Article

Invasion ecology: Origin and biodiversity effects

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Abstract

The history of invasion ecology, with respect to its mid-19th century beginning and its extended relationship with island biogeography, has not been investigated. In fact, most historical accounts begin with the publication of Charles Elton's book in 1958. Since that time, the field has undergone a phenomenal growth until it has become a major specialty area related to ecology, biogeography, and macroecology. Over the years, invasion studies have made significant contributions to knowledge in the areas of colonization, adaptation, biodiversity, evolution, and species relationships. But also, many ecologists became convinced that invasive species were responsible for native extinctions and the loss of biodiversity. However, new studies, based upon documented extinctions and their causes, have shown that invaders are rarely implicated. Instead, successful (colonizing) invaders are almost invariably accommodated by the native species that occupy the necessary habitat. Accommodation results in a gain in species diversity of the invaded area. Diversity gain generally results in a more stable system with higher productivity and a greater resistance to invasion. Furthermore, as the fossil data indicate, invasions may eventually result in additional speciation that adds to global biodiversity. These data provide evidence of a dynamic, global system consisting of successful invasions that extend from high species diversity centers outward to where diversity is less and the competition weaker.

Keywords accommodation; colonization; competition; facilitation; invasions; invasibility; speciation.

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1 Introduction

Within the past twenty years, the study of invasions by exotic organisms has become so popular that it is now a major research field within modern ecology and biogeography. Numerous journals now devote considerable space to articles on invasive species, two journals are entirely dedicated to the subject, and many new books have appeared. At the same time, some scientists and scientific writers have published articles in popular newspapers and magazines dwelling on species extinctions caused by humans and human-introduced organisms. The fact that the great majority of contemporary extinctions have taken place in locations that are

extremely space-limited, such as oceanic islands or freshwater lakes and streams, is often overlooked. As a result, there has developed among the general public, and within some conservation societies, a militaristic attitude toward invading species. That is, invaders are dangerous and must be repelled. As Brown and Sax (2004) have pointed out, invasion ecology has a need for more scientific objectivity and less emotional xenophobia.

The earliest work on invasions came with the recognition of long distance dispersal as an important biological phenomenon. With the exceptions of Darwin and Wallace, 19th century biogeographers, who divided the earth into a series of regions or provinces, seldom considered that such areas had a dynamic relationship. The long distance migrations of some birds and insects had been recorded but were not judged to be of general significance. But Darwin (1859) noted that dispersal was a phenomenon of overall importance and thought that animal and plant groups were generally younger than the places they inhabited. In this respect, he differed from the opinions of his friends Joseph Hooker and Charles Lyell. Although Darwin emphasized the importance of dispersal, he also called attention to the influence of barriers to migration which allowed for the slow process of modification by natural selection.

2 Island Biogeography

An integral, but often overlooked, part of invasion ecology is the knowledge accumulated by 150 years of island life studies. With the exception of Ludsin and Wolfe (2001), who called attention to Darwin's recognition of invasion consequences, accounts of the history of invasion ecology almost invariably begin with the advent of Elton's (1958) book. A volume entitled *Fifty Years of Invasion Ecology* (Richardson, 2011) included four chapters that were devoted to historical perspectives, but little reference was made to the invasion studies that were conducted on islands from 1858-2011. Early on, biologists began to think of isolated islands as microcosms of evolution, dispersal, and extinction that could be explored in order to understand such events on a global scale. Darwin and Wallace (1858) based their evolution theory on studies of island life. Wallace (1880) wrote the first book devoted to island biogeography. In 1948, K.W. Dammerman published his famous book on the fauna of Krakatau, illustrating the recolonization of an island that had been depleted of its biota.

While studies of island life have contributed significantly to knowledge about invasions as well as speciation, acclimatization, evolution, and extinction, there has been one unfortunate aspect. As islands were occupied by humans and the animals they introduced, large numbers of endemic island species were driven to extinction (Zhang and Chen, 2011). These events, many of which have been highly publicized, gave the impression that invasions generally produce complete (global) extinctions of native species. Reports of such extinctions, and the subsequent indication that new colonizations on islands could cause local native losses (Mac Arthur and Wilson, 1967), resulted in a strongly negative attitude toward all invasive species. However, there is now a new perspective based on the evidence that the great majority of contemporaneous extinctions were confined to islands and other restricted habitats. For example, bird and mammal extinctions recorded for the past 500 years, indicate that more than 95% took place on islands (Loehle and Eschenbach, 2012). This suggests that extinction rates on the continents have not been unusually high (three mammals and six birds).

