

Biological Invasions: Lessons for Ecology

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Anthropogenic introduction of species is homogenizing the earth's biota. Consequences of introductions are sometimes great, and are directly related to global climate change, biodiversity and release of genetically engineered organisms. Progress in invasion studies hinges on the following research trends: realization that species' ranges are naturally dynamic; recognition that colonist species and target communities cannot be studied independently, but that species–community interactions determine invasion success; increasingly quantitative tests of how species and habitat characteristics relate to invasibility and impact; recognition from paleobiological, experimental and modeling studies that history, chance and determinism together shape community invasibility.

The earth's biota is being homogenized rapidly as human activities increasingly introduce species outside their natural range. Large-scale examples include construction of the Suez Canal that connected the Red and Mediterranean Seas, and the Welland Canal that connected the Atlantic Ocean with most of the North American Great Lakes. More piecemeal exchanges of biota occur constantly as species accompany humans into non-native habitats. For most countries, the number of documented introductions is within a range of 10^2 – 10^4 species. Even The Netherlands, a very small country, has at least 300 exotics¹. These numbers are probably only the tip of the iceberg; introductions of large numbers of species go undetected. Such species transport has serious consequences for both man and nature. Indeed, Crosby² concludes that the movement of diseases, weeds, and agricultural plants and animals with Europeans was vital to the success of European imperialism.

Interest in exotic species has resurged recently because the characteristics and ecological impact of exotic species may provide clues to longstanding issues in the study of community assembly (e.g. importance of competition and predation, complexity and stability, importance of keystone species, and the influence of history on community structure). Furthermore, range expan-

sions are inextricably related to global environmental and economic issues of increasing importance – climate change, habitat fragmentation, declining biodiversity and the introduction of genetically engineered organisms.

Two classic volumes, by Elton³ and by Baker and Stebbins⁴, described many of the patterns and explanations about invading species that are still prominent in the current literature (see below). Since 1983, however, at least 13 additional volumes on biological invasions have appeared^{5–16}. Many of these have a regional (The Netherlands¹, Australia⁶, South Africa⁸, North America and Hawaii⁹) or biome (tropics¹⁴, Mediterranean¹⁵) focus, and were sponsored by the International Council of Scientific Unions' Scientific Committee on Problems of the Environment (SCOPE). Compilations of introduced species and case studies, including the sometimes dramatic ecological impact of exotics, dominate several of these volumes. Many chapters in these volumes provide *post hoc* analyses of how well a case study fits the purported characteristics of invading species. Others generalize from a few case studies about the characteristics of invaders or invulnerable communities. Yet for most characteristics, data adequate for a rigorous analysis simply do not exist. These volumes supply many fascinating examples of exotics and their impact, and provide overwhelming evidence that biological invasions are a common and important phenomenon.

Progress is emerging on several research fronts. As a result of empirical studies encompassing a range of temporal scales – from paleobiological to contemporary – the naturally dynamic character of species ranges is increasingly appreciated. After much effort in the older literature to describe the characteristics that make a species a good invader or that make a community invulnerable, ecologists are making more rapid progress with a shift in focus to the critical interaction of invader and target

community. In addition, older, more qualitative assessments of the attributes of invaders and invaded communities are giving way to quantitative tests of putative patterns. A variety of novel approaches to paleobiological analyses, microcosm experiments and modeling studies is suggesting that history, chance and determinism interact to shape ever-changing communities. However, the important roles of history and chance in community assembly mean that the ability to predict the fate and impact of a specific introduced species is still elusive.

Are exotic species ecological malignancies?

