Progresses and Controversies in Invasion Biology

Daniel Sol

Invasion biology is concerned with understanding the causes and consequences of the human-assisted introduction of organisms outside their native ranges. Ever since Elton published the foundational book "The Ecology of Invasions by Animals and Plants" (Elton 1958), the field has gained enormous importance in ecology. A major motivation in developing the discipline has been the growing concern over the environmental, economic and social impact caused by some invaders (Martin and Maron 2012). Non-indigenous species (NIS, hereafter) are an important cause of species extinction, as exemplified by the introduction of the Brown snake in Guam (Fritts and Rodda 1998) or the Nile perch in the African great lakes (Miller 1989); alter key ecosystem functions, like the nutrients cycle and fire regimes (Vitousek et al. 1987; Levine et al. 2004; Callaway and Maron 2006; Vilà et al. 2011); and generate every year millions of euros of economic loses (Pimentel et al. 2001).

Paralleling the concern over the impact of invaders, there has been an increasing appreciation that NIS represent unique opportunities for studying a variety of ecological and evolutionary processes as they occur and at unprecedented spatial and temporal scales. Thus, biological invasions have contributed to reshape important ideas in genetics, behavioral ecology, population dynamics, community ecology and evolutionary ecology (Lodge 1993; Callaway and Maron 2006; Sax et al. 2007).

In developing the discipline, two fundamental questions have almost monopolized the research agenda: Why are some species invasive and others are not? And why are some environments more invaded than others? Despite the enormous progress in answering these questions, the field remains controversial and has been criticized by its dissociation from the rest of ecology and its lack of rigor in adopting and rejecting new hypotheses and theories (Davis 2009). Some have even questioned that the field is useful at all (Valéry et al. 2013; but see Blondel et al. 2013).

D. Sol
CREAF (Centre for Ecological Research and Forestry Applications), CSIC (Spanish National Research Council), Bellaterra, Catalonia E-08193, Spain
e-mail: dsolrueda@gmail.com

The goal of this chapter is to highlight several conceptual areas that are currently dominating the field. Specifically, I focus on advancing 11 major themes in invasion biology (Table 1), which altogether provides the necessary framework to understanding what make species successful invaders (invasiveness) and what make ecosystems more or less susceptible to invasion (invasibility). While these themes clearly illustrate the progress made in the field, theoretical and empirical advances are needed in all these areas (see also Jeschke et al. 2012). Consequently, I also highlight controversies and underexploited areas that, if addressed, have the potential to reshape the field in the near future.

What Is a Successful Invader?

Progress in invasion biology has been hampered by a lack of an unifying framework to describe the invasion process, particularly between ecologists working in plants and animals (Blackburn et al. 2011). However, some consensus has now been reached (Richardson et al. 2000; Kolar and Lodge 2001; Duncan et al. 2003; Blackburn et al. 2011), which sees the invasion process as a sequence of several stages. To become a successful invader the organism must firstly be deliberately or accidentally transported (transport stage) and introduced (introduction stage) to a new location by humans; next, the organism must establish a self-sustaining population in the novel environment (establishment stage); finally, the population must increase in abundance and expand their geographic area (spread stage).

It is important to recognize the different stages because each stage influences subsequent stages (Kolar and Lodge 2001). The transport/introduction stage, for example, determines the size, structure and genetics of the founder population, which largely affect the likelihood of establishment. Moreover, the underlying processes can vary among stages. For example, while the probability of establishment is driven by population dynamics in the context of small populations and novel

Table 1 Major biological invasions themes discussed in the present chapter	
	What is a successful invader?
	Are biological invasions highly idiosyncratic?
	Is the establishment success of invaders a paradox?
	What makes a successful invader?
	Is growing fast a key feature of successful invaders?
	Do communities differ in invasibility?
	Are close relatives bad neighbors?
	Are introduced species creating an "invasional meltdown"?
	Does "enemy release" explain the increase and expansion of invaders?
	What is the role of evolution in the invasion process?
	Are exotics decreasing, maintaining or increasing biodiversity?

environments, the spread stage is more related to dispersal ability, carrying capacity and ecological interactions (Leung et al. 2012; Sol et al. 2012b). Finally, the impact of the invader can be expressed at several stages. The impact is potentially greater for widespread NIS, yet it also depends on their abundance and per capita effects (Parker et al. 1999) and hence can also be high even when the NIS are localized geographically.

It is widely accepted that a small proportion of species are introduced and establish, and a small proportion of established species spread and becomes a pest. An attempt to give numbers to these proportions is the "tens-rule", which holds that over 10 % of species transition between these different stages (Williamson et al. 1986; Williamson and Fitter 1996). The "tens-rule" has been misinterpreted by some as if it was a fundamental constant of nature, like the gravitational constant in physics. However, this was not the intention of Williamson and co-workers when they proposed the concept, as the number has scarce theoretical basis beyond the heuristic value of arguing that the probability of transition between invasion stages is low.

Why Are Biological Invasions Highly Idiosyncratic?

The search for general rules that govern invasions has often been unfruitful, with many studies -including those related to the search for features that explain invasiveness and invasibility- yielding idiosyncratic results (Williamson et al. 1986; Moles et al. 2012). Several factors can contribute to explain such idiosyncrasies, besides differences in the quality of the studies, yet the main factors relate to the routes toward extinction in introduced populations.

For an invader, a negative population growth is perhaps the most obvious route toward extinction (Figs. 1 and 2). NIS are exposed to novel environmental conditions to which they have had little opportunity to adapt (Figs. 1 and 2). If as a result there is an adaptive mismatch that negatively affects key fitness components, then the population can decrease over time and end up extinct. It follows that the same species can succeed in some environments but not in others, depending on the degree of adaptive matching. Likewise, a region can seem to be less resistant to invaders than others simply because the adaptive matching of the introduced species is higher. This can be accentuated because of the non-random selection of the species used in introductions and the places where they were introduced (Blackburn and Duncan 2001). Because the features of the pool of species introduced may differ from location to location, the search for traits that make species good invaders can yield different results depending on the region investigated.

Even if the population has the adaptations needed to survive and reproduce in the new environment, an introduced population may die out as a result of bad luck (Fig. 1). This is because most introduced populations start with a reduced number of individuals, which make them highly vulnerable to extinction by demographic stochasticity, Allee effects and genetic stochasticity (Fig. 1). Indeed,
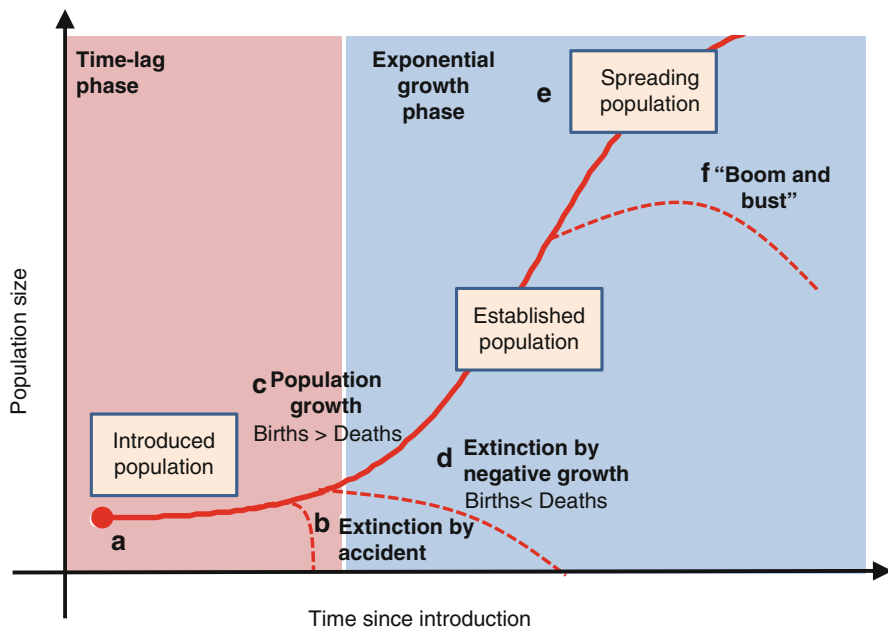
Fig. 1 A framework for the invasion process. The invasion process starts with an introduced population transported from a relatively distant region (*a*), which generally involves a low number of individuals and can have suffered a genetic bottleneck. The population can remain at low numbers for some time, even decades (time-lag phase, in red), during which is highly vulnerable to extinction by accident (i.e. demographic stochasticity, Allee effects and genetic stochasticity) (*b*). The establishment of the species is determined by a positive balance between births and deaths, which largely depends on the species' life history (*c*). However, a number of factors in addition of an appropriate life history can lead to a negative population growth conductive to extinction (*d*), such as an adaptive mismatch or a lack of adaptive plasticity to exploit the available niches. If the population is freed from competitors and enemies, it can increase exponentially in numbers (exponential growth phase, in blue) and start expanding to adjacent areas at a speed limited by dispersal capacity and evolutionary dynamics related to assortative mating (*e*). However, even populations that have initially increased and expanded can sometimes experience a 'boom and bust' in which it experiences a decline and can even go extinct (*f*)

