

Chapter 12

Ecological Factors Affecting Community Invasibility

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12.1 Introduction

What makes a community invulnerable? For over a century ecologists have sought to understand the relative importance of biotic and abiotic factors that determine community composition. The fact that we are still exploring this topic today hints at both its importance and complexity. As the impacts from harmful non-native species accumulate, it has become increasingly urgent to find answers to the more applied aspects of this question: what makes a habitat vulnerable to invasion by additional species, and which species are likely to invade? Answers to these questions will not only aid in targeting conservation efforts but will also advance our understanding of marine community ecology.

Although the relative importance of abiotic vs. biotic factors in making a habitat invulnerable varies, abiotic factors undoubtedly serve as the first “filter” to invasions, limiting establishment of non-native (=exotic) species to conditions approximating their native ranges. As obvious examples, tropical corals will not establish in boreal waters, and temperate rocky intertidal species will not colonize tropical shores. Similarly, species cannot invade a community if propagules do not arrive at the site. Other chapters in this volume cover the influence of abiotic factors and propagule supply (Chap. 7, Johnston et al.; Chap. 8, Miller and Ruiz; Chap. 19, Hewitt et al.), so we only briefly review these factors. In this chapter we focus on the question of predicting invasion success of non-native species that are (1) transported to the habitat in question (i.e., propagule supply is not extremely limiting) and (2) physiologically capable of surviving in the climatic regime. We begin with the observation that even in areas of suitable habitat within the current range of an introduced species, there is often dramatic variation in the density, presence, and overall success of the invader. We seek to explain this variation in terms of processes that control the availability of resources. These include not only abiotic and physical factors that determine base resource levels, but also interactions between species or between organisms and their environment that increase resource availability (through disturbance) or decrease resource availability (through competitive processes), or create new resources (through facilitation) (Fig. 12.1).

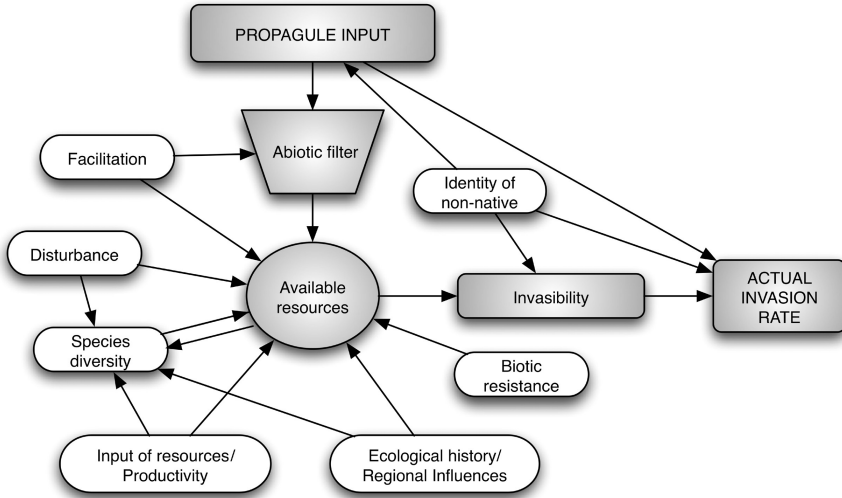


Fig. 12.1 Factors that have been shown to affect invasions of non-native species into marine communities. Assuming exotic propagules are present and able to survive the initial abiotic “filter” of the new habitat (see Sect. 12.2), their ability to invade the community can be determined by several, potentially interacting, factors that affect resource availability (Sects. 12.3–12.7), as well as the rate of propagule input and the characteristics of the exotic relative to the resident species already present (Rejmanek et al. 2005). Figures 12.3 and 12.4 illustrate how some of these factors interact to affect invasibility using specific case studies

Over the past few decades, we have seen substantial progress in understanding biological invasions, including the identification of several factors that affect community invasibility. While there is a growing body of research on invasibility in marine systems, the majority of studies are from terrestrial systems (see Fig. 12.2). Where available, we review results from marine studies; where these are scarce, we draw attention to this limitation and supplement our review with what, if anything, is known from other systems.

12.2 The Abiotic Filter

The combination of abiotic conditions under which an organism can sustain populations without immigration (“the fundamental niche”) has long been recognized as a constraint on the distribution of a species, and most non-native species are at least somewhat limited to habitats ecologically similar to their ancestral ranges (Holt et al. 2005; Peterson 2003). While this concept has been incorporated into climate- and/or habitat-matching methods aimed at predicting what habitats would be ecologically appropriate for potential invaders (Peterson 2003; Peterson and Vieglais

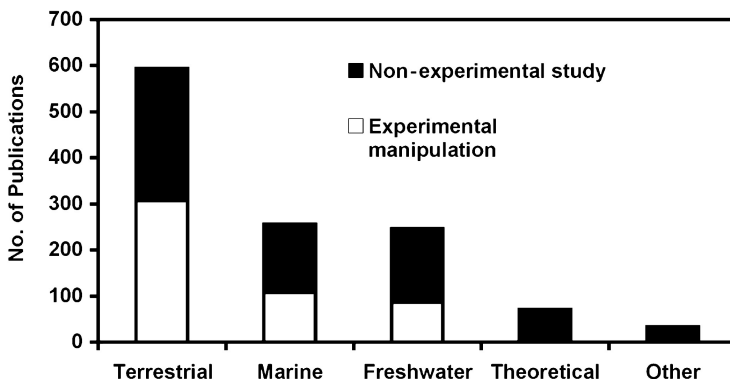


Fig. 12.2 Bioinvasion papers from the ecology literature from 1995 to 2005 by system and study type. Published papers from terrestrial systems outnumbered those from marine two to one. Of these, approximately half of the terrestrial studies involved an experimental manipulation, while only 42% of the marine and 35% of the freshwater studies did. The *white portion of each bar* represents the number of studies that included an experimental manipulation; the *black portion* represents all other types of studies. The system category “other” includes studies that either cut across all systems or did not specify a system. We searched the Web of Science using the following search terms: *invas**, *invas**, *exotic*, *alien*, *nonnative*, *non-native*, *nonindigenous*, *non-indigenous*. The analysis was restricted to 14 journals: *Ecology*, *Science*, *Nature*, *Oecologia*, *OIKOS*, *Ecological Applications*, *Biological Invasions*, *Ecology Letters*, *Journal of Ecology*, *Journal of Animal Ecology*, *Proceedings of the National Academy of Sciences of the United States of America*, *Marine Ecology Progress Series*, *Journal of Experimental Marine Ecology and Biology*, and *Hydrobiologia*

