

4 Biological Invasions: Concepts to Understand and Predict a Global Threat

GERARD VAN DER VELDE, SANJEEVI RAJAGOPAL,
MIRJAM KUYPER-KOLLENAAR, ABRAHAM BIJ DE VAATE,
DAVID W. THIELTGES, and HUGH J. MACISAAC

4.1 Introduction

Charles Elton was the modern founder of the science of biological invasions. He wrote that 'biological invasions are so frequent nowadays in every continent and island, and even in the oceans, that we need to understand what is causing them and try to arrive at some general viewpoint about the whole business' (Elton 1958). He tried to predict the outcome of global invasion processes and assumed that invasions would result in homogenization of regional floras and faunas. The prediction of homogenization was formulated earlier by Lyell (1832) who, in contrast to Elton (1958), did not consider the resulting human-caused extinctions to be a cause of concern because, in his opinion, this was a natural process (Wilkinson 2004). Interest in biological invasions has rapidly increased in recent decades and today biological invasions are a major concern in ecology and conservation. Particularly dramatic consequences of invasions have been reported from island ecosystems where endemic species suffered severely, but wetlands (marshes, lakes, rivers) and estuaries are also among the most affected systems (Moyle 1996; Williamson 1996; Ruiz et al. 1997). On the background of accelerating invasion rates, science has become increasingly interested in understanding the underlying mechanisms of biological invasions to predict invasion processes and impacts. Following a brief overview on the nature and impacts of invasions, we review different concepts regarding determinants of invasion success. We also highlight promising research areas to cope with this major threat to biodiversity in wetlands.

4.2 What is a Biological Invasion?

Biological invasions are natural phenomena and simply refer to range expansions of species into new areas. This can happen, for example, by drifting dispersal stages that eventually reach new areas (e.g. Censky et al. 1998) or when biogeographic barriers disappearing over geological times, as with the Isthmus of Panama, thereby allowing the mixing of formerly separated biota (Vermeij 1991). However, what concerned Elton and today's scientists is the human-mediated disappearance of biogeographic barriers through global transport and trade. For example, human-mediated dispersal exceeds natural dispersal to the Great Lakes by nearly 50 000-fold (Hebert and Cristescu 2002). Invasions result in the presence of an increasing number of species in areas where they have not been recorded in historical times.

There is a multitude of terms used in the scientific literature to name these species: introduced, non-indigenous, non-native, invasive, exotic, naturalized, immigrant and alien species, just to name a few. Sometimes these terms are used as synonyms but more often they are (explicit or implicit) defined quite differently (Colautti and MacIsaac 2004a; Occhipinti-Ambrogi and Galil 2004). Hence unfortunately no common terminology currently exists, making it difficult to compare studies on biological invasions. The problem is further complicated by the fact that biological invasions always happen in certain steps, which make an analysis of each appropriate (Colautti and MacIsaac 2004a). However, for the purpose of this contribution, we employ a very basic definition of introduced species: Introduced species are those that have been – intentionally or unintentionally – transported by human activities into an area where they did not occur before and where they now reproduce successfully.

How does human-mediated transport happen? One possibility is of course the intentional introduction of a species by man for purposes like aquaculture and agriculture. Another possibility is the unintentional introduction as a by-product of human activities. In aquatic systems, the transport of ballast water by ships is a major vector for introduced species globally. Larvae and also some adult stages often survive transit in ballast tanks and colonize when released into new waters (Carlton and Geller 1993). Ships can also serve as vectors by carrying fouling organisms on their hulls and anchors. This happens not only on large commercial vessels but also on smaller boats for recreational purposes (Minchin and Gollasch 2003). Fouling organisms can also be transported by drilling platforms, dry docks, navigation boys, floating debris and amphibious planes. Canals are another important pathway for invaders, connecting formerly separated biogeographical regions (Bij de Vaate et al. 2002). In addition, pet, water-garden and horticulture industries are sources of (un)intended introductions by animal releases and garden escapes (Courtenay and Stauffer 1984; Ruiz et al. 1997; Maki and Galatowitsch 2004; Rixon et al. 2005; Duggan et al. 2006).

The number of introduced species can be related to the number of introduction events and to the number of individuals introduced per event. This is why wetlands, especially freshwater, estuarine and coastal environments, are amongst the most invaded ecosystems worldwide, particularly in temperate regions (Moyle 1996; Ricciardi and MacIsaac 2000; Ricciardi 2001). These ecosystems are particularly vulnerable to invasions because they are subjected to numerous introduction vectors and activities that facilitate invasions (e.g. water diversions, shipping, recreation). Primary introductions often result from the accidental transport of species, mostly by one or a limited number of vectors. Subsequently, secondary expansion of the introduced species-range follows from the initial place of establishment and normally includes a wider range of vectors acting separately or together.

4.3 Impacts of Biological Invasions

Impacts of biological invasions can be ascribed to four different classes: ecological, evolutionary, economic and human health.

4.3.1 Ecological Impacts

Impacts of biological invasions can be found on all levels of the ecological organisation: individuals, populations, species, communities and ecosystems. The mechanisms by which an introduced species can exert impacts on native species are competition, herbivory, predation, parasitism, vectoring of pathogens and through physical or chemical modifications of habitats. Especially dramatic impacts can occur when introduced species function as keystone species or ecosystem engineers, thus affecting the functional diversity and food web structure of communities and ecosystems (Vitousek 1990; Crooks 2002). A prominent example for such a dramatic effect is the Asian clam *Potamocorbula amurensis*, which caused strong changes in phytoplankton production in San Francisco Bay and thus altered the entire food web in the bay (Alpine and Cloern 1992; Kimmerer et al. 1994; Cloern 1996). Another dramatic effect is the extinction of native species due to an introduced one. For example, the introduction of Nile perch (*Lates niloticus*) into Lake Victoria is believed to have caused up to 200 extinctions of native cichlid fishes (Kaufman 1992). Similarly, Blackburn et al. (2004) showed that the probability of native bird extinction on oceanic islands was positively correlated with the number of introduced predatory mammal species present. Indeed, introduced species are the second-leading cause of species extinction, following habitat destruction (e.g. Wilcove et al. 1998; Ricciardi and Rasmussen 1999). While the severity of introduction-induced species extinctions is hotly debated

(Gurevitch and Padilla 2004; Ricciardi 2004), it is clear that introduced species can have strong ecological impacts on native biota.

4.3.2 Evolutionary Impacts

Evolutionary impacts arise mainly by removing or lifting natural dispersal and reproduction barriers that prevented hybridization between closely related invading and native species (Mooney and Cleland 2001; Grosholz 2002; Olden et al. 2004). This prevents allopatric speciation and could restrict future biodiversity. It also alters genetic diversity and could result in outbreeding depression, one consequence of which could be reduced disease and parasite resistance. Besides these direct effects of invaders on the genetic architecture of native species, indirect effects may occur through changes in selection pressure on native populations. The introduction of predators can also affect selection for size, growth, distribution and behaviour of native species (Vermeij 1982; Trussel 1996). As an example, introduced predatory fishes often result in altered habitat use by prey species.

