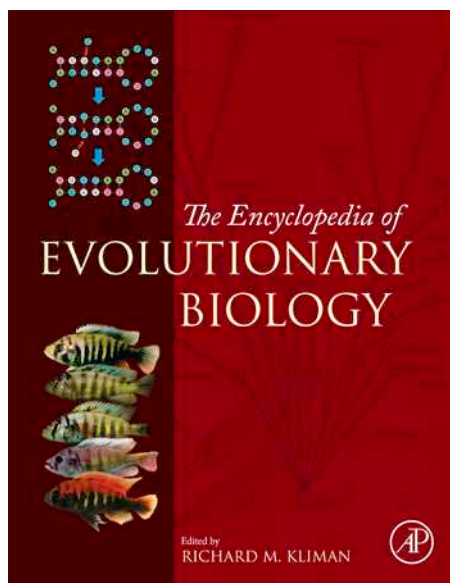


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Invasive Species, Evolution and

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Glossary

Admixture Population composed of individuals from previously separated source populations.

Biotic homogenization Increasing genetic and taxonomic similarity between regions across the globe which is promoted by species invasions.

Invasion vector Mechanism of human transport of nonnative species from their native, source region to a nonnative, recipient region.

Invasive species Nonnative species that have been introduced by humans and have established and spread in their introduced range.

Propagule pressure The total number of introduced individuals, which is a function of number of introduction events and number of propagules released during each event.

Background

The study of species invasions is important both from the perspective of biodiversity conservation and because it provides general insights into ecology and evolution (Sax *et al.*, 2005, 2007). One of the most important and defining characteristics of invasive species is that their evolutionary history with species in the invaded region is relatively short (Strauss *et al.*, 2006a,b; Sorte *et al.*, 2010a). To explore the role of evolution in species invasions in more detail, it is first important to define invasive species, the steps species must undergo to become invasive, and the scope of the invasive species problem.

Defining Invasive Species

Invasive species are defined as nonnative species that have been introduced by humans and have established and spread in their introduced range. These last two characteristics – establishment and spread – imply impacts on native communities, although impacts have been quantified for only a small proportion of introduced species (e.g., Williams and Smith, 2007). In some cases, when the term invasive is synonymous with weedy, some subset of native species could also fit this definition (Vigueira *et al.*, 2013). This article focuses on nonnative invasive species; however, certain evolutionary concepts related to invasive species will also apply to native pests.

The Invasion Pathway

Species invasions occur via a stepwise process known as the invasion pathway (Figure 1; see also Theoharides and Dukes, 2007). First, individuals of a species are transported by humans from the source region in their native range to the recipient region in their nonnative range via an introduction vector. This transport can be either intentional (e.g., plants sold in the horticultural trade; Mack and Lonsdale, 2001) or unintentional (e.g., hitchhikers in commercial shipping vessels; Westphal *et al.*, 2008). Second, colonization occurs if the transported individuals are able to survive and reproduce in

the nonnative range. Third, the introduced species is considered established if it has formed a reproducing and self-sustaining population. The final step in the invasion pathway is secondary spread, in which the species extends its range within the nonnative region. By definition, an invasive species must not only become established in its new location, but it must also expand its range beyond the original introduction site.

Whether or not a species is successful in becoming invasive depends upon its ability to pass through filters imposed by the different stages of the invasion pathway (Figure 1). For example, before even arriving in their new territory, future invasive species must find – or be chosen for – transport and

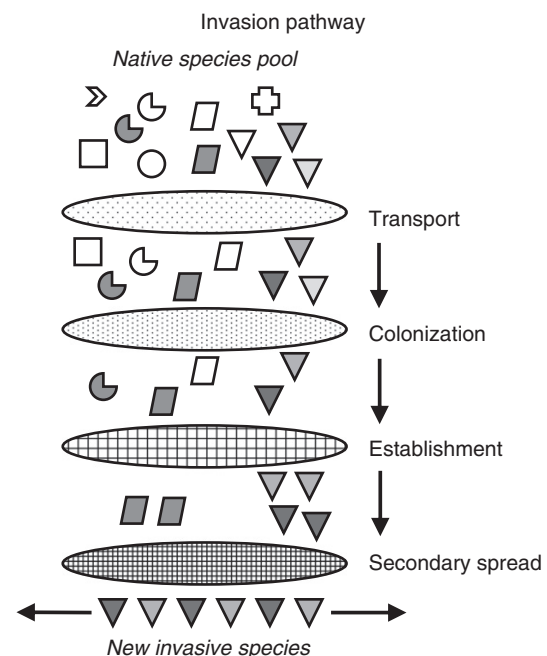


Figure 1 In order to become invasive, species (different shapes) must pass through four stages (listed on the right). Each stage acts as a filter to decrease the species pool as well as genetic diversity (indicated by shading in the shapes) within each species.

survive the journey. Once in the new habitat, invasion success depends on the ability to tolerate climatic conditions, attain resources, and avoid consumption in the nonnative range under a potentially novel set of abiotic and biotic conditions. The sequential narrowing of the potential invasive species pool is illustrated by the tens rule, which suggests that only 10% of introduced species become established, and only 10% of these become invasive (Williamson, 1996). Actual proportions rarely conform to such a simple scheme and are taxon-specific; however, establishment and subsequent invasiveness only occur in the minority of introductions (Jeschke and Strayer, 2005).