2001), the relative efficiency of modeling abiotic niche requirements (or similar methods of predicting invasions) depends on whether the abiotic requirements are conserved over time (Holt et al. 2005) or whether non-natives undergo rapid changes in their abiotic requirements in their invaded ranges (Quinn et al. 2000; Stockwell and Ashley 2004; Wares et al. 2005). Some studies do indicate widespread niche conservatism over time (Holt et al. 2005). For example, the crab *Hemigrapsus sanguineus* has nearly identical abiotic habitat requirements in its invaded and ancestral ranges (Lohrer et al. 2000). In contrast, other studies have found that abiotic habitat characteristics vary among spatially independent invasions, as is the case for the European green crab *Carcinus maenas* (Grosholz and Ruiz 1996). The degree to which a species’ abiotic requirements are conserved or can change during the course of invasions is still not well understood, but it depends on factors such as propagule delivery, initial genetic diversity, and the historical pattern of the species’ introductions (Wares et al. 2005).

Given that a non-native species has passed through the initial abiotic “filter” (Fig. 12.1), community ecology theory can provide insights on when abiotic or biotic factors may be most important in determining the course (and success) of the subsequent invasion. Abiotic factors might be of primary importance in determining the abundance of invaders, for example in physically stressed habitats where the

effects of competition and predation are typically weaker (see also Chap. 7, Johnston et al.). In Puget Sound salt marsh communities, Dethier and Hacker (2005) found that abiotic factors such as salinity and sediment type primarily controlled invasion success of the English cordgrass *Spartina anglica*, whereas biotic factors had no effect.

Variation in abiotic effects may also mediate biotic interactions, such as competition and predation, between natives and non-natives. Byers (2002b) showed that an abiotic factor (sediment type) mediated biotic impacts (crab predation) on the non-native clam *Nuttallia*. In salt marshes, relaxation of salinity stress via increased rainfall and other freshwater inputs increases growth and competitive advantage of non-native plants relative to natives (Dethier and Hacker 2005; Kuhn and Zedler 1997; Minchinton 2002). Conversely, biotic interactions can modify abiotic conditions by buffering abiotic (physical) stress (Bertness and Hacker 1994), and this modification might either facilitate or inhibit invasions (for further discussion see Sect. 12.5.2). Ultimately, it is the interplay of abiotic and biotic factors in a community (via resource availability, disturbance, facilitation, and other factors) that affects the amount of resources available for non-natives and, consequently, the invasibility of the community (Fig. 12.1).

12.3 Resource Levels

Assuming once again that a non-native species has passed through the initial abiotic “filter”, increased availability of limiting resources can influence the invasibility of a habitat. In this section, we focus on how additions of resources to resource-limited systems can facilitate invasions by alleviating resource limitation (Davis MA et al. 2000). In subsequent sections, we review how competitive interactions (Sect. 12.4), facilitation (Sect. 12.5) and disturbance (Sect. 12.6) can each alter the actual level of available resources for exotic species attempting to establish.

Because a non-native species will require certain limiting resources in order to establish and spread, it will be more successful in habitats where competition for these resources is reduced (Davis MA et al. 2000; Davis MA and Pelsor 2001; Stachowicz et al. 2002a; Stohlgren et al. 2002). Enhanced resource availability can occur either when resource use by the existing species in a community declines (e.g., due to disturbance or consumption of competitors) or when the supply of limiting resources increases faster than the native members of the community can sequester those resources (e.g., eutrophication). When resource utilization decreases or total resource supply increases, a community can become more susceptible to invasion.

Direct evidence for the effects of enhanced resource availability on marine and aquatic bioinvasions is limited to only a few case studies, though high productivity has been implicated in promoting the spread of non-native species in marine systems (Branch and Steffani 2004). The results of a nutrient addition experiment in super-littoral rock pool microcosms suggest that adding nutrients enhances invasi-

bility by increasing limiting resources (Romanuk and Kolasa 2005). Similarly, adding nutrients to an aquatic plankton community stimulated bacterial production, which in turn promoted invasion by ciliates due to decreased competition for resources (Jiang and Morin 2004). Conversely, limiting resource availability can decrease invasion success: because phytoplankton availability in the water column is reduced inside eelgrass beds due to decreased water flow, eelgrass limits the growth and survival of the suspension-feeding non-native mussel *Musculista senhousia*, reducing invasion compared to areas where eelgrass meadows are fragmented or absent and rates of food delivery are higher (Allen and Williams 2003). If we consider resource availability more broadly to include space, there is clear evidence from marine systems that if native species are unable to consume or utilize the primary limiting resource, a community may be more susceptible to invasion (Stachowicz et al. 1999, 2002a). Finally, at larger scales, nutrient runoff from the land is increasing the distribution and abundance of an exotic vascular plant (*Phragmites australis*) in New England salt marshes (Bertness et al. 2002).

Most theory and evidence supporting the role of resource availability in mediating invasibility comes from studies of terrestrial primary producers. For example, nutrient additions to nutrient-poor grasslands can promote the invasion and eventual dominance of non-native annual species (Burke and Grime 1996; Huenneke et al. 1990). In contrast, long-term observational data suggest that more productive systems may actually be characterized by reduced invasion success, likely because (within the “normal” limits of a system) native species respond to increases in resource availability by increasing growth rates, allowing them to sequester the additional resources and preventing the establishment and growth of non-natives (Cleland et al. 2004). Thus, predicting invasibility based simply on the productivity of a system without measuring unused limiting resources is problematic.