propagule pressure (i.e. variation in the quantity, composition and rate of supply of NIS, sensu Ricciardi et al. 2011) is the most consistent predictor of the probability of establishment in plants and animals (Lockwood et al. 2005). Thus, a same species can have more or less success in a novel environment depending on the number of individuals introduced. Likewise, some systems may look like if they were highly susceptible to be invaded simply because many species have been introduced there and/or the species have been released in larger numbers. Islands, for example, often present a higher number of invaders than continents, which has led to think that they were more vulnerable to invasions. However, quantitative analyses in birds have revealed that the high invasions rates on islands is primarily associated with higher propagule pressure rather than higher invasibility (Sol 2000; Cassey et al. 2004).
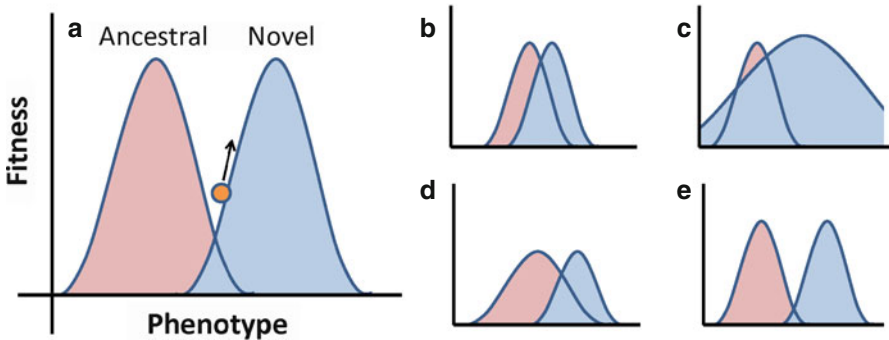
Fig. 2 The problems that a species faces in a novel environment can be metaphorically described in terms of adaptive surfaces, representing mean fitness of a population in the ancestral and novel environments as a function of the organism phenotype (**a**). The first problem is that if there is an adaptive mismatch, the population will see its mean fitness reduced (*red dot*) and hence it will run a high risk of extinction. The second problem is that natural selection is unlikely to move the population up to a new adaptive peak if there is not enough useful heritable variation and the population is too small to resist strong selective pressures. These difficulties are nonetheless reduced when (**b**) there is environmental matching between the region of origin and introduction, and hence the organism already have the necessary adaptations; (**c**) the new adaptive peak is not very demanding in terms of adaptive specializations; and (**d**) the niche of the NIS is so broad that the adaptive peaks of the environments of origin and introductions overlap to a great extent. However, there is also the possibility that niche adaptive peaks of the environments of origin and introductions are substantially different (**e**), and then we need to invoke general adaptations to environmental changes like phenotypic plasticity to understand the persistence of the organism in the novel environment

The idiosyncratic nature of the invasion process implies high uncertainties in predicting the outcome of each invasion stage (Leung et al. 2012). This is unfortunate because accurately assessing invasion success is essential to prevent and mitigate the impact of biological invasions (Kolar and Lodge 2002, Vall-llosera and Sol 2009; Leung et al. 2012). While it is not currently possible to accurately predict the outcome of a particular introduction, ecologists can still make powerful generalizations about the invasion process (Ehrlich 1989; Duncan et al. 2003; Callaway and Maron 2006; Sax et al. 2007). As we will see in the next sections, these generalizations should not be taken as laws, in the sense that physicists use the term, but as patterns that are more or less predominant despite containing some exceptions (Simberloff 2013).

Is the Establishment Success of Invaders a Paradox?

The invasion success of NIS is in a way paradoxical because we do not expect that species that come from distant regions can succeed to establish themselves in environments to which they have had little opportunity to adapt (Sax and Brown 2000); and even more paradoxical is that sometimes the invader attains higher densities

than most native species. This is less a paradox however when considering that, as expected by theory, most introduction attempts fail (Williamson et al. 1986; Veltman et al. 1996; Williamson 1996; Haight and Polasky 2010).

Still, the success of some NIS warrants explanation. The success of an invader primarily depends on whether individuals are able to reproduce at a higher rate than they die, and hence increase in numbers. Having such a positive population growth depends in turn on finding an appropriate niche in the new environment, that is, conditions that the organism can tolerate, resources that are not monopolized by native species, and a pressure of enemies that is sustainable (Shea and Chesson 2002). Thus, in addition of propagule pressure, the success of the invader may depend on both its own features and those of the recipient environment.

There are several ways by which exotic organisms can acquire a niche in a novel environment (Table 2). First, if competition for resources is strong and environmental adversity is weak, then the success of the invader relies on being competitively superior to the species with which its niche overlaps to a greater extent (Tilman 2004; Vilà et al. 2005). Second, if competition in the invaded community is weak and environmental adversity is strong, then the invader will only succeed if it has the adaptations needed to survive and reproduce in the novel environment. Third, if both competitive adversity and environmental adversity are weak, then there is no need to invoke adaptations to understand the success; this can be understood by neutral processes in which species are ecologically equivalent (Weiher and Keddy 1995). Finally, if both competitive adversity and environmental adversity are strong, then the invader would need the unlikely combination of high competitive ability and appropriate adaptations to a demanding environment.

Although there is evidence for the case-by-case importance of all these scenarios, except perhaps for the latest scenario, there has been little effort to investigate to what extent they provide a general solution to the invasion paradox (Sol et al. 2012a). Nevertheless, the few existing studies to date provide greater support for the second scenario, in which success depends on being able to fill a niche infra-utilized by native species. In plants, native and alien species often differ in the environments they use, with NIS primarily found in environments that have been modified by vegetation clearance, pasture development and livestock grazing (Pouteau et al. 2015). In birds, many NIS are not only restricted to urban or rural environments, where the diversity and abundance of native species are low (Case 1996; Sol et al.

Table 2 Scenarios accounting for the success of biological invasions

	Competitive adversity	Environmental adversity	Main process	Profile invader
Scenario 1	Strong	Weak	Biotic resistance	Strong competitor
Scenario 2	Weak	Strong	Environmental filtering	Adapted
Scenario 3	Weak	Weak	Neutrality	Ecological equivalence
Scenario 4	Strong	Strong	Biotic-Environmental	None

2012a; Barnagaud et al. 2013), but they overlap little with native species in traits associated with resource use (Sol et al. 2012a; Barnagaud et al. 2013). Although these evidence do not deny the possibility that being superior in contest competition against native species provide advantages in some cases (e.g. Sol et al. 2012a; Hernández-Brito et al. 2014), they do suggest that this is the exception rather than the norm.