3 Other Advances

Charles S. Elton deserves the title "Father of Invasion Ecology." His influential book *The Ecology of Invasions by Animals and Plants* (1958) established invasion ecology as a separate discipline, related to but distinct from succession ecology. This distinction has not been popular among some ecologists who point out that exotic and domestic invaders are both colonizers and that their effects have been fully described in the succession

literature (Davis et al., 2001). By 1958, Elton was already a famous ecologist best known for his books on animal ecology and the dynamics of animal populations. So why, in his later years, did Elton suddenly make the distinction between invasion and succession ecology? During World War II in Great Britain, Elton was asked to find better ways to control the rabbits, house mice and rats in order to protect the human food supply (Davis et al., 2001). All of these species were supposed to have originally invaded from Europe and, at the time, the country was under the threat of invasion from Germany. So, in order to emphasize the destruction caused by those pests, they were called invaders with a militaristic connotation. Elton's (1958) book focused almost entirely on notorious invaders of various kinds.

More recently, invasion ecology has benefited from advances on other fronts. Williamson (1996) published a textbook on biological invasions intended for both students and professionals. This work covers the main aspects of the subject with appropriate examples. The emphasis is on invaders as pest species, but this simply reflects the majority of published literature. Another major publication is the book *Species Invasions* (Sax et al., 2005). More recently, several other books dealing primarily with invasions, have been published. A review of ecological and evolutionary insights provided by invasions has been published (Sax et al., 2007). All of these books and the indicated review represent a small part of the enormous increase in publications on invasion biology that has taken place within the past 20 years. In retrospect, our present knowledge about species invasions represents an accumulation from continued island studies and the post-1958 revival of interest in the subject.

Along with the general increase of interest in invasions, marine invasive organisms became an important research focus, and a noticeable dichotomy developed between the fields of marine and terrestrial invasion ecology. Most of the early marine work was concerned with the damage inflicted by pest species introduced by ships into harbors and estuaries (Briggs, 2012). Despite the fact that modern invasion research in both environments has become devoted to much the same questions (influences of species diversity, disturbance, vectors, propagule pressure, competition, etc.), the results tend to be reported in different journals with very little cross-referencing. Therefore, it has become important to examine both fields to see if advances in one might be applicable to the other.

4 Marine Invasions

Some ecologists have identified exotic invaders as major threats to marine biodiversity despite scant evidence that biodiversity (here meaning species diversity or richness) is really being decreased. Molnar et al. (2008) used the Pacific oyster, *Crassostrea gigas,* as a prime example of a threat species. But this bivalve, although undesired in some places, cannot be conceived of as a threat to biodiversity. In northern Patagonia, it increased the population densities of epifaunal and infaunal organisms and also the feeding rates of bird species (Escapa et al., 2004). In the Wadden Sea, *Crassostrea* has partially replaced the native *Mytilus* and the community associated with the oysters showed superior species richness, abundance, and biomass (Reise et al., 2005). The Pacific oyster is an engineer species that enhances species diversity rather than being a threat, and there are other invader species that belong in the same category (Schlaepfer et al., 2011).

The majority of successful marine invasions, known to involve reactions by native species, appear to consist mainly of alterations in abundance or shifts in habitat (Briggs, 2010). The latter is sometimes described as niche sharing or niche compression. But in most cases, it is not clear that niche alteration is involved. As will be noted in this paper, several terms describing the relationships between invaders and native species have been proposed. Most of the interspecies reactions have been reported by observers from the Mediterranean or the Wadden Sea. Although hundreds of marine invasions have been reported worldwide, mainly from harbors or estuaries, the details of the process by which invaders are accepted into native ecosystems remain

undescribed or poorly understood. The lack is probably due to the difficulties of long-term observation in the marine environment. Competition resulting from marine invasions has been demonstrated but competitive exclusion is rare (Byers, 2009).

Observations from Eastern Mediterranean invasions (Galil, 2007) and invasions in the Wadden Sea (Reise, 2005), as well as conclusions from widespread regional vs. local data (Witman et al., 2004, Karlson et al., 2004), indicate that invasions take place almost entirely from areas of high species diversity to low diversity areas. But, even the richest communities are occasionally invasible (Briggs and Bowen, 2013). The most diverse (species rich) biotas are those in which the standards of competitive performance are highest (Vermeij, 2005). Therefore, competition can be viewed as an integral component of the colonization process, i.e., species from high species diversity areas appear to have the advantage. But the natives almost always manage to retain part of their original habitat. The common occurrence of acceptance by native species explains why invaders from high diversity hot spots can spread their influence over vast geographic areas.