12.4 Biotic Resistance and Species Diversity

Biotic resistance refers to the ability of a community of resident species to repel invaders as a result of species interactions, and it includes a variety of mechanisms. It can encompass the idea that native consumers or pathogens reduce invader fitness, but is most often conceived of as a product of competition with natives within the same trophic level. In terms of competition, the biotic resistance paradigm usually assumes that communities are both resource-limited and strongly structured by interspecific competition and resource partitioning (May and MacArthur 1972). A key aspect of this paradigm requires a comparison between the resource requirements of a potential invader and those required by the existing community. If the new species has optimum performance at resource levels that overlap minimally with the residents, then it will have a higher probability of successful invasion compared to other species with resource requirements more similar to the residents’ (Tilman 2004). For example, the dramatic success of *Hemigrapsus sanguineus* in New England has been attributed to the absence of ecological equivalents as no

other grapsid crabs are present in the intertidal there (Lohrer et al. 2000). However, this sort of attribution of causation is most usually done post-hoc. Determining the degree to which resource requirements of exotics that have not yet arrived will overlap with native species is not always straightforward: resource requirements of the invader may change in the invaded range, and biotic interactions with native species in the new habitat may alter access to limiting resources. Comparing a potential invader's performance in its native range (including resource uptake rates, resilience to varying conditions, and competitive abilities) to the performance of natives in a community at risk of invasion may increase our ability to predict whether that particular exotic will be successful in invading the community.

A single resident species may play a strong role in excluding particular invaders (Lennon et al. 2003; Lohrer et al. 2000; McGrady-Steed et al. 1997) when the characteristics of the invader and resident are sufficiently similar. In other cases a single predator or herbivore may exert a dominant influence on the abundance of non-natives (deRivera et al. 2005; Lohrer et al. 2000). A recent meta-analysis of the role of biotic resistance in plant invasions (Levine et al. 2004) suggests that these forces can be strong, but they rarely enable communities to resist invasion completely, instead acting to constrain the abundance of exotic species once they have successfully established. The results of an experiment that examined effects of the native community on an introduced oyster were consistent with this review at larger scales (across wave exposure), but not at smaller scales (across tidal elevation) (Ruesink 2007). Other experiments in marine systems that formally test the strength of biotic resistance forces are lacking. In a different meta-analysis, Parker et al. (2006) found native herbivores suppressed exotic plants, but exotic herbivores facilitated both the abundance and species richness of exotic plants. The increasing, widespread replacement of native with exotic herbivores is likely to facilitate invasions and may trigger an invasional meltdown (see Sect. 12.5.3 for further discussion).

Because there are a variety of mechanisms (competition, predation, disease) that can promote biotic resistance, it is likely that different resident species will have different effects on invaders, and those effects may interact. Ruesink (2007) simultaneously manipulated native predators and neighbors (competitors) and found these two different guilds affected introduced oysters differently. Predators reduced oyster survival, but neighbors both reduced growth and improved survival at some wave-exposed sites. Although invasion biology is beginning to address interactive effects of resident species on invaders, it is clear that we need to perform additional studies to examine the mechanisms involved and to consider the consequences of changing diversity (extinctions and invasions) on these interactions.

A corollary to the idea of biotic resistance is that, all else being equal, having more species should result in lower total resource availability, decreasing the success of new species (Case 1990; Elton 1958; Fargione et al. 2003; Fargione and Tilman 2005; MacArthur 1970, 1972; Naeem et al. 2000; Tilman 2004). Because of its intuitive appeal and the lure of a simple measure of invasion resistance, a large number of studies have addressed the question of whether more diverse communities are more resistant to invasion. The meta-analysis mentioned above estimated the effect of species diversity itself as equal in magnitude to strong individual spe-

cies effects (Levine et al. 2004). However, the analysis was limited to experimental studies, and experimental and observational approaches and small- and large-scale studies have often reached opposing conclusions, sometimes leading to contentious debate. In the remainder of this section, we focus on the relationship between resident diversity and invasibility.

12.4.1 Experimental vs Observational Approaches

Contributing to the apparent paradox between results from experimental and observational diversity-invasibility studies are the fundamentally different questions the two approaches pose, although this difference is not always recognized. Manipulative experiments ask what are the consequences of species loss for the likelihood of invasion. Surveys, on the other hand, tell us locations with species-rich native communities are characterized by conditions that promote exotic species richness. These issues are partially reviewed in Stachowicz and Byrnes (2006), and more fully in Fridley et al. (2007). Both of these questions are important from basic and applied standpoints, and a synthesis of these approaches can provide considerable insights into the conditions under which diversity is and is not an important determinant of invasion success.

Mathematical models (Case 1990, 1991; Tilman 2004; Chap. 4, Wonham and Lewis) and manipulative experiments in both marine and terrestrial systems (Britton-Simmons 2006; Kennedy et al. 2002; Levine 2000; Naeem et al. 2000; Stachowicz et al. 1999, 2002a; White and Shurin 2007) generally (but not unequivocally—see Arenas et al. 2006) support the idea that increasing diversity decreases invasibility. Stachowicz et al. (1999, 2002a) manipulated the species richness of these communities and challenged them with different potential invaders. They found that in all cases invasion success decreased with increasing resident species richness because individual species were complementary in their temporal patterns of space occupation. Individual species all fluctuated in abundance, but these fluctuations were out of phase. Thus, at least one species was always abundant and occupying space in the high-diversity treatments, whereas there were periods of high space availability in the low-diversity treatments. This mechanism appears to operate in the field, as surveys at small and medium scales showed a negative relationship between native and non-native richness (Stachowicz et al. 2002a) and showed that complementary temporal niches arise from seasonal differences in recruitment patterns at larger scales (Stachowicz and Byrnes 2006). Even a brief window of open space (2 weeks) (Stachowicz et al. 2002a) can increase invasion success by an order of magnitude (see Davis MA and Pelsor 2001 for a terrestrial example). Such seasonal or temporal niches may drive diversity effects on invasion resistance in other communities. For example, the biomass of mobile and sessile invertebrate invaders in experimental seagrass mesocosms decreased with increasing species richness of resident mobile invertebrates (France and Duffy 2006). Grazers in this system do show seasonal abundance patterns (Duffy et al. 2001;

Parker et al. 2001), which should produce more complete resource use throughout the season and may contribute to this effect.