What Makes a Successful Invader?

Even when many invaders are restricted to anthropogenic-disturbed environments, the question remains as to why they are able to survive and reproduce in those environments and most native species are not. While understanding failures is relatively easy in light of current theories, what makes some species successful invaders is less obvious. Why should an organism be able to cope with novel environmental pressures to which it has never or rarely been exposed before? One obvious possibility is that there is environmental matching between the place of introduction and that of origin of the NIS, implying that the species already possess adaptations to persist in the novel environment (Table 2, scenario 2; Fig. 2a). Although NIS typically come from distant regions, certain environmental matching is still expected. This is clear for deliberate introductions as humans are more likely to release NIS in environments where they can do better. Some environmental matching is expected even for accidental introductions, as NIS are more likely to be translocated by humans between the environments that people most often frequents. In birds, for example, species that in their places of origin occur in urbanized environments are more likely to succeed when introduced outside their native range (Møller et al. 2015), probably because these species are more readily available for introduction, are more likely to be released close to human settlements, and already possess the adaptations needed to persist in such environments. Climatic matching is also common among successful invaders. In an analysis of 50 terrestrial plant invaders, fewer than 15 % of species had more than 10 % of their invaded distribution outside their native climatic Niche (Petitpierre et al. 2012). Likewise, birds naturalized in Europe occupy a subset of the climatic environments they inhabit in their native ranges (Strubbe et al. 2013).

Another explanation for why some NIS are able to persist in novel environments is that the environment, albeit different from the native one, is little demanding in terms of survival and/or reproduction (Table 2, scenario 3; Fig. 2b), providing for instance abundant resources and few competitors and enemies. In such circumstances, the fitness of the population is not expected to decrease substantially, facilitating establishment. In urban environments, for example, the availability of food deliberately or accidentally provided by humans and the lack of specialized predators might have facilitated the success of some exotic birds escaped from captivity (Shochat et al. 2010; Sol et al. 2012a).

Finally, if the NIS has a broad ecological niche, then it is more likely that it can find the necessary resources and physical conditions in the novel environment (Table 2, scenario 2; Fig. 2c). In birds, species that are either dietary or habitat generalists are more likely to establish themselves successfully in new regions (McLain et al. 1999; Cassey et al. 2004). In Australian acacias and eucalypt trees, invasiveness is so closely associated with environmental tolerance that this feature alone can predict over 90 % of occurrences observed outside of Australia (Higgins and Richardson 2014). Ecological generalism is likely to be a common feature of NIS because generalists are more likely to be abundant close to human settlements than specialists (Evans et al. 2011), and hence more available for introduction. For the same token, communities in anthropogenic environments are often composed primarily by generalists (Sol et al. 2013), which should reduce biotic resistance (see below).

However, when the new adaptive peak is different from the ancestral one (Fig. 2d), then the population is likely to see their fitness reduced. Such 'true' niche shifts differ from the previous scenarios, which are based on 'niche unfilling' (partial filling of the native niche in the invaded range, sensu Petitpierre et al. (2012)). Although substantial niche shifts do not seem to be the most common scenario, at least in terms of climatic tolerance (Petitpierre et al. 2012), two lines of evidence suggest that some degree of shift still occurs. First, the naturalized geographical distributions of some plants and animals are outside those predicted by climatic envelops (Sax et al. 2007; Petitpierre et al. 2012). Second, as discussed later on, many NIS populations have been reported to produce plastic and/or evolutionary responses to the new conditions, suggesting that these differ in some way from the ancestral ones. What allows species to be successful under scenarios of 'true' niche shifts is insufficiently understood, yet evolutionary theory suggests that phenotypic plasticity might play a central role.

Phenotypic plasticity is the capacity of organisms to express different phenotypes in different context; thus, it facilitates that a population can persist in a new environment, thereby bringing it into the realm of attraction of the new adaptive peak (Price et al. 2003). In a meta-analysis, Davidson et al. (2011) showed that invasive plants were more plastic in a variety of traits than non-invasive species, although this plasticity was only evident when resources were abundant. In animals, much attention has been devoted to a form of plasticity, behavioural flexibility. Through innovation and learning, animals can modify their behavior and develop responses to many of the problems that they can encounter in a novel environment, such as finding alternative food sources, developing responses to new predators and accommodating the reproduction to the new environmental conditions (Sol 2003). Indeed, there is evidence for reptiles, birds and mammals that the likelihood of establishment in novel regions increases with the size of the brain (Sol et al. 2005, 2008; Amiel et al. 2011), which mediates innovative propensity and learning (Lefebvre et al. 2004). Evidence is nonetheless lacking for fish (Drake 2007).

Is Growing Fast a General Feature of Successful Invaders?

Life history describes the way organisms allocate time and energy over growth, reproduction and survival, thereby determining how the population grows and fluctuates over time (Stearns 1992). Thus, life history has long been related to the way organisms respond to environmental changes (Roff 2002). The most popular theory, proposed by Lewontin and Cohen (1969) over 40 years ago, is the population growth hypothesis. It argues that species with life histories associated with high reproductive rates should be better invaders because their populations may growth faster and hence can more easily avoid the risk of extinction by accident just after the introduction, when the population is small. Although the population growth hypothesis is based on solid demographic theory and has received wide acceptance, the confidence in the hypothesis is undermined by a lack of empirical support. In birds, where the theory has received much attention, some studies suggest a positive relationship between life history correlates of population growth and establishment success whereas others report a negative relationship or no relationship at all (Blackburn et al. 2009). One limitation of the hypothesis is assuming that demographic stochasticity is the main cause of extinction of introduced populations, when this only operates when the population is extremely small. In addition, the hypothesis ignores that a high reproductive effort may entail costs, like increased mortality, that can counter the advantages of fast population growth (Stearns 1992; Roff 2002). Demographic models show for instance that while species that prioritize reproduction over survival can increase faster in numbers when conditions are favourable, they are at the same time highly exposed to extinction because their populations exhibit greater population fluctuations (Lande et al. 2003).

   Recent work also suggests that life history can affect the invasion process by additional mechanisms than those generally considered (see Sol et al. 2012b). While prioritizing current reproductive effort provides benefits in terms of rapid population growth, a strategy that prioritize future reproduction can also afford some advantages for a species exposed to novel environment (Williams 1966; Sol et al. 2012b). In addition of reducing population fluctuations (see above), such a strategy is based on distributing the reproductive effort in a number of reproductive events, thereby reducing the fitness costs of a reproductive failure. This bet-hedging strategy facilitates population persistence when environmental uncertainties increase the probability of reproductive failure due to bad decisions (e.g. settling in an inappropriate habitat). Moreover, such a strategy reduces the fitness costs of skipping a reproduction, allowing the invader to engage in reproductive activities only when conditions are favorable (storage effect). This increases the opportunities for acquiring environmental information and for improving performance on exploiting the resources and avoiding the enemies, particularly in long-lived species with larger brains and enhanced capacity to construct learnt responses. A recent global comparative analysis of avian introductions evidenced that although rapid population growth may be advantageous during invasions under certain circumstances (i.e. low propagule pressure and environmental matching), successful invaders are generally characterized by life-history

strategies in which they give priority to future rather than current reproduction (Sol et al. 2012b). Such a strategy of expected future returns is generally achieved by investing in survival and hence attaining a long reproductive lifespan. However, it can also be achieved by reproducing more frequently, which combines the benefits of a higher reproductive effort with lower costs of losing a breeding attempt. This later strategy may explain the invasion success of species like rats and pigeons. Other strategies and mechanisms are likely to emerge in coming years.

Do Communities Differ in Invasibility?