4.3.3 Economic Impacts

Economic impacts result from the effects of introduced species on native biota, as well as funds expended to control or mitigate invasion effects (Perrings et al. 2001). Expenses may include quarantine, control or eradication programmes. In aquaculture and agriculture, introduced species can reduce harvest quantity or quality and require costly prevention or eradication methods. Introduced species can also affect technical constructions: preventing the clogging of power plant water pipes by fouling zebra mussels *Dreissena polymorpha* costs about \$ 8×10^6 per year in Canada (Colautti et al. 2006a). The wood-boring bivalve *Teredo navalis*, the shipworm, causes severe problems with harbour constructions and ships in ports worldwide and causes about U.S.\$ 205×10^6 per year damage in the USA (Cohen and Carlton 1994). In addition, in one of the most thorough economic assessments ever, Knowler and Barbier (2000) estimated that the invasion of North American comb-jelly (*Mnemiopsis leidyi*) into the Black Sea resulted in an annual 'rent' (i.e. profit) decline from U.S.\$ 17×10^6 to U.S.\$ 0.3×10^6 for the anchovy fishery of the region. In the United States, the purple loosestrife (*Lythrum salicaria*) caused an estimated damage of U.S.\$ 45×10^6 per year, exotic aquatic weeds (53 species!) cost U.S.\$ 110×10^6 per year, the European green crab (*Carcinus maenas*) U.S.\$ 44×10^6 per year, the zebra mussel (*D. polymorpha*) U.S.\$ 1000×10^6 per year and the Asian clam (*Corbicula fluminea*) U.S.\$ 1000×10^6 per year (Pimentel et al. 2004). Extrapolations of

damage and control costs for introduced species typically run into billions of dollars per year for individual countries (Pimentel et al. 2000, 2001, 2004; Colautti et al. 2006a).

4.3.4 Human Health Impacts

Human health can be affected by introduced species either directly by introduced nuisance species or indirectly by introduced species acting as vectors for human pathogens. For example, the Yellow fever (*Aedes aegypti*) and Asian tiger (*Aedes albopictus*) mosquitoes were introduced to North America and also to other localities worldwide. Asian tiger mosquitoes entered via residual water contained in scrap tyres from Japan. Besides being a nuisance species, they also serve as a vector for a range of human diseases like mosquito-borne encephalitis viruses as well as the dengue virus and possibly the West Nile virus (Moore et al. 1988; Mitchell et al. 1992; Gratz 2004; Juliano and Lounibos 2005). Another example is the unintentional introduction of the fresh water snail *Bulinus truncatus* into Ghana and Jordan, together with the trematode parasite *Schistosoma haematobium* which utilises these snails as first intermediate host and which causes schistosomiasis in humans (Burch et al. 1989; Hunter et al. 1993). Introduced species may operate in concert with other introduced or native species to impact humans, wildlife or ecosystems (Juliano and Lounibos 2005).

4.3.5 Measuring Impacts

A large gap exists in our knowledge of impacts for the majority of introduced species. Most reports on impacts are anecdotal and experimental studies are extremely rare. Part of the problem, of course, is that interest in an introduced species typically arises only after it is already abundant and has caused notable impacts. Hence, before–after, control–impact (BACI) study designs, are difficult to employ (Osenberg et al. 1994; Underwood 1994). Nevertheless, solutions for this methodological problem could be gained through comparisons between already-affected and not-yet-affected local areas and through experimental introductions in contained or quarantine areas. Better spatial and temporal considerations in biological introductions studies are required specifically; and impact studies on larger spatial and temporal scales from studies that involve more than one invading species are also required (Grosholz 2002).

When conducting impact studies, it is important to clarify what constitutes an impact. This is especially helpful if we want to compare the severity of impacts by different species or impacts of the same species at different localities. So far, no common measurement of impact is available. Parker et al.

(1999) provided a formula (Eq. 4.1) to calculate the overall impact (I) of a species, as:

$$I = R \times A \times E \quad (4.1)$$

with R being the range size, A the abundance and E the effect per individual or biomass of the invader.

Although helpful in conceptualizing factors that influence impact, the formula is not explicit with respect to the currency to measure effects or how one could compare effects of different species. This field of research needs to be explored in more detail.

The most crucial point with biological invasions is the evaluation of observed impacts. Although science can assess changes to native biota from introduced species, the evaluation of this impact is not a matter of science alone. For example, it is not the role of the scientist to determine whether invasions are good or bad, nor whether introduced species are 'evil'. Such pre-judgments have been related to xenophobic and racist motives (e.g. Simberloff 2003). Whatever the motives, scientists can only report changes induced by invaders. Whether these changes are good or bad is a matter of public and political debate. Introduced species are not by definition negative and unwanted, as most crops grown today could be classified as introduced. There is common agreement that they are beneficial. The scientist thus focuses attention principally on negative impacts of introduced species.

4.4 Examples of Biological Invasions

Typical pathways of invasions and impacts of introduced species in wetlands are exemplified by four examples from an internationally important coastal wetland, the Wadden Sea in Europe (Fig. 4.1). *Crassostrea gigas*, the Pacific oyster, was introduced to the Wadden Sea for aquaculture decades ago, but rapidly spread from culture plots to native mussel beds; and this pattern of spread now threatens native communities (Reise 1998). Since oysters are effective filter feeders and occur locally in high abundance, they exert strong trophic effects. With oyster aquaculture, the associated epifauna and infauna species, including algae and tunicates which themselves are non-native species, have unintentionally been introduced (Wolff and Reise 2002). Another prominent example of unintentional introduction via aquaculture is provided by *Crepidula fornicata*, the American slipper limpet, which arrived in Europe with early imports of American oysters in the 1870s. This species is now superabundant in parts of its range, causing high economic impacts on oyster and scallop fisheries, especially in France (Blanchard 1997; Thieltges et al. 2003). Ecological impacts are still disputed but in blue mussels (*Mytilus*

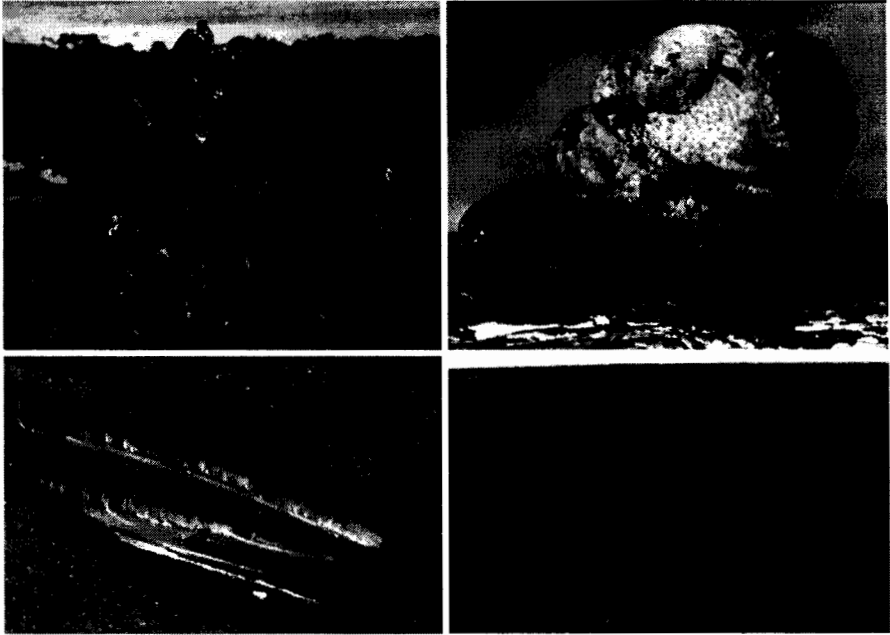


Fig. 4.1 Four examples of introduced species and their invasion pathways from a single coastal wetland ecosystem, the European Wadden Sea. **A** An intentional aquaculture introduction, *Crassostrea gigas*, the Pacific oyster, forming dense oyster beds. **B** An unintentional co-introduction with aquaculture, *Crepidula fornicata*, typical stack of American slipper limpets on their blue mussel (*Mytilus edulis*) substrate. **C** An introduction as larvae in ship ballast water, *Ensis americanus*, shells of the American razor clam. **D** An intentional introduction for coastal protection, *Spartina anglica*, cordgrass