There has been some criticism that contemporary acceptance of invaders may not be long-lasting and that future years might bring extinctions and loss of biodiversity (Ricciardi and Simberloff, 2009). In response, one can point to historic events where the consequences of large-scale invasions have been documented. Information from several historic invasions (Vermeij, 1991, 2005; Patzkowsky and Holland, 2007) showed that, once invaders became established, the relationships with the natives commonly lasted one million to several million years. Furthermore, the fossil evidence indicated that millions of years after an invasion, large numbers of the invaders had undergone speciation, thus adding to global biodiversity. Other workers found, in the Devonian Period, a long-term diversity decline due to the preferential survival of the invaders together with a depression of speciation rate (Stigall and Lieberman, 2006), but this was evidently not true for the Neogene when speciation rates were not depressed. An Ordovician study found evidence of a global richness equilibrium dictated by a combination of invasion (migration), origination, and extinction rates (Heim, 2008). Information combined from various historical and recent invasions led to the proposal of a three step process: invasion to accommodation to speciation (IAS). This process, called the IAS mechanism (Briggs, 2010), has apparently contributed to historical increases in global marine species diversity.

5 Terrestrial Invasions

Freshwater streams and lakes, even though they may be considered part of the general terrestrial landscape, exhibit an extensive history of invasion by exotic organisms. In comparison to most continental and marine habitats, freshwater aquatic habitats are extremely space-limited. This means that freshwater invasions and overfishing have resulted in numerous extinctions and ecosystem alterations (Ricciardi and MacIsaac, 2011), so the results are quite similar to those that have been discovered for oceanic islands. In general, as Strayer (2010) has pointed out in his review, classes of ecologically important invaders include molluscs that are primary consumers, fishes that affect the food web from its apex or center, decapods that are powerful omnivores, plants that have strong engineering and primary production effects, and diseases that can affect humans as well as other organisms.

Plant invasion ecology has been investigated more thoroughly and by more scientists than invasions of other organisms. The term “invasibility” has been used to describe the susceptibility of communities to exotic species (Lonsdale, 1999). The idea of invasibility stems from the biotic resistance hypothesis of Elton (1958) who suggested a negative relationship between native species diversity and invasion success. This is often true but resistance to invasion (biotic resistance) can vary depending on the amount of open space that is available (Stachowicz and Byrnes, 2006). Richardson and Pysek (2006) pointed out that factors other than species diversity must be important, and identified four that have been particularly influential: (1) disturbance, (2)

competitive release, (3) resource availability, and (4) propagule pressure. But also widely recognized is the "fluctuating resource theory of invasibility" (Davis et al., 2000).

Another term, also primarily devoted to plant invasions but with some marine animal examples, is "facilitation "(Stachowicz, 2001; Bruno et al., 2003). Facilitation has been defined as direct positive interactions between two organisms that benefit at least one. This definition includes commensalisms and mutualisms as well as mutually obligate and facultative relationships. In plant communities, facilitation may alternate with competition in response to environmental change (Callaway and Walker, 1997). A review of the literature on biotic interactions (Bruno et al., 2005) suggested that direct facilitative interactions are at least as common and as important as competition and predation in structuring communities. Richardson et al. (2000) argued that a key lesson in invasion ecology was that facilitation by numerous resident species was often required for successful colonization. But some authors (Munguia et al., 2009) believe that facilitation is not a true species interaction because the fitness of one of the species involved remains unaffected.

The term "accommodation" was initially proposed to characterize colonizing invasions in the marine environment (Briggs, 2010). Accommodation means the yielding of living space, indicating that whatever native species occupies the preferred space, it will give way to or support the invader permitting both species to become established in a location where only one existed previously. Compared to facilitation, accommodation is the broader term because it includes facilitation, as well the competition that is perceived when the native species is apparently forced to give way to or physically support the intruder. So, successful invasions can be said to be driven by dispersal (human or natural), discovery of suitable locations, and accommodation by native organisms. Sometimes, the critical factor may be substrate suitability (invasibility) or facilitation, but when the details of the species relationships are unknown, as is often the case, accommodation (as the more inclusive term) may be employed. Finally, it may be noted that both invader species and expanding native species are accommodated when they move into new ecosystems, but no differences in acceptance between the two have been reported.

Another factor, also first noted in regard to the marine environment, was the existence of fossil data indicating that historical invasions had resulted in significant increases in speciation over millions of years. Thus at least some of the local diversity increases produced by the invasions were eventually converted into global increases. Similar information is available in regard to historical plant invasions. The classic paper by Lidgard and Crane (1990) and a more recent study by Magallon and Castillo (2009) traced the rise in angiosperm species diversity through the Cretaceous. Angiosperm plants first appeared in equatorial regions about 140 million years ago (Ma). About 90 Ma, angiosperms invaded the higher latitudes and gradually became the dominant type of vegetation while the cycads, ferns, and conifers declined. The enormous gains in angiosperm species diversity that took place following their high latitude dispersal, indicated that their invasions had lasting benefits in terms of an increases in global biodiversity.