Popular science writers, environmentalists and, sometimes, ecologists vilify exotic species as ecological abnormalities, even 'malignancies' in the environment¹⁷. This characterization is understandable, given the rapid spread and impact of exotics like the zebra mussel (*Dreissena polymorpha*) in North America¹⁸ (Box 1). Nevertheless, a long-term view suggests that on all spatial scales, species range changes occur constantly and are an important structuring force of natural communities^{13,19,20}. During the last 20 million years, many episodes of mass interchanges of biotas occurred as a result of tectonic activity¹⁴. During the last 10 000 years, ranges everywhere on the earth have changed as the Pleistocene ice ages ended. The mesic forests of Wisconsin, USA, for example, have had their current species composition for only about 2000 years²¹. On timescales of decades to years, many species ranges also fluctuate as a result of alterations in climate and biological interactions¹⁴. Thus, biological invasions are commonplace in nature, and should not, in general, be viewed as abnormal events. This perspective needs to be incorporated into the theory of ecological communities.

On the other hand, humankind's acceleration of biological introductions and the extent to which it is producing global homogenization,

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may accomplish something in a few decades that movements of the earth's crustal plates could never accomplish. Thus, biological invasions do pose a threat to current ecological communities and global biodiversity. This perspective needs to be incorporated into policymaking for the regulation and management of species movements by humans.

Statistical patterns and conceptual models of invasions

What percentage of colonists (species introduced outside their native range) become invaders (establish themselves)? Statistics that merit confidence are rare: failed colonists are underrecorded; there is an overrepresentation of organisms that are easy to observe; for many taxonomic groups, no data exist; and in biological control studies, there is an overrepresentation of species likely to be successful. The lowest percentage of establishment reviewed by various authors²⁰ is about 35%, but this is certainly a gross overestimate. Williamson²² thinks the correct number is around 10%. This is roughly consistent with Vermeij's¹⁰ estimates for biotic exchanges during the Miocene to Pleistocene. For most taxa, the proportion of the potential donor biota that became established in the recipient community was <1–24%, but was as high as 46% for one taxon¹⁰. The concordance of paleobiological and contemporary estimates suggests that, averaging over many taxa, a small proportion of invaders establish themselves. But focusing on average success may hinder progress in understanding what determines invasion success. Future research should, therefore, focus more systematically on the biological significance of different percentages for different taxa and different target communities.

The two leading causes of failure to become established are inappropriate climate and predation, but the impact of competition, disease and other factors are probably underestimated because they are more difficult to measure²³.

What percentage of established exotics have an impact on the native community? Clearly, in some strict sense, every established species has an impact on the native community²⁴. However,

the percentage that have an impact large enough to be perceived by the typical ecological study is much smaller, with estimates from reviews^{11,20,24} ranging from 2 to 40%. Such estimates, like those for colonization success, are fraught with uncertainty. These estimates might increase with more careful examination of exotics or they may be inflated because studies showing no effects are not published.

Predation and habitat changes are the most often cited mechanisms of impact of exotics on native species^{11,24}. The difficulty of documenting competition and other subtle interactions may lead to their underestimation, but predation is apparently a particularly potent force as the primary cause of extinction of native species, e.g. island lizards²⁵ and African Great Lakes cichlids²⁶. Whereas many, if not most, colonists have little impact on invaded communities, three examples, in addition to the zebra mussel (Box 1), illustrate how strong the direct and indirect impacts of invaders can be.

On the island of Hawaii, the exotic nitrogen-fixing tree *Myrica faya* colonizes volcanic ash and open native forests, increasing inputs of nitrogen (N) by as much as four times in these N-limited systems²⁷. One result is that exotic earthworms are two to eight times more abundant under *Myrica* than under an abundant native tree²⁸. For some abundant native plants, however, the negative effects of *Myrica* litter accumulation and shading outweigh the positive impact of increased soil N²⁹. Thus, this exotic alters nutrient cycling, changes the physical structure of open forests, and displaces native trees.

In northern Wisconsin lakes, the exotic crayfish *Orconectes rusticus* drives native congeners locally extinct via mechanisms that include an interaction of competition for shelter and selective predation by fish^{30,31}. In addition, predation by the invader reduces the abundance of macrophytes and some invertebrates by as much as 100%^{30,32}. These changes probably reduce populations of some fishes and change the flow of energy and nutrients in lakes³³.