edulis), a major substrate for slipper limpets in the Wadden Sea, the species strongly reduces survival and growth and thus affects native mussel beds and the mussel fishery (Thieltges 2005). Besides aquaculture, ballast water of large vessels is another major vector for introduced species in wetland ecosystems. By this mode of translocation *Ensis americanus*, the American razor clam, arrived as larvae in 1978 in the German Bight. From there it spread very rapidly along European coasts, where it now constitutes the major fraction of subtidal biomass in many areas of the Wadden Sea. Impacts on native biota, however, are difficult to assess since sampling of the very fast burrowing clams is difficult. However, since it is a very abundant filter feeder, trophic effects can be expected (Armonies and Reise 1999; Armonies 2001). Other human activities, like land reclamation and coastal protection, can also serve as introduced species vectors to wetlands. Originally introduced for coastal protection in the 1920s, the cord grass *Spartina anglica* (a fertile hybrid between *S. maritima* and *S. alterniflora*) spread on the upper tidal zones of tidal flats and in the seaward ends of native salt marshes, often forming an

almost monotypic belt. The plants retain sediment and displace native species like *Salicornia stricta*, glass word, *Zostera noltii*, seagrass, and *Arenicola marina*, the lugworm, and its associated species (Reise et al. 2005).

All four species co-occur in the Wadden Sea, indicating the high abundance of invaders in a single wetland ecosystem and the multiple pathways of introduction. Along North Sea coasts, more than 80 introduced species have been identified, of which about 40 occur in the Wadden Sea (Reise et al. 2002). The full array of impacts of the invaders remains to be investigated.

4.5 Understanding and Predicting Biological Invasions

Before we can predict invasions, we have to understand the underlying mechanisms of invasion and determine whether there are general patterns or whether every invasion is a unique event. Three different questions can be asked in predicting biological invasions: (1) which species will successfully establish? (2) when, where and how fast will a species invade? and (3) what will be the impact of an introduced species? Different approaches have been utilized to address these questions:

1. Determine characteristics of the invading species that make it invasive.
2. Determine characteristics of the ecosystem that make it susceptible to invasion.
3. Investigate the relationship between invader and invaded ecosystem (key-lock approach). In this approach, it is assumed that the invading species is successful when its characteristics are suited to the specific conditions in the ecosystem that is to be invaded.
4. Explore the invasion process by addressing different stages that an introduced species pass through in order to successfully invade an ecosystem. This approach is based on the premise that during every phase, the characteristics of the invader have to fit the specific conditions of the ecosystem.
5. Comparative historical approach: finding similarities and differences in invasion dynamics across ecosystems and extrapolating them across species or systems. This remains an important objective for invasion ecology, since experimental approaches are often impractical or unethical (Unmack and Fagan 2004).

4.5.1 Invading Species Approach

Early research on invasions assumed that introduced species which spread must have certain characteristics making them successful (Rejmanek and Richardson 1996; Mack et al. 2000; Richardson et al. 2000). For example, among the attributes that have been ascribed to a successful plant invader are

a high dispersal rate, early fruiting, high fecundity, high growth rate, vegetative reproduction and a high tolerance of a wide range of physical conditions (Lodge 1993). For animal invaders, features of successful invaders that have been frequently cited include: early sexual maturity, asexual reproduction, large size, ability to colonize a wide range of habitat types, high genetic variability, high phenotypic plasticity, gregarious behaviour, omnivory, high reproductive capacity, high dispersal rates and an association with humans. Theoretical arguments to detect invasiveness characteristics in species that establish or proliferate in new habitats are given by many authors (e.g. see Colautti et al. 2006b and literature therein).

Using these attributes to explain why certain introduced species overrule natives while others do not is not always possible. None of the characteristics is by itself suited to discriminate between invasive and non-invasive species. These attributes could instead be interpreted as those of an 'ultimate invader' and it may well be assumed that species that possess more of these characteristics are more likely to be successful invaders. The 'invading species approach' is still a frequently used method to predict invasion.

Williamson (1999) pointed out serious disagreements among three studies since 1995 that sought common traits among Britain's invasive plants. One study found that large seeds favoured invasions, in a second the opposite was found, while the results of a third indicated that the size did not matter. Likewise, Colautti et al. (2006b) found little support for the concept that invasive species possess greater physiological tolerance than their non-invasive counterparts.

Propagule Pressure

A species' invasiveness can also be increased by merely repetitive and extensive introduction. Robert Pemberton, a weed scientist with the USDA Agricultural Research Service in Fort Lauderdale, Florida, recently examined old catalogues from the Royal Palm Nurseries, a well known, trend-setting company that bred and sold plants in Manatee County, Florida, from 1881 to 1937. He discovered that plants sold for just one year had only a 2% chance of establishing in the wild, while popular species that were in the catalogue for over 30 years had a 69% chance of establishing. These results are consistent with an introduction effort (or propagule pressure) hypothesis to explain invasion establishment success (Andow 2003).

Before physiological factors and positive or negative biological interactions can affect invasion success, viable propagules must arrive at the novel habitat (Lockwood et al. 2005). Colautti et al. (2006b) found that propagule pressure as well as anthropogenic activities were the best predictors of invasion success. Propagule pressure (measured as the number of introductions and the number of propagules introduced) was considered in only 29% of

studies, yet was a consistent predictor of both invasiveness and invasibility in 55 out of 64 cases. Considering that non-indigenous species are almost always introduced non-randomly, propagule biases caused by a failure to consider propagule pressure may confound current paradigms in invasion ecology (Colautti et al. 2006b). Colautti et al. (2006b) concluded that propagule pressure should serve as a null model for studies of biological invasions when referring process from patterns of natural invasions. Duggan et al. (2006) state that propagule pressure is frequently mentioned as an important determinant of invasion success for terrestrial taxa, but its importance for aquatic species is unclear. They demonstrated, however, that clear relationships exist between the frequency of occurrence of aquarium fish in shops and the likelihood of introduction and establishment. Introduced and established fish caught in the wild were also typically larger than in aquaria, in accordance with the fact that these fishes were mostly released when they outgrew their aquaria. Reducing the number of introductions is the most simple way to reduce the number of successful invasions. Lonsdale (1999) found that the number of introduced plant species established in reserves was positively correlated with the number of visitors, implicating human-mediated propagule pressure. Introduction effort was also the best predictor of invasion success for introduced birds in New Zealand (Forsyth and Duncan 2001). Given the importance of propagule pressure to invasion success for so many different taxa, it would be reasonable to conclude that the best way to reduce future invasions would be to control the number of introductions.