Scope of the Invasion Problem

Despite the fact that most species do not become invasive, those that do can have extremely large ecological impacts and economic costs (Pimentel *et al.*, 2005), and the invasion problem is increasing (Butchart *et al.*, 2010) concurrent with globalization. There were approximately 120 000 nonnative species in the United States, Europe, Australia, South Africa, India, and Brazil as of the census by Pimentel *et al.* (2002) (Figure 2), and the control of – and damages by – invasive species in those countries cost more than \$300 billion per year. Even a relatively small-scale introduction of the killer alga, *Caulerpa taxifolia*, one of the world's '100 worst' invasive species, near San Diego, California, USA, cost > \$6 million for local eradication (Williams and Grosholz, 2008).

In ecological terms, invasive species have driven declines in native populations, as well as extinctions. The impact of each invasive species is expected to increase directly with range size, population size, and per capita effect (Parker *et al.*, 1999). Although extinction causes are often equivocal and

occasionally disputed, invasive species are implicated as a leading cause of animal (particularly bird and fish) extinctions (Gurevitch and Padilla, 2004; Clavero and Garcia-Berthou, 2005). In fact, invasive species are considered one of the primary threats to global biodiversity across terrestrial and aquatic ecosystems (Sala *et al.*, 2000; Millennium Ecosystem Assessment, 2005) and, more specifically, to an estimated 42% of species on the threatened and endangered species lists (Pimentel *et al.*, 2005). Extinctions are particularly likely on islands, where potential for avoidance of invasive predators via niche displacement or rapid evolution is relatively low (Mooney and Cleland, 2001). For example, the invasive brown tree snake appears to have driven extinctions of native birds on Guam, in the tropical western Pacific Ocean (Savidge, 1987). The invasion problem is becoming exacerbated as introductions are not only continuing but are increasing in many regions (Cohen and Carlton, 1998; Millennium Ecosystem Assessment, 2005), leading to rapid biotic homogenization (see Olden *et al.*, 2004).

Evolutionary Characteristics of Invasive Species

Introduced species can be prone to founder events and population bottlenecks imposed by filters in the invasion pathway, leading to declines in genetic diversity within nonnative populations as compared to their native, source populations. In a review of 80 species of animals, plants, and fungi, diversity of alleles and heterozygosity were significantly lower in introduced populations than in source populations, although decreases were less than 20% (Dlugosch and Parker, 2008; also see Wares *et al.*, 2005). Furthermore, Dlugosch and Parker (2008) found a U-shaped relationship between genetic



Figure 2 Invasive species are a global issue, leading to economic, ecological, and evolutionary impacts on native ecosystems. Examples of recent invaders include (a) the Cuban tree frog, invasive in the USA (Florida and Hawaii) and throughout the Caribbean; (b) a suite of invasive tunicates that are now found in coastal waters worldwide and foul docks, boats, and shellfish; and (c) the cordgrass *Spartina alterniflora* which has hybridized with a native species, *Spartina foliosa*, and is shown here invading San Francisco Bay, California, USA.

(allelic) diversity and time since first introduction, suggesting that selection and genetic drift continue the loss of genetic diversity during the first several decades after colonization. Over longer time scales, multiple introductions can cause genetic diversity to rise again via the mechanisms discussed below. Thus, it is perhaps not surprising that a lag phase often occurs between the colonization and spread stages in the invasion pathway (see Crooks, 2005), in which population growth and subsequent spread are inhibited either directly by low population sizes or by low level of genetic variation within the populations.

Propagule pressure – or the total number of introduced individuals – is one of the best supported correlates of invasion success (Kolar and Lodge, 2001; Lockwood *et al.*, 2005; Colautti *et al.*, 2006) and can counteract the effect of founder events on genetic diversity within introduced populations (Roman and Darling, 2007). Simberloff (2009) reviewed examples – from birds to ungulates – of cases where introductions failed until the number of introduced individuals exceeded a minimum threshold. Increased propagule pressure is associated with increased population sizes and increased genetic diversity within populations (Simberloff, 2009). Furthermore, multiple introductions may lead to the formation of admixtures, new populations composed of individuals from previously separated source populations. Such introduced admixture populations can have equivalent (Dlugosch and Parker, 2008) or even increased levels of genetic diversity as compared to individual source populations (Kolbe *et al.*, 2004; Gillis *et al.*, 2009).