The introduction of another aquatic decapod, the opossum

shrimp (*Mysis relicta*), into Flathead Lake, Montana, changed the flow of energy between the lake and the terrestrial ecosystem. Through a complex set of trophic interactions, the introduction of the shrimp reduced salmon numbers, which decreased dramatically the numbers of eagle and grizzly bear that fed on salmon³⁴.

Thus, *Myrica*, *Orconectes* and *Mysis* are keystone species and affect population, community and ecosystem processes in the invaded community. These examples may be unusual only in that they are relatively well studied.

Are there characteristics that are common to successful colonists, to invaders that have a large impact on the invaded community, and to communities that are invulnerable? From particular case studies, many authors have proposed general answers to these questions (Box 2). One of the most oft cited generalizations is that successful colonists have high r , but this is not supported by correlative analysis¹⁵. Predators, particularly vertebrate predators, seem to be overrepresented among exotics that have a large community impact. This is especially true for islands, probably because island communities are depauperate in vertebrates, particularly mammals^{27,30}. The crayfish and shrimp examples above, however, show that predators need not be vertebrates to have a large impact.

It is increasingly recognized that the characteristics of the target community are as important to the fate and impact of an introduction as the characteristics of the introduced species. Many authors think that disturbance predisposes a community to invasion, but many counterexamples show disturbance is not a requisite¹⁷, and can even hinder invasion, e.g. exclusion of trees from fire-maintained prairie. Some authors¹⁶ have argued that disturbance enhances invasibility for plants more than for animals, but large extinction events during the last 20 million years have apparently enhanced invasibility for animals as well as for plants¹⁰. Thus, conflicting evidence on the role of disturbance typifies the evaluation of many generalizations (see Box 2), and emphasizes that such patterns are probabilistic. The

role of disturbance and other factors probably also differs among taxa and community types.

In paleobiological reconstructions¹⁹, the strong asymmetries in the direction of invasion between newly joined communities are consistent with the large impact of exotics on islands: both patterns suggest that less speciose, less biologically 'sophisticated'¹⁹ communities – those in which species are less adapted to multiple competitors and predators – are more prone both to invasion and to be changed by invasion. That is, the percentage of species from the more speciose community that becomes established in the less speciose community is greater than the percentage of species from the less speciose community that becomes established in the more speciose community. Thus, more-saturated communities are hypothesized to resist invasion and to be the source of successful colonists into other communities¹⁹. The degree to which this description of invaders – highly competitive, defended against predation – is inconsistent with the still widely held view that invaders are typically pioneer species (see Box 2) calls for further study. Certainly, paleobiological evidence and recent studies on islands provide strong evidence that biological interactions are very important in determining success of colonists. For most other purported characteristics of invaders and invaded communities, data are inadequate for rigorous testing.

The difficulty of testing for patterns from real case histories has led to a potentially fruitful increase in the use of mathematical and experimental models of invasions. Case¹⁰ shows that for multispecies Lotka–Volterra communities, Elton's argument that more-speciose communities are more resistant to invasion is correct. Case¹⁰ argues that the ways in which his Lotka–Volterra communities are unrealistic only make his conclusions conservative. These results emphasize the importance of the characteristics of both the colonist species and the target community in determining invasion success.

Microcosm experiments in which the order and rate of invasions are

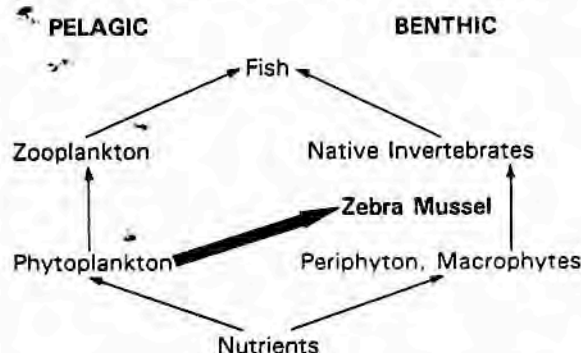
Box 1. Spread and impact of zebra mussels in North American freshwaters (from Nalepa and Schloesser¹⁸)

In about 1985, the zebra mussel (*Dreissena polymorpha*), a filter-feeding Eurasian bivalve, became established in the North American Great Lakes system, probably having been introduced in ballast water. Since then, zebra mussels have continued to spread into all five American Great Lakes, and many rivers and lakes of the eastern United States. In the 19th century, zebra mussels spread with human commerce from the Caspian and Black Seas region into much of Europe, but the ecological impacts were not well documented. In North America, the spread of zebra mussels has been far more rapid and its impact far greater than most exotics.