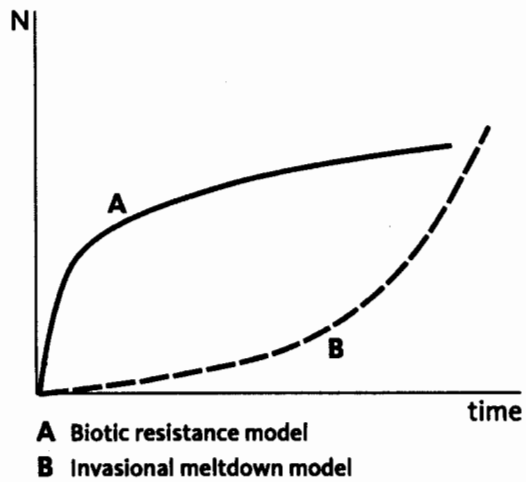
4.5.2 Invaded Ecosystem Approach

Species Richness: Biotic Resistance Model

A long-standing theory to predict invasion success is that ecosystems with high native diversity – with their dense, interconnected webs of ecological relationships – can resist invasions better than those with fewer species (Elton 1958; Lodge 1993; Fig. 4.2). Subsequent works on species packing in a community by Robert MacArthur (1970) and others were consistent with this concept. Why should diversity affect invasibility? One might expect more diverse assemblages more fully utilize the available resources, thus leaving less space for individuals of new species (Levine and D'Antonio 1999). This is an extension of the 'empty niche' concept in ecology.

Stachowicz et al. (1999) provided support for this theory. He created artificial marine epifaunal ecosystems with anywhere from zero to four North Atlantic sessile suspension-feeding invertebrates, with all systems beginning with the same initial cover of native species. Space was the limiting factor in these systems. He then introduced a known invader, the Pacific tunicate

Fig. 4.2 Temporal trend in the cumulative number of successful invasions, as predicted by the biotic resistance model and the invasional meltdown model (after Ricciardi 2001)



Botrylloides diegensis into these communities. The more species initially present, the lower was the tunicate's subsequent survival (Stachowicz et al. 1999). In addition, Kennedy et al. (2002) found in their grassland plots that invasion success increased in plots with decreasing diversity. Species diversity appeared to enhance invasion resistance by increasing crowding and species richness in localized plant neighbourhoods. Both the establishment (number of invaders) and success (fraction of invaders that are large) of invading plants were reduced. These results suggest that local biodiversity represents an important defence mechanism against the spread of invaders. However, the resulting effects on biodiversity depend on the spatial scale considered: while local species richness increases with species introductions, globally the opposite effect can be observed (Sax and Gaines 2003).

The invasion processes on islands, which usually have fewer species than comparable areas of mainland, offer some support for this theory (Elton 1958). Islands are often the most heavily invaded. However, a large problem with studies that find that invaded communities are less diverse than their non-invaded counterparts is that the results are likely to reflect the impact of the invader on the native diversity and not that of diversity on the invader. In other words, cause and effect may be confounded. More diverse communities are also more likely to contain species with a strong impact on invasibility, whether deterring or facilitating invasions. How invasibility varies with diversity in natural systems is further complicated by the fact that variation in diversity is controlled by and thus covaries with disturbance, resource availability, physical stress, competitors and consumers. Also, low-diversity patches may often be the least invisable when the low diversity results from competitive dominance by one or a few species (Levine and D'Antonio 1999). Some recent studies contradict the island:continent paradigm. For example, Lonsdale (1999) determined that

island:mainland nature accounted for only 13 % of the variance in introduced species richness, while native species diversity and habitat area accounted for much more variation (23 % and 22 % respectively). Similarly, Blackburn and Duncan (2001) found that island:mainland status were unable to explain patterns in the invasion success of introduced birds on islands; and they concluded that there was little support for the biological resistance hypothesis. Simberloff (1995) argued that islands were more heavily impacted by invasions (rather than being more invaded) than comparable mainland areas because the invasions often involved certain taxa (e.g. predatory mammals) that were missing entirely from islands and that these absences predisposed the islands to greater impact once those species were introduced.

Invasion theories about resistance have always been made on the basis of island-like or very small-scale invasions. Island-like models cannot be generalized to systems in which species arrive in greater frequencies or densities similar to the case on the mainland (Hewitt and Huxel 2002). Many assumptions are made when building assembly models which try to explain and predict invasions. Some of these assumptions are:

1. The Lotka–Volterra equilibrium is present in the invaded ecosystem, which assumes well mixed populations, so that all species interact with a potential invader. This restricts the applicability to the neighbourhood scale at which all component species interact.
2. The interactions of the invader are similar to those of the resident species.
3. A community is invulnerable if the invader persists at equilibrium. Invaders that fail to persist in communities at equilibrium may still strongly impact these systems.
4. In all of the models, the communities have reached equilibrium prior to the invasion, a state rarely reached by natural systems (Levine and D'Antonio 1999).

Hewitt and Huxel (2002) utilized assembly algorithms similar to those used in previous studies (the Lotka–Volterra model from Drake 1990), which made several more assumptions including: (5) only one species invaded per time-step and (6) invasions occurred at low densities relative to Lotka–Volterra equilibrium densities. In this study, they allowed either two species to invade per time-step (assumption 5 tested), or single species invasions at relatively high inoculation rates (assumption 6 tested). Their results showed that invasion resistance only occurred when the invasion process was restricted to single species invading at low densities (Hewitt and Huxel 2002). Moore et al. (2001) simulated plant community assemblages and tested four different mechanisms of co-existence. Their results suggest that species richness does not necessarily correlate with saturation (number of niches occupied) and is a poor predictor of invasion resistance.

Levine and D'Antonio (1999) reviewed theoretical and empirical work linking species diversity and invasions. They found that it was not possible to

prove experimentally the existence of biotic resistance; and empirical studies have not produced consistent results. Similarly, Ricciardi (2001) found that there is no convincing evidence that rich aquatic communities resist invasion when organisms are introduced frequently. If abiotic conditions are suitable and dispersal opportunities exist, aquatic species will likely invade regardless of the composition of the resident community (Ricciardi 2001). Therefore, as human activities and transports continue to decrease the isolation of regional floras and faunas from each other, the numbers of species and densities of introduced invaders will increase and result in higher susceptibilities to invasion in recipient ecosystems (Hewitt and Huxel 2002). For example, the toxic dinoflagellates (including *Alexandrium catenella* and *Gymnodinium catenatum*) were spread across Australia by ballast water, while the mussel *Mytilus galloprovincialis* and even some fish species also used ships for travelling around the world (Apte et al. 2000; Lockett and Gomon 2001). Carlton and Geller (1993) termed the mass transfer of species globally in ballast tanks 'ecological roulette'.