In addition to the invasion process influencing genetic diversity, there is some evidence that genetic diversity also influences invasion success. For example, genetic diversity has been linked to colonization ability in the plant *Arabidopsis thaliana* (Crawford and Whitney, 2010) and productivity and clonal spread in a perennial grass (Lavergne and Molofsky, 2007). It is important to note, however, that there are a number of counter-examples to the trends presented above. Successful invasions of a broad range of species – including a European solitary bee to North America and the North American muskrat to Europe – are thought to have derived from only one to a few introduced individuals (see Simberloff, 2009). There are also examples where invasion success was associated with decreases rather than increases in genetic diversity (e.g., Schmid-Hempel *et al.*, 2007), particularly when loss of genetic variation increased the frequency of a genotype that proved to be beneficial (e.g., increase population sizes) in the nonnative habitat (e.g., Tsutsui *et al.*, 2000).

Evolution of Invasive Species

The invasion process drives evolution in invasive species via both non-selective and adaptive evolutionary mechanisms. The genetic characteristics of invasive species, discussed above, are indicators of the types of non-selective mechanisms at work. Low genetic diversity may indicate the influence of genetic drift, the random change in allele frequencies that more strongly impacts smaller populations. Genetic drift is likely in founder populations, including of introduced species, due to their small sizes (Sakai *et al.*, 2001). High genetic

diversity, on the other hand, has been related to the number of separate introduction events occurring over time (Dlugosch and Parker, 2008). Gene flow can be high when introduced individuals are sampled from a large geographic area and also when multiple introductions create admixtures, with increased propagule pressure decreasing the negative impacts of genetic drift and increasing potential for adaptive evolution in the nonnative range. Invasive success can be increased by hybridization both within and between species, including between natives and nonnative (Ellstrand and Schierenbeck, 2000; Schierenbeck and Ellstrand, 2009). For example, hybrids of the introduced cordgrass *Spartina alterniflora* and native species *Spartina foliosa* grow larger and are more invasive than either of the parent species in San Francisco Bay, California, USA (Grosholz, 2002; Figure 2).

Adaptive evolution is promoted in invasive species as they experience strong selection pressures at each stage in the invasion pathway. Initial transport might favor individuals that associate with and survive human transport, whereas secondary spread has been associated with increases in reproduction (Colautti and Barrett, 2013) and innate dispersal ability (Phillips *et al.*, 2006). For example, cane toads with longer legs are the first to arrive at and colonize new populations in Australia, and this shift in toad morphology could explain why the invasion front is extending faster over time (Phillips *et al.*, 2006). Within its nonnative habitat, a successful new invader must be capable of surviving environmental conditions, attaining resources, and avoiding predation. Novel environments and biotic interactions can select for shifted climatic tolerances (e.g., Sexton *et al.*, 2002; Lee *et al.*, 2003; Sorte *et al.*, 2011) or increased predator defense (e.g., Miehls *et al.*, 2014). On the other hand, some invasive species experience relaxed selection in the nonnative habitat due, for example, to release from their native enemies or competitors (the enemy release hypothesis (ERH); Keane and Crawley, 2002) or encounters with naïve prey (Cox and Lima, 2006). The evolution of increased competitive ability (EICA) hypothesis describes how this relaxation could allow a reallocation of resources from, for example, predator defense to competitive traits such as faster growth rate (Blossey and Nötzold, 1995). A review of pair-wise experiments suggested that invasive plants were better competitors than native species (Vilà and Weiner, 2004) and a meta-analysis of several hundred species indicated that invasive species had higher values for performance-related traits than non-invasive and native species (Van Kleunen *et al.*, 2010). However, the role of evolution in these competitive and trait differences is unknown, and there are many counter-examples. For example, Seabloom *et al.* (2003) found that native perennials were better competitors than invasive annual grasses, and they attributed the greater dominance of invasive species in their system to differential propagule pressure.