In contrast to these findings, an experimental study of marine algae found that native algal functional group richness did not affect invasion success of other, non-resident natives, and that functional group identity most strongly affected invasion instead (Arenas et al. 2006). They found that resource availability did control invasion success, but algal identity (and not richness) controlled resource availability. However, the clever experimental design, which assembled polycultures from small monocultures of each functional group chipped from the rock, did not include all possible functional groups (ephemeral green algae, one of the native invaders, was not included). The design also decreased the likelihood of canopy layering, in which understory species (which had low space availability but high light levels) and canopy species (which had low light levels but high bare substrate) might have acted to complementarily reduce overall resource levels and invasion success. In fact such multivariate complementarity was found in a study of algal invasion into communities of varying functional group richness on the west coast of North America (Britton-Simmons 2006). A third macroalgal study found an overall negative effect of species richness on invasion, even though algal richness enhanced invader settlement by facilitation; apparently this was due to the extremely low survival of settlers in diverse patches (White and Shurin 2007). Thus on balance, experimental marine studies from a diverse suite of taxa (sessile inverts, mobile inverts and algae) generally concur with terrestrial experiments (Fridley et al. 2007) in finding a negative effect of increasing diversity on invasion success, and that this is mediated in large part by complementary resource use among taxa.

Unlike controlled experiments that manipulate only one factor (richness), observational studies, while they cannot unambiguously assign causation, enable an assessment of whether the mechanistic effects of richness identified in experiments are sufficiently strong to generate patterns in the context of natural variation in other important factors. Compared with terrestrial systems, there have been surprisingly few observational studies of resident diversity and invasion in the sea. A survey of sessile marine invertebrates in Tasmania found a positive correlation between the number of native species and the species richness (and to a lesser extent the abundance) of settlers (including both native and non-native species; Dunstan and Johnson 2004). They attributed the positive correlation to a combination of interspecific facilitation and low richness communities being dominated by a few large colonies, which were difficult to displace (Dunstan and Johnson 2004). Likewise, a similar study performed across several spatial scales found that the strength and direction of the relationships between native and exotic plant richness and cover in estuarine plant communities varied among sites and sampling scale (Bruno et al. 2004). Both these studies suggest that any negative effects of diversity are weak relative to other factors, and thus do not generate a negative relationship between native and invader richness in the field. In contrast, several studies have found negative correlations between native richness and invader abundance (White and Shurin 2007) or invader richness (Stachowicz et al. 2002a). Both of these studies also found that reduced diversity increased invasion success in experiments,

suggesting that native richness can be strong enough to generate patterns in some cases but can also be overwhelmed by other factors.

A paired experimental and observational approach to this question can clearly produce important insights, but experiments may be limited in their ability to rigorously manipulate multiple factors. Using a multiple regression approach, Stachowicz and Byrnes (2006) examined the context dependency of richness effects on invasion. They found that substrate heterogeneity and the availability of primary space markedly influenced the slope relationship. Specifically, the substrate heterogeneity and additional settlement space generated by a structurally complex bryozoan (*Watersipora subtorquata*) caused the native-invader richness relationship to shift from negative to positive (Fig. 12.3). Thus a negative relationship was only found when facilitators were rare and space was limiting, suggesting that the conditions

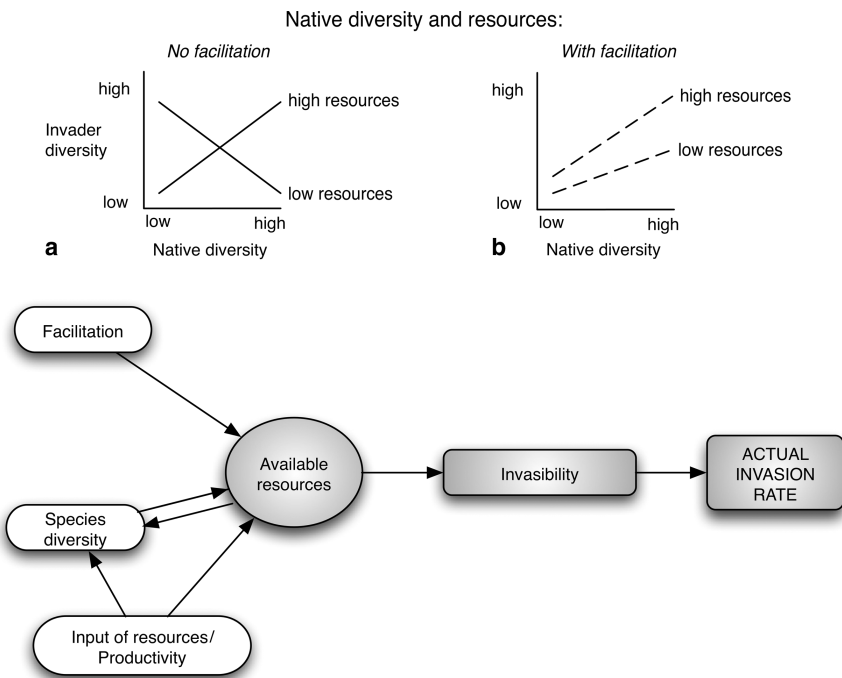


Fig. 12.3 Native diversity can interact with the resource pool to determine invasibility of a system. This concept derives from experiments in sessile invertebrate communities, where space is an important resource. **a** In a community where the amount of available space is limited, a more diverse assemblage of native species more fully co-opts the limiting resource, reducing invasion success through competition and biotic resistance. Where there is abundant space or very high levels of propagule supply, competition and biotic resistance are relatively unimportant and both native and invader diversity are determined by extrinsic factors (e.g. recruitment, disturbance, flow), creating a positive correlation (Levine 2000; Stachowicz et al. 2002a; Stachowicz and Byrnes 2006). **b** Where facilitation increases the availability of limiting resources (e.g., by providing space for secondary settlement), resource limitation is alleviated, overwhelming the negative effects of diversity on invasibility (Stachowicz and Byrnes 2006; see Sect. 12.5.1)

under which the effect of species richness on invasion is dominant are somewhat restricted. Terrestrial studies often agree, finding that the positive effects of heterogeneity or resource levels on both native and exotic richness drive the native-exotic richness correlation, particularly at larger spatial scales, whereas smaller scale negative relationships are often found, reflective of the limited heterogeneity at that scale (e.g., Shea and Chesson 2002; Davies et al. 2005; Fridley et al. 2007).