Facilitating Invasions: 'Invasional Meltdown' Model

Up to this point, the focus has been on biotic resistance: negative interactions between native and non-indigenous species, mostly resource competition and interference. It is also possible, however, for the opposite process, facilitation, to increase invasion rate as communities become more diverse (Bruno et al. 2003). This means that a species already established in a community (native or non-native) facilitates invasion by a second species. If this is the case with two non-native species, invasional meltdown may occur, with every new introduced species making it easier for subsequent ones to establish. This results in an accelerating accumulation of introduced species rather than a deceleration, as envisioned in the biotic resistance model (Simberloff and von Holle 1999; Fig. 4.2).

There is a great variety of ways in which different non-native species can facilitate one another. For example, animals pollinate and disperse plant seeds; and animals or plants may modify habitats in ways that prove beneficial to invading species (Simberloff and von Holle 1999). Introduced species frequently interact with each other and facilitative interactions are at least as common as negative ones (Simberloff and von Holle 1999). Ricciardi (2001) found that direct positive (mutualistic and commensal) interactions among introduced species are more common than purely negative (competitive and amensal) interactions. In addition, many exploitative (predator-prey) relations appear to be strongly asymmetric in benefiting one invading species at a negligible cost to another. Combined with an increasing invasion rate in the Great Lakes, this information supports the invasional meltdown theory. The invasion history of the Great lakes is explained better by the invasional melt-

down model than by the biotic resistance model. Further work is required to identify the generality of meltdown phenomena (Simberloff and Von Holle 1999). If biotic resistance to establishment exists only at a low frequency of attempted introductions, then invasional meltdown might have a threshold effect of inoculation pressure, beyond which the phenomenon may occur often. Such a case may apply with vectors that transport large numbers and large populations of species, as is the case with ballast water. In addition, biotic resistance may operate only at small spatial scales (Levine and D'Antonio 1999), while invasional meltdown could operate at multiple scales, ranging from communities to ecosystems (Simberloff and Von Holle 1999). One caution is warranted when considering the possibility of 'invasional meltdown'. Serial introductions of species from the same source pool may produce the same pattern in new areas, even with non-interacting species, as produced by invasional meltdown. Thus investigators ought to demonstrate that the species interact in a facilitative manner prior to accepting this hypothesis.

Abiotic Resistance Model

Until now, the focus has been on biotic resistance (or facilitation) rather than abiotic resistance. Moyle and Light (1996) argued that, in the case of fish invasions, abiotic resistance plays a much larger role in invasion processes than biotic resistance. They predicted that the most successful invaders in streams will be those adapted to the local hydrologic regime and mentioned several examples in North America. They also stated that all fish assemblages are invulnerable regardless of the diversity of the resident fish assemblages, suggesting an important role for propagule pressure. Invasive fish species have become established in a range of streams, from those with initially no fish, to those with complex fish assemblages (Moyle and Light 1996).

Abiotic resistance was a focus of Lennon et al. (2003), who investigated the impact of the supply rate of limiting nutrients (trophic state) on the invasion success of an exotic zooplankton species (*Daphnia lumholtzi*) in native plankton communities. This species is an aggressive invader in North America, primarily in reservoirs in the southern United States, which tend to be more eutrophic than lakes and reservoirs in the north. The authors initially tried to link the establishment success of *D. lumholtzi* with the trophic state of the system, assuming that a higher nutrient concentration increases the chances of successful establishment. Surprisingly, *D. lumholtzi* was associated with systems that had low nutrients, low zooplankton biomass and high zooplankton species diversity. The authors proposed that invasion success of *D. lumholtzi* was inhibited by another cladoceran species, *Chydorus sphaericus*, thereby implicating an interaction between trophic state, community composition and invasion success. Havel et al. (2005) proposed that a combination of factors, including physicochemical properties, connectivity and high levels of

disturbance, have facilitated the spread of *D. lumholtzi* through reservoirs in the United States.

Disturbance (Human or Natural)

Disturbance is the process that leads to partial or total destruction of the individual or group of individuals. Disturbance is a broad term with many components and magnitudes and with much temporal variation. Often, it is the process leading to bare ground or areas of altered light conditions; and consequently disturbance is another factor that may influence invasibility. Many researchers have found, for example, that non-native species colonize disturbed areas more than pristine ones. Harper (1969) suggested that disturbance is the main determinant of plant community structure, with the important element of time influencing the level of diversity able to establish after the perturbation.

Moyle and Light (1996) predicted that successful invasions in aquatic systems are most likely to occur when native assemblages of organisms have been temporarily disrupted or depleted; as such a much wider range of species can invade in aquatic systems with high levels of human disturbance than in systems with a low level of disturbance. They mention that reservoirs (high-disturbance systems) on California's rivers often support three to four species of predatory black bass (*Micropterus* spp), while rarely more than two species are found together in natural systems. Although Lozon and MacIsaac (1997) found no support for disturbance facilitating animal invasions, there was strong support for plant communities. Colautti et al. (2006b) found that disturbance was significantly associated with invasibility of plant communities. Pollution can be considered as a disturbance leading to underexploited resources. Van der Velde et al. (2000, 2002) noticed that invasions by alien macroinvertebrates in the River Rhine occurred after a period of pollution followed by water quality improvement and these invasions accelerated again after a chemical spill followed by further water quality improvement. Strayer et al. (2005) found also that restoration efforts of large-river ecosystems led to systems heavily invaded by alien species, based on a study in the Hudson River.

Fluctuating Resource Availability

The "fluctuating resource availability" hypothesis states that a community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources (Davis et al. 2000). This increase in resources occurs either by reduced consumption and/or by increased availability (Fig. 4.3).

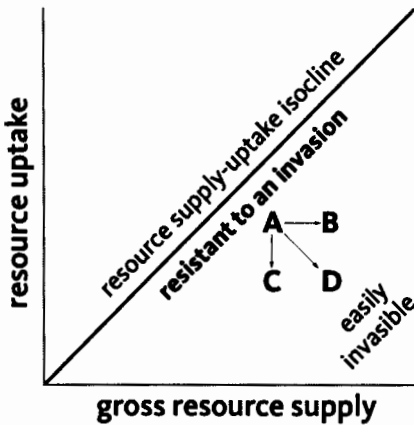


Fig. 4.3 The theory of fluctuating resource availability holds that a community's invisibility or susceptibility to invasion increases as resource availability (the difference between gross resource supply and resource uptake) increases. Resource availability can increase due to a pulse in resource supply (A→B), a decline in resource uptake (A→C) or both (A→D). In the plot shown, resource availability, and hence invisibility, increases as the trajectory moves further right and/or below the supply/uptake isocline (where resource uptake = gross resource supply). Modified after Davis et al. (2000)

Fluctuation in resource availability is identified as the key factor controlling invisibility. The theory is mechanistic and quantitative in nature, leading to a variety of testable predictions, some of which are mentioned here.

1. Environments subject to pronounced fluctuations in resource supply will be more susceptible to invasions than environments with more stable resource supply rates.
2. Invasibility will increase following disturbances, disease and pest outbreaks that increase resource availability by increasing resource supply and/or reducing the rate of resource capture by the resident vegetation.
3. There will be no necessary relationship between the species diversity of a plant community and its susceptibility to invasion. Since complete exploitation and very incomplete exploitation of resources can occur in both species-rich and species-poor communities, there is no reason to expect any consistent pattern between species richness or diversity of a community and its susceptibility to invasion.
4. There is no general relationship between the average productivity of a plant community and its susceptibility to invasion because competition intensity has not been found positively correlated with community productivity (Goldberg et al. 1999).