Species-rich communities have long been thought to be more resistant to the establishment of NIS, a theory known as the 'biotic resistance' hypothesis. As more species are present in a community, the niches will be better filled and competition for resources like food, breeding sites or shelter will be stronger (Elton 1958). This would reduce the likelihood of establishment of additional species.

The existence of 'biotic resistance' has been demonstrated in microcosm and mesocosm experiments. Levine (2000), for example, designed a field experiment in which exotic plants were introduced into tussocks where the number of resident plant species had been manipulated in situ. As species richness increased, the likelihood of germinating and surviving the breeding season declined in two out of the three studied invaders.

However, ecological interactions rarely enable communities to resist establishment of NIS but only limit their abundance, at least in plants (Levine et al. 2004). Indeed, stochastic niche theory argues that local diversity is rarely limited by competition (Tilman 2004). Rather, with the addition of large numbers of propagules of novel species, many more species are predicted to coexist locally than ever would occur with natural assembly (Tilman 2004).

Moreover, observations at large spatial scales often show a positive (instead of the predicted negative) correlation between exotic and native species richness. In the tussocks studied by Levine (2000), the natural incidence of all three exotic plants was greater on more diverse tussocks. Such patterns may suggest that other features of the habitat can also be important, if not more important, than biotic resistance. At higher spatial scales the relative effect of biotic interactions diminishes and environmental factors gain importance in shaping regional biodiversity. If the environmental factors that favours higher number of native species also increase niche opportunities for the establishment of NIS, then the existence of a positive correlation between exotic and native species richness do not necessarily deny the importance of biotic resistance (Shea and Chesson 2002).

The nature of such environmental factors is not well-known yet, although some possibilities have been advanced. First, a structurally heterogeneous region may provide a greater array of microenvironments (Davies et al. 2005), increasing the likelihood that the invader encounters a favourable niche not monopolized by native species. In plants, there are more alien plant species and they are more abundant at fragment edges than in the interior of fragments (Vilà and Ibáñez 2011). Second, climatic conditions are also expected to influence both native and exotic species

richness by limiting the number of species that can persist in the region when these conditions are most extreme. This can in part explain why invaders are scarcer on the top of mountains (Bartomeus et al. 2011). Finally, disturbance, whether temporal or permanent, is thought to facilitate invasion by simultaneously opening resource opportunities and decreasing competition from resident native species (Tilman 2004). Habitats altered or entirely created by humans may be particularly susceptible to invasion, as the resulting communities have had less time to assemble, and hence to adapt to the local conditions and to each other; moreover, these communities are also more likely to have fewer species with broader niches and lower competitive abilities (Shea and Chesson 2002).

There is indeed evidence that environmental heterogeneity, climate conditions and anthropogenic disturbances can be common factors favouring both native and exotic species richness. Bartomeus et al. (2011), for instance, identified habitat heterogeneity, high precipitation, low altitude, elevated human density and anthropogenic disturbances as common factors favouring both native and exotic plants in Catalonia (see also Pino et al. 2005). However, these common factors did not seem to be the whole explanation for the positive relationship between exotic and native species richness. When these common causes were controlled for with structural equation modelling, the positive relationship did not turn out negative (Bartomeus et al. 2011).

As alternatively, it is possible that the positive correlation between exotic and native species richness also reflects the difficulties of separating invasibility from invasion rate. Human activities may not only create new niche opportunities for both exotic and native species adapted to disturbances, but also facilitate the transport (intentionally or unintentionally), introduction and spread of exotic and native species adapted to such environments. Rejmánek (2003), for example, showed that a positive native–exotic plant richness association previously reported for North American plants turned out negative when human population density was included along with latitude in a model predicting exotic species richness. The analyses of Bartomeus et al. (2011) of plants from Catalonia are also consistent with the importance of human-driven effects. When the comparison was restricted to native plants associated with anthropogenic-disturbed ecosystems (i.e. ruderal plants), the positive relationship between native-exotic species richness became stronger (from an $R^2 = 0.11$ to 0.52) and the fraction explained by common factors also increased substantially (58.3 %). The important role of human activities in creating a positive native-exotic richness association is not surprising given that biological invasions are induced by human activities, and highlights the need of distinguishing invasiveness from invasion rates when testing the biotic resistance hypothesis.

Darwin Naturalization Hypothesis: Are Close Relatives Bad Neighbors?

In the Origin of species, Darwin (1859) proposed the hypothesis that NIS should be more successful in communities in which their close relatives are absent. The rationale of the hypothesis is that close relatives are more likely to occupy niches that

would otherwise facilitate the establishment of NIS, an idea known as Darwin's naturalization hypothesis (DNH). The DNH has been demonstrated experimentally (Jiang et al. 2010). Analysing laboratory bacterial communities, Jiang et al. (2010) showed that the frequency of successful invader establishment was best explained by average phylogenetic distance between the invader and all resident species, consistent with the absence of empty niches. Invader abundance was also related to phylogenetic distance between the invader and its nearest resident relative, possibly indicating reduced availability of the optimal resources.

However, when we move from the controlled conditions of the laboratory to natural conditions the results become less clear, with different studies either supporting or refuting it (Jiang et al. 2010; Sol et al. 2014). This lack of firm support comes in part from using a scale of analyses too large for competition to be relevant or from not considering the possibility that the adaptations to become invasive are little phylogenetically conserved (Sol et al. 2014). In addition, the two basic assumptions of the hypothesis, that competition is a major process involved in biological invasions and that competition is more intense between close-related species, have been called into question by some authors (Duncan et al. 2003; Levine et al. 2004; Gilbert and Lechowicz 2005). As already mentioned, biotic resistance may reduce the establishment of species but rarely enables communities to resist invasion (reviewed in Levine et al. 2004). In addition, exotic species are unlikely to encounter close relatives in the recipient community when they come from distant regions (Valiente-Banuet and Verdú 2007). Finally, the strength of competition will not only depend on the presence of close-relatives, but also on their abundance (Tilman 1997) and the form in which they compete (Sol et al. 2012a; Jones et al. 2013). While competition with close-relatives is expected to increase with exploitative competition, as a result of increase in niche overlap in species with similar phenotypes, interference competition can be stronger among species with different phenotypes (e.g. differences in body size)(Jones et al. 2013).

Moreover, although competition is often assumed to be the primary source of biotic resistance, it is increasingly acknowledged that other mechanisms can also underlie the phenomenon and even be more important (Levine et al. 2004). The pressure from enemies (i.e. pathogens, parasites and predators) appears to be highly influential in this regard. Exotic birds, for example, appear to be more likely to fail on oceanic islands with species-rich mammalian predator assemblages (Cassey et al. 2005).

Not only evidence for the DNH is scarce, but some contrary results have also been accumulating showing that introduced organisms more closely related to native species are more likely to become invasive. Indeed, this possibility was already advanced by Darwin (1859), as NIS can share with their native relatives traits that pre-adapt them to their new environment (Table 2, scenario 2). As example, Duncan et al. (2002) analysed a complete list of seed-plant species introduced to New Zealand and found that those with congeneric relatives were significantly more, not less, likely to naturalize. Again the assumption here is that phylogenetic distance reflects ecological distance, which has been rarely tested. If phylogenetic distance accurately measures similarity in traits related to invasiveness, closely

related species should generally exhibit similar invasion potential. However, they often do not (Sol 2007). Although the differences can simply reflect differences in propagule pressure or in place of introduction rather than fundamental intrinsic differences (Fig. 2), evidence that close-relatives exhibit similar invasion potential is lacking.

Are Introduced Species Creating an "Invasional Meltdown"?

The emphasis on biotic resistance has led to under-appreciate the importance of positive interactions in the invasion process. Nevertheless, such perception is changing. In a review of invasions in the Great Lakes, Ricciardi (2001) showed that direct positive (mutualistic and commensal) interactions among introduced species are more common than purely negative (competitive and amensal) interactions. In terrestrial plants, positive interactions between NIS are also common, albeit in this case negative interactions are far more common (Kuebbing and Nuñez 2015).