12.4.2 Large- vs Small-scale Studies

The change in the slope of the native-exotic richness relationship from negative to positive as one moves from small to large-scale observational studies is a bit more vexing than the difference between experimental and observational studies. There appear to be multiple, non-mutually exclusive explanations for the shift from a nearly universally positive slope at large spatial scales to variable slopes at smaller scales. Competition-based models suggest that at small scales, species interactions are strong, resulting in biotic resistance; across large scales, increased resources reduce interaction strengths, resulting in a higher probability of invasion success (Byers and Noonburg 2003). Indeed most studies of interspecific competition in sedentary or sessile organisms would support the idea that the effects of competition occur primarily at a neighborhood level. In contrast, Fridley et al. (2004) caution that random assembly of communities of neutral species also produce a negative relationship between native and exotic diversity at the smallest scales and a positive relationship at larger scales, so biological mechanisms are not required to produce these results.

Davies et al. (2005), building on the arguments of Shea and Chesson (2002), explained the invasion paradox as a consequence of spatial environmental heterogeneity. They showed that native and exotic richness at large scales were both positively influenced by variance in soil resources (such as soil depth), suggesting that shifts in competitive dominance of different species over a range of resource levels favor the coexistence of natives and exotics on scales where such heterogeneity emerges (Chesson 2000; Huston and Deangelis 1994; Tilman 2004). This theory and the temporally-based analogue of Davis J et al. (2002) are specific cases of more general ideas relating to the persistence of rare species (i.e., an invader) in a variable environment (Chesson 1994). The result is a consistently positive native-exotic richness relationship at large scales, where heterogeneity is virtually guaranteed. At smaller scales plots may be homogenous or heterogeneous, leading to higher variability in diversity-invasibility patterns. In their study of landscape scale patterns in shoreline plant communities, Bruno et al. (2004) found native and exotic richness were negatively correlated within some, but not most, sites (small scale), and were positively correlated across sites (larger scale). They suggested three mechanisms: (1) exotics could be facilitated by residents (see Sect. 12.5), (2) the factors that promote high native richness (e.g., high propagule supply, resource availability and favorable environmental conditions) could also enhance success of

exotics (see Sect. 12.4.1 and Fig. 12.3a), and (3) sampling artifacts could be driving positive native-exotic relationships (this section). The authors point out that none of these mechanisms preclude biotic resistance by native species, therefore a positive relationship should not necessarily lead to the rejection of the diversity-invasibility paradigm. Further, the shoreline habitats of New England are subject to frequent disturbance, which often acts to increase available resources and reduce competition, increasing invasibility (see Sect. 12.6).

A major cause of variation in small-scale heterogeneity may be the presence or absence of biogenic habitat structure (see also Sect. 12.5). In small-scale field surveys of native and invader richness, the slope of the relationship between native and invader diversity can change with the availability of resources (space) and the presence of habitat-forming foundation species (Stachowicz and Byrnes 2006). In these systems, negative relationships between native and exotic richness are only found when primary space is limiting and structure-forming species like mussels and head-forming bryozoans that provide habitat heterogeneity and additional settlement space are rare. We further explore the role of facilitation and resource provision in the next section.

12.5 Facilitation

So far we have focused on species interactions that decrease resource availability, but by their presence most species also create some resources. There are obvious examples that cross trophic levels, such as the presence of a plant providing food for herbivores, but others are more subtle and can act within guilds or trophic levels. For example, while a mussel holds space, its hard shell provides additional attachment surface that can alleviate space limitation for other sessile suspension feeders. Invasion biology, like ecology in general, has often focused on negative, resource-consuming interactions like competition and predation to the exclusion of facilitative interactions among species (Bertness and Callaway 1994; Bruno 2005; Bruno et al. 2003; Rodriguez 2006). However, native and exotic species can provide habitat or offer a refuge from physical stress or predation and thus could either directly facilitate non-native species or inhibit them by facilitating native competitors or predators (see also Chap. 16, Crooks; Chap. 17, Grosholz and Ruiz). In this section, we examine the direct and indirect effects of the presence of different types of positive interactions on available resources for exotic species in marine communities.

12.5.1 *Increasing Resource Availability*

Marine systems provide numerous examples of foundation species enhancing biological diversity by providing structure and substrate, and by reducing the effects of disturbance for organisms (Bruno and Bertness 2001; Bruno et al. 2003;

Rodriguez 2006; Stachowicz 2001). Both in subtidal and intertidal habitats, native mussels provide additional surface area for sessile invertebrates and a dense structural matrix for many smaller mobile invertebrates (Paine and Suchanek 1983). Mussel and oyster farms have severe problems with non-native fouling organisms such as the solitary sea squirts *Ciona intestinalis* (Carver et al. 2003) and *Styela clava*, as the hard shells provide ideal substrate for colonization by sessile invertebrates. Native kelp in the Gulf of Maine provides a substrate for the non-native bryozoan *Membranipora membranacea* (Berman et al. 1992) that normally resides on kelp in the Pacific (Dixon et al. 1981; Hepburn and Hurd 2005). The alga *Chondrus crispus* is host to a variety of non-native bryozoans and tunicates (Stachowicz and Whitlatch 2005). These relationships are commonly assumed to be parasitic or competitive, but they can be mutualistic, as the epibionts can provide associational defenses (Wahl and Hay 1995) or provide nutrients via their excretions (Hepburn and Hurd 2005; Hurd et al. 1994). Native species that support invaders as epibionts facilitate invasions in the same way that the construction of artificial jetties, breakwaters, oil platforms, and marinas and docks do – by adding available resources (space).