Resource availability may be variously high or low in either productive or unproductive habitats, with invisibility also then being either high or low in these habitats. It is not yet clear how this theory can be applied to animals and to what extent behaviour reduces the dependence of animal invaders upon a supply of unused resources. Davis et al. (2000) concluded that the elusive nature of the invasion process is caused by the fact that it depends upon resource enrichment of the habitat or release of resource usage by the inhab-

itants of the habitat. These two reasons occur only intermittently. Whether or not invasion actually occurs is a function of propagule pressure and the characteristics of the invading species. If a species is totally unfit for a certain environment, then the invasibility of that environment may be great but the species will never invade. Characteristics in an invading species that make it suited for the environment will support its invasiveness in a correspondingly vulnerable ecosystem (Heger and Trepl 2003). This interaction needed for a successful invasion is discussed in the next paragraph.

4.5.3 Relationship Between Invader and Invaded Ecosystem (Key-Lock Approach)

Both the invading species approach and the invaded ecosystem approach are concerned with the properties of only one component of a biological invasion. There seem, however, to be cases in which neither of these general characteristics sufficiently explains the success of an invasion. In these cases, the relationship between features of the ecosystem and characteristics of the invader is crucial for the invasion success. When there are empty niches in an ecosystem, an invader with the right characteristics to fit into such a niche has the possibility to be successful, assuming a sufficient supply of propagules. The concept of the niche was developed decades ago as an explanation for how species coexist in ecological communities.

It is difficult to determine exactly the range of a certain species' niche (including all possible niche axes) and it is still harder to quantify niche overlap between species (Lohrer 2001). Even when these niches are quantified, community composition cannot be predicted. There are other factors influencing community composition, including competition, disturbance and environmental variability, predation and timing and number of invading propagules. Even with these limitations, niche theory has value when applied to modern ecological investigations. Lohrer (2001) created a hierarchical niche-based framework (NBF) that seeks to explain *a posteriori* why particular species successfully invade habitats (Fig. 4.4). The models are differentiated hierarchically by: (1) the amount of niche overlap in the invaded habitat, (2) the type/amount of change in niche breadth and (3) the nature of resource limitation. Ideally, every new invasion should be explained by only one of the models in the framework. Lohrer (2001) proposed that, when the niche-based framework is widely applied, invasion ecologists may begin to elucidate patterns necessary for making predictions. Binggeli (1997) suggested that most of the highly successful invaders do not have an ecologically equivalent species in the ecosystem invaded. Thus, ecosystem characteristics may be important to the success of the invader, who in turn must possess the 'right' characteristics to invade a particular ecosystem. This is what the relational key-lock approach comprises (Heger and Trepl 2003).

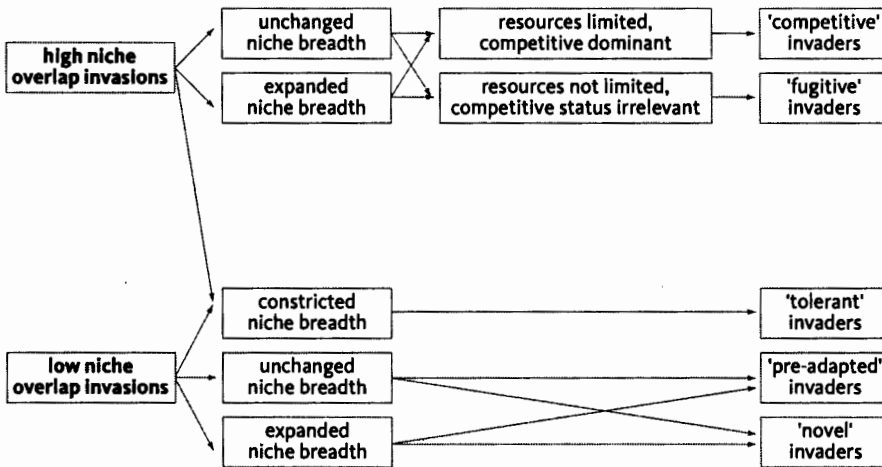


Fig. 4.4 Hierarchical niche-based framework (NBF). The models are differentiated according to: (1) the amount of niche overlap in the invaded habitat – the uppermost level, (2) the type/amount of change in a niche breadth between native and invaded habitats – the second level and (3) the nature of resource limitation – the final level. There are ten possible paths, each representing a unique invasion scenario. Modified after Lohrer (2001)

A major disadvantage of this approach is that it does not take into account factors for community composition other than the niche of a species, such as the increase in probability of establishment with number of release events or number of individuals released (Grevstad 1999). Demographic factors whose influence depends on population size or density such as demographic stochasticity, Allee effects and genetics also play an important role in the establishment of invading populations (Grevstad 1999). In addition, escape from natural enemies (predators, parasites) may influence invasion success (Binggeli 1997), although authors must be careful in ascribing invasiveness to 'enemy release' (Colautti et al. 2004b).

What happens, however, if a species manages to invade in a food web which already contains an equivalent species? Would one be redundant and driven out by competition or would both manage to coexist? In computer terms, redundancy means: the provision of multiple interchangeable components to perform a single function in order to cope with failures and errors. Translated to ecosystems, it could be the co-existence of equivalent competitors having the same or largely overlapping niches. Loreau (2004) suggested that neutral co-existence of equivalent competitors, non-linear per capita growth rates and lack of correlation between functional impact and biomass may provide the basis for the existence of functional redundancy in natural ecosystems. Difficulty of determining the existence of functional redundancy is that species may appear to perform the same function under a restricted set of

conditions, yet their functional roles may vary in naturally heterogeneous environments (Wellnitz and LeRoy Poff 2001).

Duncan and Williams (2002) compiled a list of 1511 native plant species of New Zealand that occur in genera with at least one introduced species. They separated the introduced genera into those containing at least one naturalized (introduced from another region and persisting without cultivation) species and those without and also into those containing at least one native species and those without. A noticeably smaller number of naturalized genera were found to contain native species but the naturalization rate was much higher for these same genera (45 % in genera with native species, 18 % in genera without natives). Within families, genera containing at least one native species showed a significantly higher rate of naturalization than genera without native species. This contradicts Darwin's naturalization hypothesis. A possible explanation also considered by Darwin is that introduced species with native congeners are more likely to share features with them that allow them to survive in New Zealand, compared with introduced species that lack those relatives here. These shared traits may pre-adapt the plants to their new environment, helping to outweigh the potential disadvantage of stronger competition from close relatives (Duncan and Williams 2002). This might also be the case for animals. An example comes from Declerck et al. (2002), who researched patterns of diet overlap between populations of introduced and native fishes in shallow ponds. Chironomid larvae were the most important food source for all species but, by differential consumption of chironomid size classes, niche differentiation between introduced fishes was attained. In contrast, high diet overlap was found between the functional groups of one of the indigenous species and several introduced fishes, indicating a high potential for interspecific exploitative competition (Declerck et al. 2002). The introduced species established a successful self-sustaining wild population in a place with congeneric native species, which is opposite to that expected from Darwin's naturalization hypothesis.