The importance of mutualistic interactions is exemplified in ectomycorrhizal plants, whose invasion success has been limited in some regions by the absence of appropriate fungal symbionts (Traveset and Richardson 2011). Positive interactions are useful to understand the rapid invasion of some environments, an issue of great importance from a conservation perspective. Simberloff and Holle (1999) coined the term "invasional meltdown" to describe situations in which NIS facilitate one another's invasion instead of limiting invasions as the species accumulation increases biotic resistance (Ricciardi 2001; Simberloff 2006).

However, a full "invasional meltdown", in which interspecific facilitation leads to an accelerating increase in the number of introduced species and their impact, has yet to be conclusively demonstrated (Simberloff 2006). Better supported is nonetheless a weaker version of meltdown that argues that one invader facilitates population persistence of one or more other invaders without itself receiving an evident benefit (Simberloff 2006). For example, Grosholz (2005) used field and laboratory experiments to demonstrate that a recently introduced crab favoured the rapid proliferation of an introduced bivalve that had been rare for nearly 50 years. The effect was not direct but occurred through the positive indirect effects of predation by the introduced crab on native bivalves.

Does "Enemy Release" Explain the Increase and Expansion of Invaders?

One of the most puzzling observations in invasions biology is that some NIS perform better in their new ranges than in their native ones. A recent analysis indeed reported that invasive plants and animals tended on average to be more abundant in their introduced ranges (Parker et al. 2013). A possible explanation for why NIS can

proliferate in the new environment is that they are released from the pressure of co-evolved enemies (i.e. pathogens, parasites and predators), an idea known as the "enemy release" hypothesis (ERH, Elton 1958; Maron and Vila 2001). In the case of pathogens and parasites, an introduced host can be released from these enemies if for instance mortality during the transport mostly affects infected or parasitized individuals (Mitchell and Power 2003).

Although there is little doubt that enemies can be important agents of population control, whether NIS are generally released from their enemies remains less clear. At a biogeographic scale all NIS will lose some enemies (Colautti et al. 2004). However, community studies often show that NIS are no generally less affected by enemies than native species in the invaded community (Colautti et al. 2004). For example, Clay (1995) found that grasses native to the United States have, on average, fewer pathogen species than co-occurring NIS. In other cases, evidence either supporting or contradicting the enemy release hypothesis is inconclusive because the study do not quantify the impact of enemies on both NIS and native species, and still more rarely include controls that experimentally exclude enemies (Keane and Crawley 2002). The assumption of the enemy release hypothesis that few specialist enemies shift to attack NIS is also frequently falsified (Keane and Crawley 2002). Many invasive species are generalists unlikely to have co-evolved with enemies.

Some release from the pressure of enemies is expected in anthropogenic disturbed environments, where NIS attain highest success, as these environments typically contain simplified communities in which enemies are scarcer or even controlled for humans. However, this should not only benefit NIS but also native species.

What Is the Role of Evolution in the Invasion Process?

Evolution has often been dismissed as an important factor in the success of invaders because of the idea that genetic variation in small introduced populations should be reduced (see Moles et al. 2012). Indeed, bottlenecks have been demonstrated in many introduced populations. In a literature review, Puillandre et al. (2007) found lower genetic diversity in introduced populations than in native populations in 80 % of the 72 studies they examined. Bottlenecks can limit the success of invaders by inbreeding depression and by reducing genetic variation available for natural selection to adapt the population locally (Allendorf et al. 2013).

However, the predicted genetic reduction is not always observed (Roman and Darling 2007). In fact, genetic variation can be substantially enhanced when propagule pressure is high (Moles et al. 2012), as this increases the probability that individuals come from different source populations. For example, in a review of aquatic invasions, only 16 of 43 invasive species had reduced genetic diversity (Roman and Darling 2007). Genetic variation can also increase by hybridization. (Ellstrand and Schierenbeck 2006). Hybridization has for example been suggested to explain the rapid spread of mosquitos responsible of the transmission of the West Nile virus (Allendorf et al. 2013). In occasions, bottlenecks can themselves contribute to rapid

adaptation by providing raw material for natural selection through genetic drift and epistatic interactions (Sax et al. 2007).

Another reason why evolution has often been dismissed as an important factor in biological invasions is the common believe that adaptive change proceeds slowly. However, rapid adaptive evolution has been repeatedly demonstrated in introduced populations (Reznick and Ghalambor 2001; Moles et al. 2012). Reznick and Ghalambor (2001) found that many of the examples of contemporary evolution involves biological invasions. Colautti and Barrett (2013) indeed reported experimental evidence for earlier flowering in the North American invasive plant *Lythrum salicaria*. In this species, northern populations had been found to flower earlier than southern populations. Reciprocal transplant experiments demonstrated the characteristic "home site advantage" in which the organism attains higher fitness in their home region, thereby showing the adaptive nature of earlier flowering.

During the spreading stage, evolution can proceed particularly faster when there is heritable variation in traits affecting dispersal. Individuals at the forefront of the expansion encounter a low density of individuals and hence will tend to mate assortatively with respect to the dispersal trait (Phillips and Suarez 2012), favoring rapid evolutionary divergence. In cane toads (*Bufo marinus*) introduced to Australia, the annual rate of progress of the toad invasion front has increased about fivefold since the toads first arrived (Phillips et al. 2006). This seems to have resulted from selection for longer limbs: Toads with longer legs move faster and are the first to arrive to new areas.

The study of biological invasions has largely contributed to the debate of whether evolution is contingent or follows consistent routes. Several studies on introduced insects and plants have for instance reported the re-establishment of latitudinal clines in life history traits similar to those found in their native ranges. A classic example is the restitution of the Bergman's rule (i.e. increase in body size with latitude) in *Drosophila suboscura* introduced to North American (Huey et al. 2000). In other cases, however, consistent evolutionary routes have been harder to demonstrate. The EICA hypothesis, for instance, argues that because of the enemy release, invaders do not need to invest in defense and can relocate resources to be more efficient and competitive in the novel environment (Blossey and Nötzold 1995). Despite receiving considerable interest, the EICA hypothesis has surprisingly received little unambiguous support. Some studies do provide evidence that introduced species has lost enemy resistance, yet they fail to show that this loss increases fitness (Maron et al. 2004). Even in cases that demonstrate fitness benefits, the explanatory power of the hypothesis appears to be low. Colautti and Barrett (2013), for example, showed that in introduced *L. salicaria* the fitness benefits of earlier flowering in response to shorter growing seasons is significantly higher than those of reducing defense investment.

Despite the progress, our understanding of the exact role of evolution in the invasion process is deficient. Hendry et al. (2008) conducted a meta-analysis and found that plastic responses were more frequent than genetic change when organisms confront human-induced changes (mostly involving NIS). There is thus an urgent need to understand the mechanisms of rapid evolutionary adaptation rather than simply

document new cases. We do not even known at what stage of the invasion process is evolution more important, although several lines of evidence suggest that evolution should be more relevant at the last stages of the invasion process. At earlier stages, selection should lead to weaker evolutionary responses, as the population is smaller, and strong selection can lead the population to extinction. Indeed, the often observed time-lags in which the population remains at low numbers before explodes (Sakai et al. 2001) could in part be attributed to insufficient opportunities for local adaption.

Are Exotics Decreasing, Maintaining or Increasing Biodiversity?

NIS can impact on native species through a variety of mechanisms including predation, competition, hybridization and habitat alteration (Vilà et al. 2011). However, their role in reducing biodiversity remains controversial. Biological invasions involve both species additions and extirpations, and hence the resulting regional and local diversity results from the balance between both processes (Case 1996). If some areas hold lower species richness than it could really hold because many have been unable to colonize the area, then human-assisted invasions may increase diversity with little biodiversity loss.