Provision of habitat for exotic species by already established non-native species follows similar patterns. The non-native mudsnail *Battilaria attramentaria* provides settlement substrate for the non-native slippershell *Crepidula convexa* and the invasive anemone *Diadumene lineata* in the mudflats of tidal estuaries in Washington State (Wonham et al. 2005). Often, these exotics facilitate the establishment of other non-native species in habitats where they could not have otherwise existed (see Fig. 12.3b). On boats covered with anti-fouling paint, the non-native bryozoan *Watersipora subtorquata* can settle in areas where the paint has chipped, and then create large foliose heads that provide settlement substrate and a means of dispersal for other non-native species (Floerl and Inglis 2005). The non-native worm *Ficopomatus enigmaticus* creates rocky reefs in the middle of soft-sediment estuaries, enabling a variety of other exotic species to enter an otherwise inaccessible habitat (Schwindt and Iribarne 2000).

In general, when exotic, habitat-forming species invade habitats lacking other foundation species, the consequences for community invasibility will be dramatic. However, when other native facilitators are present, the outcome is less clear. For example, although the invasive mussel *Mytilus galloprovincialis* serves the role of a foundation species in Sydney Harbor, it does not contain as high of an abundance or richness as adjacent native algal turfs (Chapman et al. 2005), nor does it contain any species that the turfs lack. In contrast, native-exotic hybrids of *Spartina* cordgrass in San Francisco Bay produce taller and denser stems, greatly decreasing habitat suitability for native infaunal species (Brusati and Grosholz 2006). Because interactions between habitat-forming species and their associates are relatively generalized, we see no reason why exotics or natives should, as a rule, benefit more from such interactions. However, even subtle differences in the types of habitat structure provided can dramatically alter composition of associated faunal communities, so comparative studies of the relative effects of native and non-native foundation species on the success of exotic (and native) species is clearly an area in need of greater attention.

12.5.2 *Ameliorating Physical Stress*

Species that have large individuals or that form dense aggregations often buffer the physical environment, making it more hospitable for smaller or less stress-tolerant species. For example, in physically stressful intertidal habitats canopy-forming algae and plants are known to facilitate the persistence of many species by reducing heat, desiccation, and/or salt stress (Bertness and Callaway 1994; Bertness and Hacker 1994; Bertness and Shumway 1993). Similarly, the non-native alga *Caulerpa taxifolia* experiences higher growth in the presence of native seagrasses due to lower water velocity that reduces blade fragmentation (Ceccherelli and Cinelli 1998, 1999). But as *Caulerpa* grows it can become larger than the seagrass bed that facilitated it, eventually overgrowing it, suggesting that these sorts of facilitative interactions may be most important during the early establishment phase of an invasion, as is true more broadly of the “nurse plant” effect (Callaway 1995). In many cases, exotic foundation species can stabilize the substrate (e.g., seagrass, marsh cordgrass or mat-forming bivalves), fundamentally altering water flow and disturbance regimes among many other effects. We provide examples of how these negatively affect natives and may positively affect exotics in Sect. 12.6.

12.5.3 *Facilitation Cascades and “Invasional Meltdown”*

There is some evidence that facilitation can lead to positive feedbacks among invaders that progressively increase the invasion susceptibility of a community. Resident organisms can make a habitat more easily invaded if they suppress the densities of potential predators or competitors of a newly arrived, non-native species. These types of facilitators can reduce the effect of both diversity and biotic resistance on invasion resistance. These facilitation interactions tend to be more likely in ecosystems that have been heavily affected by anthropogenic activities or are already heavily invaded, leading to “invasional meltdown” (Simberloff and Von Holle 1999).

For example, one of the major factors enabling the invasion of the Japanese alga *Codium fragile* ssp. *tomentosoides* in the Gulf of Maine was a dramatic increase in the native urchin *Strongylocentrotus droebachiensis* (Harris and Tyrrell 2001; Sumi and Scheibling 2005). Rising urchin densities were caused at least in part by declines in urchin predators due to overfishing (Steneck et al. 2002). *Codium* is a low-preference food for these urchins and is avoided until other native algae, particular the dominant bed-forming *Laminaria saccharina*, have been dramatically reduced or eliminated (Sumi and Scheibling 2005). This state change was facilitated by a second non-native species, the epiphytic bryozoan *Membranipora membranacea*, which encrusts native kelp, increasing its palatability to herbivores and its susceptibility to mechanical breakage (Dixon et al. 1981; Levin et al. 2002), facilitating *Codium* establishment. Interestingly, once established, *Codium* provides

substrate for a variety of non-native epibionts, propagating a cycle of invasional meltdown in the Gulf of Maine (Harris and Jones 2005; Mathieson et al. 2003).

A single species can also have impacts by both altering the competitive landscape and removing direct predators under different scenarios. The exotic European green crab *Carcinus maenas* has been implicated in at least two scenarios of facilitation of other exotic species. Much like urchins in the previous example, on the west coast of North America *Carcinus* has been shown to reduce the density of native clams, *Nutricola* sp., thereby releasing the formerly suppressed, non-native clam *Gemma gemma* (Grosholz 2005). On the east coast of North America, instead of reducing competitors, *Carcinus* removes a variety of small gastropods that would, in its absence, reduce the abundance of non-native fouling organisms through predation (Osman and Whitlatch 1998, 2004; Stachowicz and Whitlatch 2005).

12.6 Disturbance

Ecologists have long recognized that disturbances can facilitate non-native species (Byers 2002b; Clark and Johnston 2005; Elton 1958; Grosholz 2002; Occhipinti-Ambrogi and Savini 2003; Chap. 7, Johnston et al.). Although disturbance can be defined in many ways, we focus here on those forces (natural or human-caused) that remove native biomass and/or change environmental conditions, thereby increasing or creating available resources.

Despite the well-documented effects of natural disturbance on marine communities (Connell 1978; Dayton 1971; Sousa 1979), there are only a few documented cases of natural disturbances facilitating non-native invasions in marine systems (Nichols et al. 1990; Valentine and Johnson 2003). In contrast, there are numerous examples of anthropogenic disturbance such as physical disturbance, over-harvesting, and the presence of non-native species contributing to invasion success (Byers 2002a). It has been suggested that coastal areas such as estuaries, bays and lagoons are hotspots for invasions due to not only to the high rate of human-mediated transfer between these areas but also high rates of disturbance that either remove native biomass or alter physical conditions (e.g., pollutants, dredging, development, etc.) in such a way to facilitate exotic species (see Fig. 12.4; also see Chap. 33, Preisler et al.). As a corollary, one explanation for the relatively small number of invaders along the coast of Chile is a scarcity of sheltered areas that are more likely to attract human development and associated disturbance (Castilla et al. 2005).