Although there is an increasing number of observations consistent with adaptation, it is important to note that natural selection is not the only explanation for observed phenotypic differences (Keller and Taylor, 2008). Phenotypes are reflections of both genotypes and environmental conditions, and many reports of phenotypic variation are based solely on observational data used to compare individuals of a species from within versus outside its native range or between multiple invasive populations. To determine whether phenotypic

variation is driven by genetic differences versus environmental plasticity, researchers often employ transplant – or ‘common garden’ – experiments in which the environmental factor is removed or accounted for in the experimental design (e.g., Sexton *et al.*, 2002; Lee *et al.*, 2003; Colautti and Barrett, 2013 cited above). Parker *et al.* (2003) used common-garden experiments to compare morphological traits across 10 populations of an invasive weed inhabiting a range of elevations across the Sierra Nevada Mountains, California, USA. They found that the great majority of phenotypic variance was at the individual (not family or population) level, indicating that differences between samples collected from the field were primarily due to phenotypic plasticity. There is even evidence that invasive species have higher levels of phenotypic plasticity than noninvasive species, as indicated by a meta-analysis of 75 plant species pairs (Davidson *et al.*, 2011). Clearly, population-level differences of invasive species across their native and nonnative ranges could reflect influences of myriad processes, including genetic drift, gene flow, hybridization, phenotypic plasticity, and natural selection.

Invasive Species as Drivers of Native Species Evolution

Observations across time (before and after invasion) and space (within vs. outside invasive species’ ranges) have uncovered evidence of invasive species impacts on native species, including cases of rapid evolution in native populations (Mooney and Cleland, 2001; Lambrinos, 2004; Strauss *et al.*, 2006b; Vellend *et al.*, 2007). As an example, Phillips and Shine (2006) suggested that native black snakes in Australia have evolved increased resistance to cane toad toxin and decreased prey preference for the toads after less than 23 generations. Invasive species have also impacted native populations via positive interactions. A native checkerspot butterfly in Nevada, USA incorporated the invasive European weed *Plantago lanceolata* into its diet, and breeding studies indicated a genetic basis to the butterfly’s feeding preference (Singer *et al.*, 1993). In some cases, utilizing novel resources requires further adaptation, and a native Australian soapberry bug has evolved longer mouthparts in order to feed on an invasive vine (Carroll *et al.*, 2005). Hybridization between invasive and native species appears to be widespread (Mooney and Cleland, 2001), such as the *Spartina* cordgrass example, above. Invasive species can even promote hybridization between two native species by providing a novel resource and, thus, leading to novel niche overlap between native species that would otherwise not meet nor reproduce (Schwarz *et al.*, 2005). It is, therefore, clear that invasive species have driven evolution of native species although, as for the evolution of the invasive species themselves, the relative contribution of genetic adaptation to observed changes is often unknown.

Implications for the Future: Applying an Evolutionary Perspective to Invasive Species Management

In the words of Charles Elton, called the ‘father’ of invasion biology, “we are seeing one of the great historical convulsions

in the world’s fauna and flora” (Elton, 1958, p. 31). Invasive species are contributing to the homogenization of both species and genetic material on a global scale, including driving extinctions of native species and diversification in their invaded habitats. They are an ecological, economic, and evolutionary threat of our own making: while we facilitated invasions initially, we now spend billions of dollars on their control. In so doing, we are driving adaptation of characteristics that allow the invasive species to avoid control and persist in their invaded range (Lee, 2002), including mimicry of the crops they invade and resistance to herbicides and pesticides (Vigueira *et al.*, 2013). Furthermore, we are indirectly contributing to the increased threat of invasive species by our role in driving global climate change, which appears to favor invasive species over native species (Sorte *et al.*, 2010b, 2013).

Future attempts to prevent, control, and eradicate invasive species could benefit from the incorporation of an evolutionary perspective (Whitney and Gabler, 2008). Although protocols are increasingly being implemented to prevent unintentional introductions of nonnative species, intentional imports continue, including through the horticultural trade (Bradley *et al.*, 2012). Importation suitability should be informed by Weed Risk Assessments, which, in the version used by the Australian government, includes population biology characteristics such as hybridization potential and reproductive strategies. Many invasive species start out as seemingly innocuous species introductions, and eradication efforts would ideally start during the establishment and lag phases. Efforts to prioritize nonnative species for control and eradication could be aided by an understanding of population genetics and ecological interactions, in order to identify species that are likely to become invasive, cause ecological and evolutionary damage (i.e., hybridization, extinctions, etc.), and evolve resistance to control methods (Allendorf and Lundquist, 2003). Finally, issues of invasive species developing evolved resistance should be acknowledged, with control practices including fluctuation of multiple herbicides, pesticides, or biological control agents, and potentially assisted spread of nonresistant genotypes (Stockwell *et al.*, 2003). A multipronged approach to invasive species management that incorporates an evolutionary perspective will help us to meet future challenges as invasion rates continue to increase (Millennium Ecosystem Assessment, 2005; Simberloff *et al.*, 2013).

See also: Ecological Fitting and Novel Species Interactions in Nature. Pest Management, Evolution and

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