6 Extinctions

Aside from cases on oceanic islands, freshwater lakes and streams, and other similarly restricted habitats, there appears to be a virtual absence of invasion caused extinctions (Gurevitch and Padilla, 2004). In cases involving marine organisms, land plants, and smaller terrestrial animals, evidence for invasion caused extinctions is weak or nonexistent, except on islands (Vermeij, 2005). There is no evidence that competition from exotic plants has caused any native species extinctions (Davis, 2003) and, even on islands, plant and animal extinctions are primarily caused by predation rather than competition (Sax and Gaines, 2008). In the marine environment there have been no cases of native extinction resulting from competition by exotic species (Sagoff, 2005; Briggs, 2007, 2012). In fact, there have been very few contemporary, marine extinctions from any cause.

But during the past 50 years, government supported, commercial fishing has resulted in the collapse of about a thousand populations that once supplied most of the world's seafood. For the collapsed species, now existing as small remnants of their former population sizes, the future is bleak. They suffer from the loss of genetic diversity, inbreeding depression, and depensation (Allee effect). Because marine species were eliminated by historic climatic changes, continued global warming is likely to result in the extinction of small populations that already have a precarious existence. They may be considered evidence of an extinction debt that must be paid as the climate change becomes more severe (Briggs, 2011). Small terrestrial populations await a similar fate.

7 A Dynamic World

For both land and sea, it has become apparent that exotic species, which succeed in colonizing a native ecosystem, rarely cause extinctions and are instead accommodated by the native species that occupy the appropriate niches or habitats. The accommodation process results in a gain in the species diversity of the invaded area. Furthermore, as the fossil data indicate, invasions may eventually result in additional speciation that adds to global diversity. In terrestrial systems, diversity gain generally results in a more stable system with higher productivity and a greater resistance to invasion (Tilman et al., 1996; Lehman and Tilman, 2000; Stachowicz and Tilman, 2005). This is true in the marine environment as well (Vermeij, 2005; Worm et al., 2006). Among ecologists, there is a broad consensus that a positive relationship exists between species diversity and ecosystem stability (Hooper et al., 2005). Invasions have been observed in almost all parts of the world and increases in diversity may continue to build up until the next drastic climate change, which may already be on the way. In the sea, there is a global dispersal system consisting of successful invasions that branch from high species diversity centers outward to where diversity is less and the competition weaker (Briggs and Bowen, 2013); and diversity in peripheral ecosystems is apparently dependent on a continuous flow of species from regional sources (Karlson et al., 2004). Invasion may be as crucial to the long-term development and vigor of communities and ecosystems as mutation is to the long-term evolution of populations and species (Vermeij, 2005).

8 Conclusions

Although invasion ecology had its origin in the mid-19th century when the importance of species dispersal became apparent, and made significant progress during the ensuing 150 years of island studies, it did not become recognized as a separate discipline until the appearance of the 1958 book by Charles Elton. Over the years, invasion studies have contributed greatly to the general areas of ecology, colonization, adaptation, evolution, and species diversity. On land and in the sea, invader species add to local diversity. The mechanism that allows this to happen has been called invasibility or facilitation or accommodation. In the sea, it seems that the addition process must have a competitive component because successful (colonizing) invasions take place almost entirely from areas of high species diversity areas to those of lesser diversity. On land, competition is also important because various kinds of plant competition have been described, but the relationship between regional and local species diversity is not quite as clear. In both environments, exotic invaders were noted to cause species diversity increases in local communities. Facilitation is widespread but may not occur in most cases of successful invasion. The term "accommodation" includes facilitation, niche sharing, niche compression, and mutualism; thus, it is applicable to almost all invasions that result in colonizations.

In the sea, paleontological studies have shown that accommodation leads to long-term relationships between invader and native species and, in the long-term, speciation produces increases in global species

diversity. On land, the greatest change in plant diversity took place beginning with the evolution of the angiosperm flora about 140 Ma. As the angiosperms invaded the higher latitudes, they underwent an enormous increase in species diversity. This suggests that the causes and ultimate effects of historic invasions may be quite similar in both terrestrial and marine environments, and that the invasion to accommodation to speciation (IAS) process may be applicable to each. It may be observed that, while marine and terrestrial ecology remain separate disciplines, there is a pervasive similarity in regard to invasive species. The result of almost all contemporary (colonizing) invasions is accommodation, not elimination. The natural world of invasion and native reaction is more in keeping with the admonition "love thy neighbor" instead of "man the ramparts."

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