The characteristics that distinguish a successful invader are often difficult to recognize (Box 2). Zebra mussels, however, are doubly unique among freshwater bivalves in North America. First, larvae are free-swimming, and second, adults (which grow to 4–5 cm) attach themselves to firm substrates, e.g. boat bottoms, with byssal threads. These attributes allow larval and adult zebra mussels to disperse easily, and allow adults to occupy space like no other freshwater species in North America.

In lakes St Clair and Erie, where zebra mussels occur at densities of 100 000–400 000 m⁻², their filtration of phytoplankton has greatly increased water transparency (see simplified lake food web below). Now light reaches more of the bottom, allowing colonization by rooted vascular plants. Native unionid clams, many species of which are endangered, become covered by zebra mussels, and populations have declined. In contrast, total macroinvertebrate abundance is ten times greater in the presence of zebra mussels. Negative impacts on fish populations, while predicted, have not been documented. Ducks have reduced some local European populations of zebra mussels. However, adult mussels appear to have few predators, and the extent to which zebra mussels are a trophic dead end is an important question.

Overall, current evidence suggests that zebra mussels profoundly change pelagic and benthic communities, and shunt carbon and nutrients from the pelagic to the benthic zone. Clearly, zebra mussels will eventually inhabit many, if not most, of the lakes and streams of temperate North America. The magnitude and long-term impacts on community structure and ecosystem function are important topics of research.



manipulated, strongly support the importance of both invader and community characteristics, and the corollary that the history of a community strongly influences its invasibility^{10,30}. Whereas Drake¹¹ asserts that microcosm results support the importance of deterministic 'assembly rules', what is most striking about the mathematical and experimental results is that any 'rules' operate in a context established in large part by chance. Two similar communities may, in fact, have gotten that way by different paths and may be on different trajectories¹⁰. Therefore, as Drake^{10,11} points out, inferring causation from contemporary patterns is rife with pitfalls.

Can we predict the outcome of a species colonization?

'Ecologists can make some powerful and wide-ranging predictions about invasions ... On the other hand, ecologists cannot accurately predict the results of a single invasion or introduction event.'⁴² This

quotation from Ehrlich¹² accurately synthesizes the state of ecologists' study of invasions in particular and community structure in general. Some generalizations are supported by several types of evidence: for instance, all other things being equal, a given species is more likely to succeed in invading a species-poor community than a species-rich community. Yet, because all patterns are characterized by large variance and exceptions, we cannot with any confidence predict the outcome of any particular introduction. For successful prediction, every potential invader and target community must be intensively studied, perhaps, Simberloff⁴³ suggests, with the equivalent of a PhD dissertation. Given the thousands of introductions occurring every year, clearly a serious mismatch exists between the need for study and the resources of ecologists.

Conclusions: lessons for ecology

Recent research has shown that range changes are an integral part

Box 2. Widely-cited generalizations about biological invasions

From individual case studies and surveys of studies, many ecologists have proposed qualitative descriptions of invading species – species that establish self-sustaining populations outside their native range. Such species are said to be characterized by the following (simplified from Lodge²⁰):

- r-selected traits
- high dispersal rate
- single-parent reproduction
- vegetative reproduction
- high genetic variability
- phenotypic plasticity
- large native range
- eurytopy
- polyphagy
- human commensalism

Many of these generalizations are intuitively appealing and are cited widely. However, the British SCOPE volume⁷ has led the way in quantitative analysis of these and other patterns, and found that exceptions are numerous. Some of the few patterns that have been tested statistically (e.g. high r (Ref. 35)) have been rejected.