4.5.4 Invasion Processes Differentiated in Time

The approaches described in the previous paragraphs explain several aspects of invasions, but they fail to regard invasions as processes. The characteristics of invading species, the invaded ecosystems and the interplay of both are in most cases derived from the analysis of some aspects of the invasion process, ignoring that various steps of an invasion may differ in quality and thus every step may require different characteristics from the invader (Heger and Trepl 2003).

The model of steps and stages (Heger and Trepl 2003) visualizes the invasion process as a staircase, with stages that are derived from a chronological differentiation of an idealized invasion process (Fig. 4.5A). The steps differ in

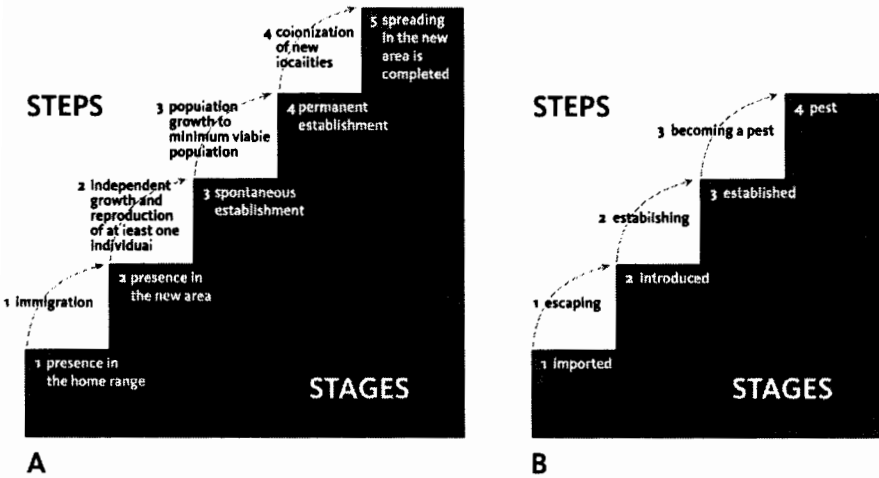


Fig. 4.5 **A** Chronological discrimination of an idealized invasion process into steps and stages. Different stages are reached by overcoming a sequence of steps in the course of the invasion. The height of each step depends on the ability of the species to overcome environmental limitations. Modified after Heger and Trepl (2003). **B** Chronological discrimination of an invasion process into steps and stages. *Imported* Species found in collections or accidentally brought into the country, *introduced* (or casual) found outside control or captivity as a potentially self-sustaining population, *pest* with a negative economic effect. Based on Williamson and Fitter (1996)

perspective: the first and second steps consider single individuals and investigate the possible difficulties facing an individual and the third step considers the founder population, which is confronted with problems on different levels. The fourth step concerns all new populations of the invading species and therefore considers problems of yet another quality (Heger and Trepl 2003). A successful species must pass all the different stages, taking all the steps and facing different problems at each step. Many introductions fail at the lower steps, never reaching the upper steps. The model aims to serve as a tool to define the difficulties facing a plant invader, but also pertains to animal invaders. However, the possible threats and characteristics which increase the probability of a successful invasion must be adapted for animals. It is very much focused on the invader and less on the invaded ecosystem. This is not necessary and can easily be changed: for instance, the model of biotic resistance can be incorporated into the steps and stages model. Biotic resistance is hypothesized to occur at two stages of invasion: at the establishment stage (stage 2: independent growth and reproduction) and, if establishment is successful, during subsequent population growth, when the abundance of the invader (and thus its community-wide impact) is limited by resident species richness (step 3: population growth to minimum viable population; Levine and D'Antonio 1999).

Kolar and Lodge (2001) defined four transitions (steps in the invasion sequence) in their model of chronological discrimination: transportation, release, establishment and spread. To begin the invasion process, a species must be moved away from its home range and transported into a new environment by a (human) vector. With each sequential transition, a large proportion of species fails (Kolar and Lodge 2001). When those barriers have been overcome, the species starts interacting with the invaded ecosystem. These interactions, along with other factors, determine whether that species will establish itself in the new environment (attaining a self-sustaining population). When the species does not spread from its point of establishment, it is called non-invasive; when it does, it is called invasive. This distinction is however quite imprecise because spread is partly a function of time since establishment, which is not always known. Small population size is important both to endangered species and invasive species. In both cases, consecutive periods of high mortality can drive the population (species) to extinction; this effect can be exacerbated by (and contributed to) demographic stochasticity (Mack et al. 2000). For example, having inappropriate sex ratios (for dioecious species) or age classes dominated by non-reproductive individuals could doom an introduced population even if environmental conditions were highly suited for the species' survival. However, even if sufficient propagules of appropriate sex ratio and reproductive status are introduced, successful establishment is still not guaranteed. Environmental stochasticity also affects colonizing populations and may cause invasion failures (Crawley 1989). The combined effects of demographic and environmental stochasticity may render invasion success very difficult to predict using classic, deterministic approaches. Indeed, stochastic population models may perform better in predicting invasion success than can deterministic models when inoculum sizes are very small (Crawley 1989). The model of Kolar and Lodge (2001) is meant to distinguish between stages in the invasion process because they are likely to differ in quality. Simultaneous examination of all transitions may hinder the detection of patterns. The definition of the transitions and of associated stages shown in the scheme remains unclear. The scheme does not explicitly discriminate between stages and transitions (Heger and Trepl 2003). The stage: 'survives transport and introduction' may be split up into two sub-stages: 'survives transport' and 'survives introduction'; and, since these two stages both face different threats, a species may be adapted for transport and not for introduction.

The model of steps and stages by Williamson and Fitter (1996; Fig. 4.5B) is slightly simplified compared to that of Heger and Trepl (2003) but serves well as a 'bottleneck' model for predicting where most species will fail in the invasion process. The word 'pest' however can be replaced by 'invasive' and is corresponding with the step 'spreading in the new area is completed'. In the same way, 'imported' corresponds with 'presence in the new area', 'introduced' corresponds with 'present in the new area' and 'established' corresponds with

'permanent establishment'. It seems only one step from Heger and Trepl (2003) is missing: step 2, which is spontaneous establishment.

