coralligenous framework, including most taxonomic groups such as bryozoans,

serpulid polychaetes, sponges, cnidarians, mollusks, and tunicates (Boudouresque et al. 2017). Sea warming has increased the frequency of heat waves that have been linked to severe mass mortality events in coralligenous benthic invertebrates over broad geographical scales (Garrabou et al. 2009; Crisci et al. 2011). In turn, some invasive species can thrive in the coralligenous habitat, but only introduced algal species are currently threatening the coralligenous ecosystems. Remarkably harmful is the red turf alga *W. setacea*, which forms a dense and thick carpet over encrusting calcareous algae, thus inhibiting photosynthesis and growth of the main framework builders, and the recruitment of animal species inhabiting the coralligenous community (Airoldi et al. 1995; Ballesteros et al. 1998; Piazzì et al. 2002). New mass mortality events depleting animal forests in coralligenous habitats are expected under projected climate warming scenarios, and invasive algal species are increasing through the Mediterranean (Marbà et al. 2015), suggesting the ongoing transformation of coralligenous animal forests into algal-dominated forests. Although the impact of invasive species is increasingly recognized in shallow-water Mediterranean coralligenous ecosystems, little is known of the presence of non-native species beyond the continental shelf (Galil et al. 2019). However invasive fish may spread to depths and impact unique, diverse, and fragile mesophotic animal forests (Gori et al. 2017; Galil et al. 2019).

10.5 *Carijoa*

The snowflake coral *C. riisei* (Fig. 1b) is a tropical stoloniferous zooxanthellate octocoral (Order Alcyonacea, Family Clavulariidae) that occurs in shallow water. It was considered native to the tropical western Atlantic and throughout the Caribbean (Bayer 1961), but recent molecular studies indicate that it is actually native to the Indo-West Pacific (Concepcion et al. 2010; Quintanilla et al. 2017). It is thus nonindigenous from Florida, USA, to Santa Catarina, Brazil, as well as on some Atlantic islands (Galván-Villa and Ríos-Jara 2018), and on oil platforms off Gabon, Southeast Atlantic (Friedlander et al. 2014). In the Pacific, *C. riisei* has invaded the southern part of India, the Hawaiian Archipelago, and Tropical Eastern Pacific (Panamá, Colombia, and Ecuador—Quintanilla et al. 2017; Mexico—Galván-Villa and Ríos-Jara 2018). According to genetic evidence, the introduction to the Hawaiian Islands occurred from the Indo-Pacific, separately from its arrival to the Caribbean (Concepcion et al. 2010). Furthermore the Colombian Eastern Pacific invasion was probably derived from the Atlantic (Quintanilla et al. 2017).

In Hawaii, *C. riisei* was first reported in 1972 at Pearl Harbor. Since then, it has spread throughout the archipelago and heavily impacted MAFs. According to Grigg (2003), a survey of the Maui Black Coral Bed carried out in 2001 showed that up to 90% of *Antipathes dichotoma* Pallas, 1766, and *A. grandis* Verrill, 1928, colonies had been overgrown by the snowflake coral and died. They are commercially valuable species (\$30 million) used to make precious coral jewelry (Grigg 2004). It is believed that epifauna provides a beachhead which *C. riisei* uses to settle on

black corals; it then spreads vegetatively, its' stolons smothering the natives (Kahng and Grigg 2005), transforming the MAFs into “virtual graveyard for black coral” (Grigg 2003). Shallower, *C. riisei* was observed to overgrow other scleractinian plate corals (*Leptoseris* sp. and *Pavona* sp.), transforming the seascape into “an underwater “prairie” of white polyps” (Kahng and Grigg 2005). In Pacific Colombia *C. riisei* can overgrow the native octocoral fauna, such as the sea fans *Pacifigorgia* Bayer, 1951 and sea whips *Leptogorgia* Milne Edwards, 1857 on oceanic and coastal rocky reefs. In fact, large-scale mortality of native octocorals, particularly of *Pacifigorgia* spp. and *Muricea* spp., has been reported (Quintanilla et al. 2017), and at one site, >87% of octocorals [*Pacifigorgia* spp. and *Leptogorgia alba* (Duchassaing & Michelotti, 1864)] died as a result of *C. riisei* interaction (Sánchez and Ballesteros 2014).

According to Quintanilla et al. (2017), the invasive success of *C. riisei* is attributable to its fast stoloniferous growth mode, generalist filter-feeding behavior, few natural predators, and a symbiotic interaction with the sponge *D. anchorata* which has cytotoxic compounds (Calcinai et al. 2004). Kahng et al. (2008) further demonstrated that under favorable conditions *C. riisei* exhibits high polyp fecundity and has asynchronous, continuous spawning of gametes which may allow it to dominate ephemeral space through high and continuous production of larvae.

11 Conclusions, Perspectives, and Challenges for Future Research

The expansion of global trade will increase the number of marine biological invasions, and MAFs will be increasingly impacted by those species that create, modify, or exclude them. However we still know very little-to-nothing about invasive species and their impacts on MAFs in many deeper and less accessible systems, such as shallow-water, benthic communities in Antarctica (Aronson et al. 2007; Hughes et al. 2020), mesophotic reefs (Loya et al. 2019; Soares et al. 2019), and deep sea ecosystems in general (e.g., Galil et al. 2019), including hydrothermal vent communities. This may be because we know little about these systems or that they are less susceptible to invasion, or both. Whichever, these systems urgently need to be better addressed (Galil et al. 2019; Hughes et al. 2020).

We have difficulty and must also address how we recognize “deep invasions” in MAFs (Carlton 2009). Furthermore, we need to better distinguish which mechanisms create novel or modify existing MAFs, be they impacts of “traditional” biological invasions (jumps through barriers by vectors along pathways) or range expansions caused by human-induced change.

Global warming, particularly, has been predicted and/or has now resulted in the formation, modification, or exclusion of MAFs through poleward expansion of tropical and subtropical species toward temperate reefs (Greenstein and Pandolfi 2008; Burrows et al. 2011; Vergés et al. 2014; Takao et al. 2015; Canning-Clode and

Carlton 2017) and temperate species toward the poles (Aronson et al. 2007). An additional challenge is distinguishing these human-mediated range expansions from natural processes such as dispersal not mediated by human activities (Lonhart 2009). Further baseline studies of less well-known MAF systems, coupled with predictive modeling, are crucial to detect and forecast future ecosystem changes as a result of human-mediated range expansion and invasion.

Given the usual high diversity of interacting species they harbor, MAFs offer a natural laboratory for the study of the evolutionary effects on invasions in the marine realm. Studies of the invasive holobiont as a whole are currently incipient, but new, cheaper molecular tools should open up this field for future studies which will better understand the complex multiple mechanisms, including the chemical ecology, of the holobiont invasion. Understanding the history, pathways and vectors and the reproduction strategies of invasive MAF-forming species and those of invasive predators on native MAFs are crucial for developing methods for their control.

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