Indeed, empirical work by Sax and collaborators indicate that at the regional level, exotic additions have often increased biodiversity, suggesting that at least at this spatial scale there is no species saturation (Brown and Sax 2007; Sax and Gaines 2008). Except for birds in oceanic islands, in which the number of native extinctions has been largely matched the number of established NIS, an increase in species richness has been reported for plants, freshwater fishes and mammals. Alien plants, for example, have doubled native biodiversity in oceanic islands.

A relevant question is therefore whether alien species richness will continue to increase as new species are added or has instead reached an equilibrium point. According to classical island biogeography theory, a saturation point can be maintained through the balance between extinctions and colonizations, where the number of species that colonize lead to the extinction of an equal number of species already present (extinction-based saturation)(Sax and Gaines 2008). The extinction-based saturation does not seem prevalent, however. In both plants and freshwater fish, species richness has increased because few native species have gone extinct whereas many exotic species have become naturalized. Even in birds from oceanic islands, where colonizations have largely matched extinctions, this is not extinction-based saturation because most extinctions were not caused by the introduced birds but by other factors like human hunting or introduced mammals (Duncan and Young 2000; Owens and Bennett 2000). However, the conclusion that extinction-based saturations are rare should be taken with caution as there are currently high uncertainties in how long extinctions take to manifest, the so-called extinction debt.

Alternatively, a saturation point can be maintained through biotic resistance, where species richness restricts additional introductions. Sax and Gaines (2008)

called this later process colonization-based saturation. Although such type of saturation is in line with the observed reduced local extinction observed in plants and fresh-water fish, there is little unambiguous indication for species saturation in natural communities (Sax and Gaines 2008). The only firm evidence currently available comes from the studies of *Anolis* lizards from the Caribbean (Helmus et al. 2014). While no anole has gone extinct on Caribbean islands in the last decades, except possibly one, at least 18 species have established, probably arriving as commensals of humans in cargo shipments. As a result, species richness has increased in average from 4.72 to 5.41 species. Interestingly, islands impoverished in native species have gained the most exotic species, strengthening the species–area relationship by which larger islands can harbour more species. This suggests that the communities have reached a saturation point, although it remains to be tested whether this has been achieved through biotic resistance.

As pointed by Sax and Gaines (2008), a local increase of biodiversity with the addition of NIS is not necessarily good from a conservation perspective as many unique endemic species may have been lost and replaced by more cosmopolitan species. Moreover, rather than the number, the identity of the species and their role in the ecosystem appear more relevant to understand how NIS affect the structure and function of ecosystems. Four possibilities exist here: (1) all species from the community play different roles, so the addition and removal of any species has always certain impact on the ecosystem; (2) species belong to different functional groups, and hence the replacement of a native species for a NIS should have little effect if they belong to the same group (as they do redundant functions) and high effect if belongs to a different group; (3) the NIS becomes a key species in the ecosystem, either because replaces a native species playing such a role or because plays a role different from all other species; and (4) all species are ecologically equivalent and hence there is no effect of the entrance of an invader. Understanding how frequently these alternatives occur is important not only from a conservation perspective, but also to help guarantee ecosystem services that are essential for human societies. While evidence exist for each of these possible outcomes, NIS typically lead to an increase, not a decrease, in ecosystem function (Ehrenfeld 2010; Vilà et al. 2011). Particularly troubling is the existence of examples for the third scenario, which can lead to cascade effects through the whole ecosystem. Zebra mussels (*Dreissena polymorpha*), for example, alters aquatic ecosystems by acting as a powerful filter that increases light and nutrients, allowing the proliferation of plants and algae (Ludyanskiy et al. 1993).

Concluding Remarks

The field of biological invasions has experienced an enormous progress in the last decades. Much of the progress comes from adopting ecological and evolutionary theories as a working framework and from improving the rigor in adopting and rejecting new hypotheses and theories. This has led to reject some ideas that were taken by granted in the past, like the view that islands are easier to invade than

continents or that NIS are competitively superior to native organisms. Although many ideas in invasion biology still remain controversial, we now start having a reasonable understanding of the processes of invasiveness and invasibility (Fig. 3). An important advance has been acknowledging that human influences are pervasive and varied throughout the invasion process, and hence that an anthropocene pespective is needed if we aim to understand the biogeography of biological invasions (Stuart et al. 2012).

Valéry et al. (2013) have recently called into question the need of the biological invasions discipline on the grounds that native species should also be called invasive whenever they outbreak. However, as pointed out by Blondel et al. (2013), there is no reason for unifying concepts and terminology to include native species. Rather,
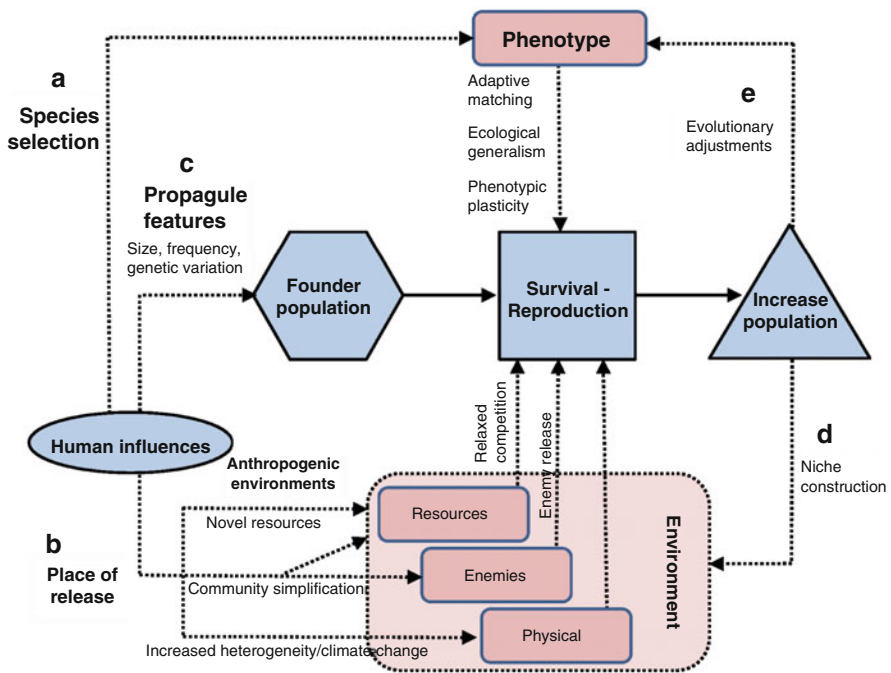

Fig. 3 General framework to understand the success of NIS. The likelihood that a NIS can increase in numbers in the novel environments depends on resource availability, enemies and the physical environment. Human activities can increase this likelihood in three ways: (**a**) selecting the type of organisms that are introduced, which should often favor organisms pre-adapted to the new environment and/or that exhibit high ecological and phenotypic plasticity; (**b**) determining the environments where they are released, which will often exhibit anthropogenic disturbances that increase invasibility through increased environmental heterogeneity, simplification of the native community (releasing the NIS from many enemies and competitors) and enhanced resource opportunities; and (**c**) affecting the size and structure of their founder populations, which determines the importance of Allee effects and demographic and genetic stochasticity. The organism itself can to some extent modify their new environment through niche construction (**d**), as well as improve fitness through an evolutionary rescue (**e**)

as suggests the evidence summarized in this chapter, the discipline of biological invasions departs from other disciplines at two levels. The first is the uniqueness of the processes that investigates, particularly regarding the importance of anthropogenic influences, magnitude of distances at which the organisms are moved, and the extent of which NIS differentiate from native species and exhibit adaptive mismatch respect to the novel environment, all of which requires a specific framework (Fig. 3). The second is the unique focus on preventing and mitigating the impact of organisms outside their native ranges, which makes challenging anticipate consequences. While we are still far from being able to predict the outcome of any introduction event, for some groups like plants and vertebrates we at least can identify situations where the risk is high that the species successfully establishes itself in a new environment (Kolar and Lodge 2002, Vall-llosera and Sol 2009; Leung et al. 2012). Because the entrance of NIS seems inevitable, concern over the impact of invaders will continue being an important reason fueling research on biological invasions.