Richardson et al. (2000) developed a model with six major barriers that a non-native species must overcome in order to become invasive (Fig. 4.6). This model has the advantage of distinguishing between the settlement of non-native species in environments made by humans and in natural environments. However, since only barriers are described, the stages in between are less clear. In this model, a species is called casual ('alien plants that may flourish or even reproduce occasionally in an area, but which do not form self-replacing populations and which rely on repeated introductions for their persistence') when it has crossed a geographical barrier. Only when the next barrier is overcome (abiotic or biotic barriers at the site of introduction) can a species may be called casual. The first barrier 'geographic' corresponds with the first step in Heger and Trepl (2003): 'immigration'. The second barrier 'environmental (local)' corresponds with the second step 'independent

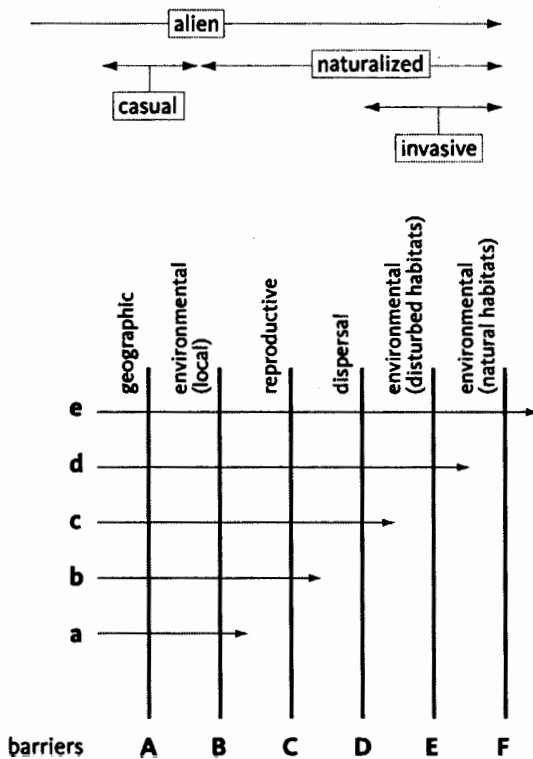


Fig. 4.6 A schematic representation of major barriers limiting the spread of introduced plants. The barriers are: A major geographical barriers (intercontinental and/or intra-continental, approximate scale >100 km), B environmental barriers (abiotic and biotic) at the site of introduction, C reproduction barriers (prevention of consistent and long-term vegetative and/or generative production of offspring), D local/regional dispersal barriers, E environmental barriers in human-modified or alien-dominated vegetation, F environmental barriers in natural or seminatural vegetation. Arrows a–e The paths followed by taxa to reach the different states from introduced to invasive in natural vegetation. Crossing the barriers is not irreversible: for example, climatic fluctuations can either pose new barriers, or enable the new taxon to spread. Modified after Richardson et al. (2000)

growth and reproduction of at least one individual', the third barrier 'reproductive' corresponds with 'population growth to minimum viable population' and the fourth barrier 'dispersal' corresponds with 'colonization of new localities'. In Richardson et al. (2000), however, there are two more barriers – a natural and a disturbed environmental barrier – which are actually different parts of barrier four (dispersal). Many species are better equipped to invade disturbed habitats, while others more easily invade natural habitats.

4.5.5 Comparative Historical Approach

To what extent do patterns of invasion in one region generalize to other regions? Answering this question is a key goal of invasion biology because it underlies whether we can make progress via comparative studies or must instead cope with a large set of anecdotal evidence or unrelated case studies. Prediction would be virtually impossible if the latter were true. However, historical reconstructions of the progress of invasions show remarkable similarities between diverse taxa and (eco)systems.

To illustrate this, Unmack and Fagan (2004) have investigated the Gila and Yaqui river basins (western North America) with respect to fish communities, comparing the native/non-native ratio of both basins from 1850 until today. The two basins are similar in size, physiography and ecology, but differ in the timing of regional development. Trends observed in the native/non-native ratio in both basins resemble each other (both are roughly linear), but a time lag of about 41 years exists between them. The Gila basin contains more alien fish species than the Yaqui basin; it is in a further invasion stage. Based on those data, the predictions can be made that the future of the Yaqui will echo the present-day situation of the Gila. Unfortunately, lack of this type of data and the differences in ecosystems limits the frequency that the comparative historical approach can be used.

It is questionable whether ecologists are able to identify mechanistic explanations for the phenomena observed and then be able to make predictions on the basis of universal laws. Ecological phenomena always have the component of uniqueness, particularity and historicity. Hence, a probably more suitable approach could be the so-called 'method of case studies' successfully employed in applied issues of ecology (Shrader-Frechette and McCoy 1993). The comparison of case studies allows one to identify certain patterns or analogies to be made on the ground of good knowledge on the biology and ecology of the species in question. This method seems also highly suitable to research on biological invasions and might be much more rewarding than purely mechanistic approaches (Shrader-Frechette 2001).

4.6 Shadows on the Prospects of Prediction

Several phenomena have until now escaped from prediction models. One of these is the 'time-lag' phenomenon; non-native species living inconspicuously in their new habitat for decades, until the population suddenly explodes and spreads like wildfire. Two types of lag phases may be recognized: (1) a period between the first introduction and the first spread and (2) the period preceding the switch to a significantly higher rate of population growth according to Kowarik (1995). Time-lags between the introductions of exotic plants, their establishment and subsequent spread are commonly observed in many species (Binggelli 2000). In woody plants, major changes in a biotic factor (e.g. grazing, pollinator) or an abiotic factor (e.g. hurricane, flood, logging) usually determine the duration of time-lags and there is little published evidence to support the importance of other factors and genetic adaptations in particular. Human activities and detection (e.g. interest in and ability to detect the spread of an invasive) are also common explanations for some observed time-lags (Binggelli 2000). The zebra mussel (*Dreissena polymorpha*) is another case in point. Scientists predicted its arrival into the Great Lakes from Europe via ballast water in 1981, yet no invasion occurred. It is still not clear why the animal finally invaded when it did in 1986. One possibility is a change in the environment which makes it more suitable to non-native species, although it is often unclear what that is. In the case of the zebra mussel, ironically, improving water quality may have allowed the species to survive in key European source regions and/or in the Great Lakes. Alternatively, the species may not have had appropriate dispersal opportunities from Europe until shortly before it established in the Great Lakes. Therefore, it is not clear whether the species benefited from a change in introduction effort or environmental conditions, or both (Andow 2003; MacIsaac et al. 2001). To predict time-lags, it is necessary to draw a list of species for which time-lags have been recorded elsewhere (Kowarik 1995).

Another strange phenomenon is the occasional collapse of substantial populations of invasive non-indigenous species. For example, the widespread invasive snail *Achatina fulica* and pondweed *Elodea canadensis* appear to be characterized by a rapid expansion followed by rapid decline. For the snail, disease might be the cause but, for the pondweed, the decline is yet unexplained (Simberloff and Gibbons 2004). Zebra mussel (*D. polymorpha*) populations in European systems may be differentiated into those with relative stable, long-term population dynamics and those that exhibit great variance in interannual population density (Ramcharan et al. 1992). Possible reasons for the periodic crashes include density-dependent endogenous cycles, predators, parasites or pathogens.

4.7 Conclusion

Are biological invasions unique events or can we find certain patterns that make predictions possible? Invasion biology is so intricately linked with human history, global trade and ever-decreasing transport barriers that a historical perspective is essential to understand the ecological process at hand. One should also learn from the physiology, behaviour and previous invasions of a possible invader to estimate the invasibility of valuable ecosystems. Chronological discrimination could be a useful tool in predicting invasions, especially when there is more research into the different threats posed by the different stages and more use of existing models on animal invaders. The key-lock approach is very useful as an explanatory tool. Predictions are still quite inaccurate and have an observational nature. Recent studies on propagule pressure generally meet with success in explaining vulnerability of ecosystems to invasion, although in reality it is very likely that more than one mechanism simultaneously affects invasion success. More experimentation would enable greater use of theoretical models with lower false + or - error rates. As pointed out by Rose (1997) 'nothing in biology makes sense except in the light of history'. For the prediction of future invasions, we should learn from history; and history has left us with a great deal to study.

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