To understand the role of disturbance in invasion success, it is important to identify whether the mechanism by which disturbance acts is direct (changing environmental suitability) or indirect (increased resource availability by reduction of native abundance). We first review examples of disturbance increasing available resources. Returning to an earlier example, seagrass beds are often fragmented as a result of physical disturbance from dredging and development; the non-native mussel, *Musculista senhousia*, grows best in disturbed eelgrass beds as compared to continuous

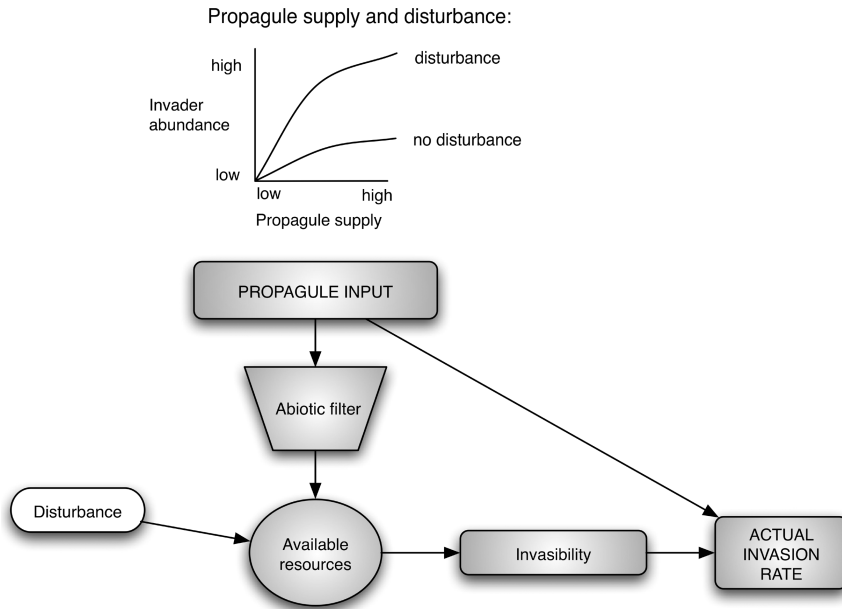


Fig. 12.4 Disturbance and propagule supply can interact to modify invader success. Invasion increases with propagule supply, but in the absence of disturbance or other factors that release resources, high levels of propagule input are needed for successful invasion because individual survival rates are low. Where disturbance is stronger, fewer propagules may be required for successful establishment. For example, in an experiment that controlled propagule supply, physical disturbance was shown to increase the invasion success of the introduced species *Bugula neritina* in sessile, marine invertebrate communities (see Sect. 12.6) (Clark and Johnston 2005; Chap. 7, Johnston et al.)

beds with slower flow rates and reduced food availability (Allen and Williams 2003; Reusch and Williams 1999). In another experiment that simulated anthropogenic impacts, physical disturbance increased space availability and the recruitment success of the non-native bryozoan *Bugula neritina*, although chemical pollution did not (Clark and Johnston 2005). In addition, non-native species can be a cause of disturbance to natives, facilitating the establishment of other non-natives, as discussed previously for the bryozoan, *Membranipora membranacea* (see Sect. 12.5.3).

In addition to removing species, natural or human-mediated disturbances can change habitat conditions and result in mismatch between native species and their environment (Byers 2002a). Such a situation can lead to a competitive advantage for non-native species if they are successful under the new conditions (Byers 2002a). In an experiment that controlled nonnative propagule supply, Crooks et al. (unpublished data) found that native diversity declined significantly with increasing concentrations of copper, a common pollutant from boat-bottom paint, while exotics did not. Although there are few experimental data, evidence from marine

systems suggests that human-mediated eutrophication enhances the survival and growth of non-native species by creating conditions that are unfavorable for native species (Allen and Williams 2003; Byers 2002a; Occhipinti-Ambrogi and Savini 2003). In addition to disturbing native species directly (see above), the presence of other non-native species can also result in abiotic and/or biotic environmental change that is detrimental to native species (Byers 2002a; Grosholz 2002; Levin et al. 2002; Neira et al. 2005). In particular, non-native foundation species such as the *Spartina alterniflora*-*S. foliosa* hybrid in San Francisco Bay, (Brusati and Grosholz 2006; Neira et al. 2005) or the mussel *Musculista senhousia* (Crooks and Khim 1999) can greatly alter habitat characteristics (e.g., sediment organic content, light availability, physical and structural complexity) reducing the fitness or abundance of natives, and in some cases, facilitating exotics. A major source of disturbance (anthropogenic and natural) that can directly facilitate invasions is rising ocean temperatures as a result of global climate change (Harley et al. 2006). Temperature increases from climate change have facilitated range expansions of many tropical and subtropical organisms into temperate areas (Barry et al. 1995; Beare et al. 2004; Perry et al. 2005; Southward et al. 1995). In many instances, the success of non-native species may depend on the magnitude of temperature extremes (minimum and maximum) in certain seasons, instead of increases in mean temperature. For example, warmer winter temperatures accelerated the seasonal timing of recruitment of invasive tunicates in New England, such that in warm years exotics recruited before natives, whereas in colder years the reverse was true (Stachowicz et al. 2002b). Temperature extremes had similarly opposing effects on the magnitude of recruitment of native and exotic species. In no cases was there any effect of annual mean temperature on recruitment of natives or exotics. In concert, the results suggest that decreasing severity of New England winters over the past two decades has likely facilitated the shift in dominance of fouling communities to recent invaders. Finally, interactions between human-driven alterations in biotic pressure (e.g. overfishing of top predators) and climate (ocean warming) is also thought to have accelerated shifts in entire communities, for example the dramatic shift to an exotic-dominated community assemblage in the subtidal areas of the Gulf of Maine discussed above (Sect. 12.5.3) (Harris and Tyrrell 2001).