Yet, ecologist should avoid at the same time committing the "appeal to nature fallacy" of considering that something is good simply because it is natural and bad because it is not (Brown and Sax 2005). Many invaders are innocuous and have come to stay, yet they still have important value for addressing scientific questions. Indeed, as shown throughout the chapter, NIS offer unique opportunities for studying a variety of ecological and evolutionary processes in real time and at an unprecedented scales. Some of the ideas that the discipline has contributed to reshape include community assemblage rules, ecological cascades and the speed of contemporary evolution (Callaway and Maron 2006; Reznick et al. 2008; Helmus et al. 2014). Thus, despite claims for the end of invasion biology, the field still has much to offer and I anticipate that the enormous current interest in the discipline will continue growing in the coming years.

References

Allendorf FW, Luikart G, Aitken SN (2013) Conservation and the genetics of populations. Wiley-Blackwell, Sussex (UK)

Amiel JJ, Tingley R, Shine R (2011) Smart moves: effects of relative brain size on establishment success of invasive amphibians and reptiles. PLoS One 6:e18277

Barnagaud J, Barbaro L, Papaïx J (2013) Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds. Ecology 95:78–87

Bartomeus I, Sol D, Pino J, Vicente P, Font X (2011) Deconstructing the native-exotic richness relationship in plants. Glob Ecol Biogeogr 21:524–533

Blackburn TM, Cassey P, Lockwood JL (2009) The role of species traits in the establishment success of exotic birds. Glob Chang Biol 15:2852–2860

Blackburn TM, Duncan RP (2001) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. J Biogeogr 28:927–939

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339

Blondel J, Hoffmann B, Courchamp F (2013) The end of invasion biology: intellectual debate does not equate to nonsensical science. Biol Invasions 16:977–979

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889

Brown BJH, Sax DF (2007) Do biological invasions decrease biodiversity? Conserv Mag 8:16–17

Brown JH, Sax DF (2005) Biological invasions and scientific objectivity: reply to Cassey et al. (2005). Austral Ecol 30:481–483

Callaway RM, Maron JL (2006) What have exotic plant invasions taught us over the past 20 years? Trends Ecol Evol 21:369–374

Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. Biol Conserv 78:69–96

Cassey P, Blackburn TM, Duncan RP, Gaston KJ (2005) Causes of exotic bird establishment across oceanic islands. Proc R Soc Lond B 272:2059–2063

Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL (2004) Global patterns of introduction effort and establishment success in birds. Proc R Soc Lond B 271:S405–S408

Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. Science (New York, NY) 342:364–366

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Lett 7:721–733

Clay K (1995) Correlates of pathogen species richness in the grass family. Canadian Journal of Botany 73:S42–S49

Darwin C (1859) The origin of species. J. Murray, London

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecol Lett 14:419–431

Davies KE, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. Ecology 86:1602–1610

Davis M (2009) Invasion biology. Oxford Univ Press, Oxford

Drake JM (2007) Parental investment and fecundity, but not brain size, are associated with establishment success in introduced fishes. Funct Ecol 21:963–968

Duncan RP, Blackburn TM, Sol D (2003) The ecology of bird introductions. Annu Rev Ecol Evol Syst 34:71–98

Duncan RP, Williams PA, Wikelski M, Wong V, Chevalier B, Rattenborg N, Snell HL, Janvier P, Arsenault M (2002) Darwin's naturalization hypothesis challenged. Nature 417:608–609

Duncan RP, Young JR (2000) Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. Ecology 81:3048–3061

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annu Rev Ecol Evol Syst 41:59–80

Ehrlich PR (1989) Attributes of invaders and invading processes: vertebrates. In: Drake JA, DiCastri F, Groves RH, Kruger FJ, Mooney HA, Rejma´nek M, Williamson MH, (eds) Biological invasions: a global perspective. Wiley, New York, USA, pp 315–328

Ellstrand NC, Schierenbeck KA (2006) Hybridization as a stimulus for the evolution of invasiveness in plants? Proc Natl Acad Sci U S A 148:35–46

Elton CS (1958) The ecology of invasions by animals and plants. Wiley, New York

Evans K, Chamberlain D, Hatchwell BENJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? Glob Chang Biol 17:32–44

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Ann Rev Ecol Syst 29:113–140

Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. Ecology 86:1848–1855

Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proc Natl Acad Sci U S A 102:1088–1091

Haight RG, Polasky S (2010) Optimal control of an invasive species with imperfect information about the level of infestation. Res Energy Econ 32:519–533

Helmus MR, Mahler DL, Losos JB (2014) Island biogeography of the anthropocene. Nature 513:543–546

Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. Mol Ecol 17:20–29

Hernández-Brito D, Carrete M, Popa-Lisseanu AG, Ibáñez C, Tella JL (2014) Crowding in the city: losing and winning competitors of an invasive bird. PLoS One 9:e100593

Higgins SI, Richardson DM (2014) Invasive plants have broader physiological niches. Proc Natl Acad Sci U S A 111:10610–10614

Huey RB, Gilchrist GW, Carlson ML, Berrigan D, Serra L (2000) Rapid evolution of a geographic cline in size in an introduced fly. Science (New York, NY) 287:308–309

Jeschke J, Gómez Aparicio L, Haider S, Heger T, Lortie C, Pyšek P, Strayer D (2012) Support for major hypotheses in invasion biology is uneven and declining. NeoBiota 14:1–20

Jiang L, Tan J, Pu Z (2010) An experimental test of Darwin's naturalization hypothesis. Am Nat 175:415–423

Jones EI, Nuismer SL, Gomulkiewicz R (2013) Revisiting Darwin's conundrum reveals a twist on the relationship between phylogenetic distance and invasibility. Proc Natl Acad Sci U S A 110:20627–20632

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Kolar CK, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kolar CS, Lodge DM (2002) Ecological predictions and risk assessment for alien fishes in North America. Science (New York, NY) 298:1233–1236

Kuebbing SE, Nuñez MA (2015) Negative, neutral, and positive interactions among nonnative plants: patterns, processes and management implications. Global Change Biol 21:926–934

Lande R, Engen S, Saether B-E (2003) Demographic and environmental stochasticity. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233–246

Leung B, Roura-Pascual N, Bacher S, Heikkilä J, Brotons L, Burgman MA, Dehnen-Schmutz K, Essl F, Hulme PE, Richardson DM, Sol D, Vilà M, Rejmanek M (2012) TEASIng apart alien species risk assessments: a framework for best practices. Ecol Lett 15:1475–1493

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Lewontin RCC, Cohen D (1969) On population growth in a randomly varying environment. Proc Natl Acad Sci U S A 62:1056–1060

Lockwood JL, Cassey P, Blackburn TM (2005) The role of propagule pressure in explaining species invasions. Trends Ecol Evol 20:223–228

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol (Personal Edn) 8:133–137

Ludyanskiy ML, McDonald D, MacNeill D (1993) Impact of the Zebra Mussel, a Bivalve Invader. Bioscience 43:533–544

Maron JL, Vila M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373

Maron J, Vilà M, Arnason J (2004) Loss of enemy resistance among introduced populations of St. John's Wort (Hypericum perforatum). Ecology 85:3243–3253

Martin TE, Maron JL (2012) Climate impacts on bird and plant communities from altered animal–plant interactions. Nat Climate Change 2:195–200

McLain DK, Moulton MP, Sanderson JG (1999) Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. Evolutionary Ecol Res 1:549–565