Similarly, general descriptions of invadable habitats have been offered (simplified from Lodge²⁰):

- climatically matched with native habitat
- early successional
- low diversity of native species
- absence of predators
- disturbed

These habitat generalizations, too, suffer exceptions and lack of statistical testing. Yet, many empirical and some theoretical studies support the idea that communities with low species richness are more invadable than those with high species richness^{19,36}, that predators often prevent establishment^{11,24–26}, and that disturbances enhance invasibility^{19,38}. These are probabilistic patterns, however, and provide little guidance in making predictions about the success of any particular introduction. Prediction will emerge only from intensive study of particular potential invaders and target communities.

of natural communities that are accelerated by humans. Exotic species will therefore cause increasing economic disruption, and become a more important focus of ecological study and natural-resource management. For example, annual mitigation costs for biofouling of water intakes by zebra mussels are forecast to reach \$2–4 billion for the American Great Lakes alone (see Box 1). Global changes in climate will both cause more range changes, and respond to range changes of species that alter ecosystem processes like gas and water vapor fluxes. Because some exotic species cause extinction of native species, increasing introductions will lead inevitably to further reductions in global biodiversity.

Thus, progress in the ecological study of invasions is essential to understanding what determines the dynamics of ecological communities, and to predict ecological and economic impact of range changes.

As ecologists are recognizing, the study of invasions can be profitably studied with correlative approaches, mathematical models and experimental microcosms. As reviewed above, the characteristics of the community and of a colonist are both critical to the success of invasion and the impact of a successful colonist¹⁰. The complexity of the interaction between species and community – each of which alone is difficult enough to characterize – is a central reason why predictions about specific introductions are so difficult to make.

Regarding community characteristics, paleobiological evidence suggests that many communities are not saturated – many invasions simply increase species richness¹⁹. On the other hand, much evidence suggests that some communities are saturated: biological interactions, especially predation by natives, are often the cause of failed colonization¹¹; probability of success declines with the species richness of the target community¹⁰; and mass extinctions enhance invasion success¹⁹. The prevalence of exotics on islands results, in part, from the facts that predators (especially vertebrate predators) are rare on islands, and that island communities are, in general, low in species richness. However, a paradox about the role that predation by natives plays in resisting invasions should be addressed in future research: in contrast to predation's role in resisting invasion (see above), microcosm¹⁹ and field¹¹ studies demonstrate that predation can enhance community invasibility by allowing the coexistence of competitors.

Regarding colonist characteristics, there seem to be few, if any, general characteristics of successful colonists. Among successful animal colonists, predators are more likely to have a large impact on the native community^{24,25}. Identification of potential keystone species from among colonists should be pursued. Such species might include: top predators; species that differ

markedly from natives in resource use, e.g. zebra mussel and *Myrica*; species that would alter disturbance intensity, e.g. pigs that root forest floor, grasses that enhance fires; and species, especially plants, that would provide a novel habitat, e.g. trees invading a herbaceous community^{24,27}. That the impact of such species blurs the boundaries of population, community and ecosystem ecology is an important lesson for all ecologists.

An emerging lesson for community ecology is that the outcome of any introduction into a community depends not only on deterministic interactions of one species with the abiotic and biotic environment. The outcome depends also on the path by which the native community arose. Thus, every ecological community is captive to the historical contingencies of the order and rate of invasions by which it was assembled. These details usually are difficult, if not impossible, to learn. Therefore, predictions about the outcome of colonizations will always suffer uncertainty, and, at best, will emerge only from focused studies on particular potential invaders and target communities.

Acknowledgements

I thank Mark Williamson for helpful correspondence, and James Drake, Anna Hill and Andrea Midgett for improvements to the manuscript. My work on invasions has been supported by the US National Science Foundation (BSR 8500775 and BSR8907407) and the US Environmental Protection Agency.

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