Another important consideration for predicting habitat invasibility is the timing of disturbance in relation to the arrival of invader propagules (Clark and Johnston 2005; Chap. 7, Johnston et al.). For example, experimental removal of the native algal canopy just prior to recruitment of the non-native kelp *Undaria* facilitated the introduction to a greater degree than when the disturbance occurred after the recruitment pulse (Valentine and Johnson 2003). Presumably early life history stages of many invaders cannot persist long in established communities of natives, but may thrive when native biomass is decreased. Interestingly, disturbance is not critical for the persistence of *Undaria* in this system; once established, *Undaria* can persist even in the absence of grazing urchins (Valentine and Johnson 2005). Prolonged disturbance can reduce natives to sufficiently low abundance that even if the disturbance ceases, recolonization by natives is slow and perhaps recruitment

limited, so systems remain dominated by exotic species unless natives are artificially restored (Seabloom et al. 2003).

We close this section with several generalizations that have recently emerged from work on the disturbance – invasibility relationship in freshwater and terrestrial environments that have yet to be fully examined in marine systems (Lozon and MacIsaac 1997). First, non-native species may be more likely to be associated with human disturbances than natural ones (Lozon and MacIsaac 1997), which is supported by the qualitative trend in the marine literature. Second, disturbance is more important to the success of plant than animal invasions in terrestrial systems (Lozon and MacIsaac 1997); similar comparisons might hold for mobile vs sessile organisms in marine communities, but few comparative data are available. Third, assessing causation to disturbance, per se, is difficult because disturbance often co-varies with many other factors that also influence resource supply and niche space (e.g., biotic resistance, species diversity, propagule supply (Clark and Johnston 2005; Connell 1978; Davis MA et al. 2002; Klein et al. 2005; Naem et al. 2000) and because invaders themselves may cause significant changes in disturbance regimes. Careful, multifactorial experiments will be needed to help address this issue.

12.7 Historical Context

In this chapter we have reviewed how abiotic conditions (resource availability and disturbance) and biotic interactions (competition and facilitation) and the interaction between the two affect the relative abundance of invaders in marine communities. We would be remiss, however, if we did not emphasize that a community's history – on both geologic (Daehler and Strong 1996; Vermeij 1991a, 2005) and ecological timescales (Davis MA and Pelsor 2001; Grosholz 2005; Vitousek et al. 1996) can affect the probability and course of an invasion.

Large-scale geological invasions of species (i.e., biotic interchanges) between two or more regions have occurred several times in the past, for instance the Trans-Arctic interchange between the North Pacific and North Atlantic via the Bering Strait 3.5 Ma (Vermeij 1991a, b). Vermeij observed that most of these interchanges involved asymmetrical movements of species from one geographic donor region to another receiver region, and he found that the number of invaders to a region was proportional to the number of species that had gone extinct there (the “ecological opportunity” hypothesis). Species poor regions were disproportionately invaded by species from species rich invasions. For example, the rocky-shore fauna of the Northwest Atlantic suffered a catastrophic extinction event in the early Pliocene, dramatically reducing species diversity. During the subsequent Trans-Arctic interchange the majority of species involved (for example, 261/295 of mollusc fauna) migrated from the North Pacific to the Northwest Atlantic (Vermeij 1991a, b). On a shorter geologic timescale, many have noted that the exceptionally high invasion rate of U.S. Pacific coast estuaries may be related to the fact that the estuaries are geologically “young” (i.e., they formed less than 10,000 years ago) and are therefore

species poor (Cohen and Carlton 1998; Daehler and Strong 1996). And on an even shorter timescale, the degree of “saturation” of a community (or lack thereof) appears to be relevant for ecological timescales as well. Moyle and Light (1996) noted that freshwater fish invaders were more successful in streams that had recently suffered a catastrophe (e.g., a major flooding event), and human-caused extinctions and local extirpations have also been shown to make a community susceptible to invasion (as discussed in Sect. 12.6).

12.8 Conclusion

Most of the studies we have reviewed focus on one or perhaps two of the various factors affecting habitat invasibility; studies that consider the interaction among factors are rare. Yet Fig. 12.1 clearly illustrates that many factors simultaneously affect resource availability both directly and indirectly. A major priority for invasion biology (and community ecology) is to assess the relative roles of these factors in determining community composition, and how these relative roles change across environmental gradients. A promising avenue for untangling these relationships is to conduct factorial experiments with factors that are often related, for example, disturbance and propagule supply (Clark and Johnston 2005). Where multifactorial experiments are not feasible, or where larger spatial scales are desirable, careful correlative studies that measure a range of covariates can be very useful (e.g., Stachowicz and Byrnes 2006).

A number of the relationships in Fig. 12.1 have been depicted as unidirectional when in fact they may be bi-directional, leading to the potential for feedback. For example, disturbance affects diversity but diversity may also affect the susceptibility of communities to disturbance (Sect. 12.6). Given that each of the factors alone can affect invasibility in different ways, it seems important to understand how their interactive effects might differ from their effects in isolation (see Figs. 12.3 and 12.4 for conceptual models).

Finally we suggest that a diversity of approaches and study systems will aid in developing more robust generalities in invasion biology. Our focus on resource availability is driven in part by the bias in invasion ecology toward the study of sessile or sedentary taxa; if mobile taxa are less resource-limited, then perhaps other factors drive differential patterns of invasion in these groups (but see France and Duffy 2006). Similarly, more explicit recognition of the benefits as well as the limitations of both experimental and observational approaches will clarify our thinking and reduce misunderstandings. Indeed, the literature in both invasion biology and general ecology shows that studies that combine these approaches often reach robust conclusions (Levine 2000; Stachowicz et al. 2002a; White and Shurin 2007). We urge experimentalists to complement their studies with larger scale experiments, and vice-versa. Simultaneous application of both approaches in the same system should enhance our ability to connect pattern and mechanism in invasion biology.

Acknowledgements We thank L. Rodriguez and two anonymous reviewers for comments on a previous draft of the manuscript and the editors for the invitation to participate in this project. We also acknowledge support from the National Science Foundation Biological Oceanography Program (to JJS) and Graduate Research Fellowship program (to SVO, ARH, and KMH).

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