Miller DJ (1989) Introductions and extinction of fish in the African great lakes. Trends Ecol Evol (Personal Edn) 4:56–59

Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. Nature 421:625–627

Moles AT, Flores-Moreno H, Bonser SP, Warton DI, Helm A, Warman L, Eldridge DJ, Jurado E, Hemmings FA, Reich PB, Cavender-Bares J, Seabloom EW, Mayfield MM, Sheil D, Djietror JC, Peri PL, Enrico L, Cabido MR, Setterfield SA, Lehmann CER, Thomson FJ (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. J Ecol 100:116–127

Møller AP, Díaz M, Flensted-Jensen E, Grim T, Ibáñez-Álamo JD, Jokimäki J, Mänd R, Markó G, Tryjanowski P (2015) Urbanized birds have superior establishment success in novel environments. Oecologia. doi:10.1007/s00442-015-3268-8

Reznick DN, Ghalambor CK (2001) The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112–113:183–198

Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc Natl Acad Sci U S A 97:12144–12148

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Whonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Parker JD, Torchin ME, Hufbauer RA, Lemoine NP, Alba C, Blumenthal DM, Bossdorf O, Byers JE, Dunn AM, Heckman RW, Hejda M, Jarosík V, Kanarek AR, Martin LB, Perkins SE, Pysek P, Schierenbeck K, Schlöder C, van Klinken R, Vaughn KJ, Williams W, Wolfe LM (2013) Do invasive species perform better in their new ranges? Ecology 94:985–994

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler C, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348

Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. Nature 439:803

Phillips B, Suarez A (2012) The role of behavioural variation in the invasion of new areas. In: Candolin U, Wong B (eds) Behavioural responses to a changing world. Oxford Univerisity Press, Oxford, pp 190–200

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agricul Ecosyst Environ 84:1–20

Pino J, Font X, Carbó J, Jové M, Pallarès L (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). Biol Conserv 122:339–350

Pouteau R, Hulme PE, Duncan RP (2015) Widespread native and alien plant species occupy different habitats. Ecography 38:462–471

Price TD, Qvarnström A, Irwin DE (2003) The role of phenotypic plasticity in driving genetic evolution. Proc R Soc Lond B 270:1433–1440

Puillandre N, Dupas S, Dangles O, Zeddam J-L, Capdevielle-Dulac C, Barbin K, Torres-Leguizamon M, Silvain J-F (2007) Genetic bottleneck in invasive species: the potato tuber moth adds to the list. Biological Invasions 10:319–333

Rejmánek M (2003) The rich get richer. Front Ecol Environ 1:122–123

Reznick DN, Ghalambor CK, Crooks K (2008) Experimental studies of evolution in guppies: a model for understanding the evolutionary consequences of predator removal in natural communities. Mol Ecol 17:97–107

Ricciardi A (2001) Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Can J Fisheries Aquat Sci 58:2513–2525

Ricciardi A, Jones LA, Kestrup ÅM, Ward JM (2011) Expanding the propagule pressure concept to understand the impact of biological invasions. In: Richardson DM (ed) Fifty Years of Invasion Ecology: The Legacy of Charles Elton, Blackwell, Oxford, pp 225–235

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distribut 6:93–107

Roff DA (2002) Life history evolution. Sinauer Associates, INC, Sunderland

Roman J, Darling JA (2007) Paradox lost: genetic diversity and the success of aquatic invasions. Trends Ecol Evol 22:454–464

Sakai AKK, Allendorf FWW, Holt JSS, Lodge DMM, Molofsky J, With KAA, Baughman S, Cabin RJJ, Cohen JEE, Ellstrand NCC, Cauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive specie. Ann Rev Ecol Syst 32:305–332

Sax DF, Brown JH (2000) The paradox of invasion. Glob Ecol Biogeogr 9:363–371

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471

Sax D, Gaines S (2008) Species invasions and extinction: the future of native biodiversity on islands. Proc Natl Acad Sci U S A 105:11490–11497

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Shochat E, Susannah B, Warren PS, Faeth S (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208

Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Lett 9:912–919

Simberloff D (2013) Invasive species what everyone needs to know. Oxford University Press, New York

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Sol D (2000) Are islands more susceptible to be invaded than continents? Birds say no. Ecography 23:687–692

Sol D (2003) Behavioural flexibility: a neglected issue in the ecological and evolutionary literature? In: Reader SM, Laland KN (eds) Animal innovation. Oxford University Press, Oxford, pp 63–82

Sol D (2007) Do successful invaders exist? Pre-adaptations to novel environments in terrestrial vertebrates. In: Nentwig W (ed) Biological invasions. Springer, Heidelberg, pp 127–141

Sol D, Bacher S, Reader SM, Lefebvre L (2008) Brain size predicts the success of mammal species introduced into novel environments. Am Nat 172 Suppl:S63–S71

Sol D, Bartomeus I, Griffin AS (2012a) The paradox of invasion in birds: competitive superiority or ecological opportunism? Oecologia 169:553–564

Sol D, Duncan RP, Blackburn TM, Cassey P, Lefebvre L (2005) Big brains, enhanced cognition, and response of birds to novel environments. Proc Natl Acad Sci U S A 102:5460–5465

Sol D, Lapiedra O, Gonzalez-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112

Sol D, Lapiedra O, Vila M (2014) Do close relatives make bad neighbors? Proc Natl Acad Sci 111:E534–E535

Sol D, Maspons J, Vall-llosera M, Bartomeus I, Garcia-Pena GE, Pinol J, Freckleton RP (2012b) Unraveling the life history of successful invaders. Science 337:580–583

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob Ecol Biogeogr 22:962–970

Stuart YE, Losos JB, Algar AC (2012) The island-mainland species turnover relationship. Proceedings. Biolog Sci/R Soc 279:4071–4077

Tilman D (1997) Community invasibility, recruitment limitation, and grassland diversity. Ecology 78:81–92

Tilman D (2004) A stochastic theory of resource competition, community assembly and invasions. Proc Natl Acad Sci U S A 101:10854–10861

Traveset A, Richardson DM (2011) Mutualisms: key drivers of invasions … key casualties of invasions. In: Richardson DM (ed) Fifty years of invasion ecology: the legacy of Charles Elton. Blackwell Publishing Ltd, Oxford, pp 143–160

Valéry L, Fritz H, Lefeuvre JC (2013) Another call for the end of invasion biology. Oikos 122:1143–1146

Valiente-Banuet A, Verdú M (2007) Facilitation can increase the phylogenetic diversity of plant communities. Ecol Lett 10:1029–1036

Vall-llosera M, Sol D (2009) A global risk assessment for the success of bird introductions. J Appl Ecol 46:787–795

Veltman CJ, Nee S, Crawley MJ (1996) Correlates of introduction success in exotic New Zealand birds. Am Natural 147:542–557

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708

Vilà M, Gómez A, Maron JL (2003) Are alien plants more competitive than their native conspecifics? A test using Hypericum perforatum L. Oecologia 137:211, 2005, 145:175

Vilà M, Ibáñez I (2011) Plant invasions in the landscape. Landsc Ecol 26:461–472

Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA (1987) Biological invasion by Myrica faya alters ecosystem development in Hawaii. Science (New York, NY) 238:802–804

Weiher E, Keddy P (1995) Assembly rules, null models, and trait dispersion: new questions from old patterns. Oikos 74:159–164

Williams GC (1966) Adaptation and natural selection. Princeton University Press, Princeton

Williamson MH (1996) Biological invasions. Chapman and Hall, London

Williamson MH, Brown KC, Holdgate MW, Kornberg H, Southwood R, Mollison D (1986) The analysis and modelling of British invasions. Philos Transac R Soc Lond B Biol Sci 314:1167

Williamson MH, Fitter A (1996) The varying success of invaders. Ecology 77:1661–1666