# The success of animal invaders

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Zebra mussel, kudzu, fire ant, gypsy moth, common carp—whether you are a farmer, outdoors enthusiast, cottage owner, or ecologist, you have undoubtedly witnessed the spread and adverse impacts of invasive species. As long as humans have migrated, we have carried species from their homeland to provide some familiar comforts of home in new lands. This trend was exemplified by the acclimatization societies of North America in the 19th century, which systematically imported and introduced Old World species. The expansion of global trade and tourism during the past century has fostered an explosion of unintentional (mostly invertebrate) species introductions, further accelerating the spread of species beyond their native range, as has been documented for the Laurentian Great Lakes (Fig. 1). The article in this issue of PNAS by Jeschke and Strayer (1) provides a much needed assessment of invader success patterns for vertebrate species exchange between the continents of Europe and North America.

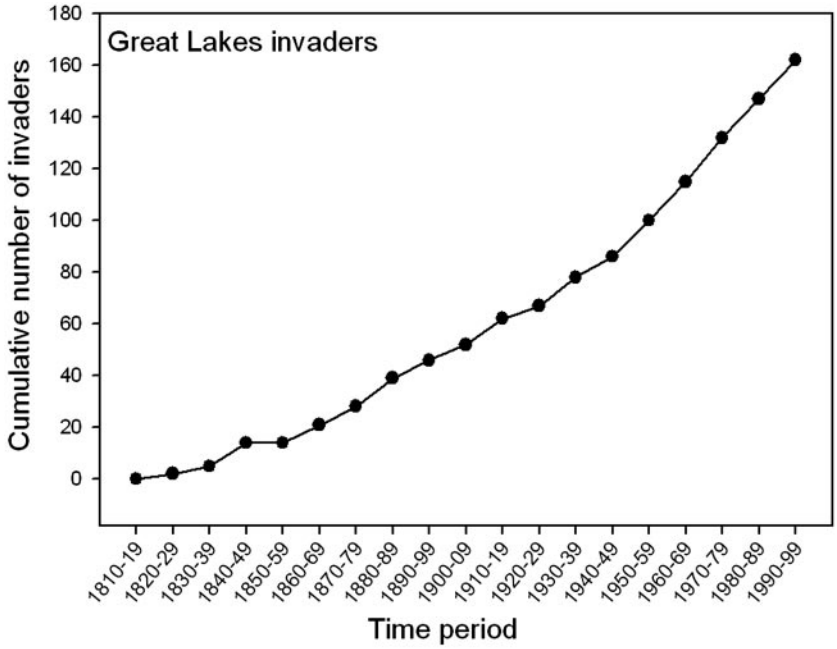


**Fig. 1.** The accelerating rate of species invasions during the past two centuries in North America's Laurentian Great Lakes. Adapted from Riccardi (22).

The introduction and spread of invasive species, both intentional and unintentional, is emerging as among the most dramatic ways that humans are transforming the planet (2), and nonnatives are now recognized as a central agent of human-caused global change (3). What's more, the combined effect of the spread of nonnatives and the extinction of rare species is causing ecological communities worldwide to become increasingly similar (4). In other words, the global biota is being homogenized. In light of these trends, there is an urgent need to better understand invasive species spread and success. Although efforts have been made to describe the attributes of successful invaders and invasible ecological communities (5), ecologists have lamented the difficulty in making quantitative predictions about invaders (6), and broad-scale statistical patterns of invader success remain poorly known.

The article by Jeschke and Strayer (1) makes several important contributions to our understanding of invasive species. It is now widely accepted that a small proportion of introduced species establish, and a small proportion of established species spread or become pests (6). This belief has been presented more formally as the oft cited "tens rule" (7), which holds that ≈1 of 10 imported species "escapes" to the wild, 1 of 10 of these introduced species becomes established in the wild, and 1 of 10 established species spreads and becomes a pest. Although this rule of thumb was developed by Williamson and Fitter (7) on the basis of examination of plant invaders in the United Kingdom, this rule has been broadly applied (probably beyond the original intent of the authors) and has influenced invasive species thinking and policymaking at many levels. Jeschke and Strayer find that this rule simply does not hold for vertebrate exchange between these continents. A small fraction (<5%) of the North American and European faunas have been introduced in either direction. But of those lucky few species that have managed to make the transatlantic journey, half have become established, and of those that establish, half have spread and become invasive. Although the tens rule is based on plants and has one more "step" than does the analysis of Jeschke and Strayer, the most conservative application of this rule predicts that 1 of 100 introductions would become invasive. Jeschke and Strayer find that, for vertebrates, approximately one of four introductions becomes invasive.

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This analysis also tests two important hypotheses about invader spread at broad spatial scales. The ecological imperialism hypothesis (8) postulates that species of European origin would be at an advantage when introduced into the New World, because they would encounter species assemblages with which they had coevolved back in the Old World. The biotic resistance hypothesis is the converse, that the more species-rich and less disturbed ecosystems of North America provide "biotic resistance" to an influx of European invaders, an idea that dates back to the pioneering work of Charles Elton, who suggested that diverse and undisturbed systems are less invasible (9).

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Neither of these hypotheses was supported by Jeschke and Strayer (1), because similar patterns of invader success were observed in the two directions. Still, this finding does not refute the observation that a handful of species that coevolved with European civilization have subsequently thrived in environments created by Europeans on other continents. Similarly, the role of biodiversity and native species loss appears to be very important in mediating invader success, although findings are highly scale-dependent. Local-scale species losses appear to increase invader success; however, at larger scales, more diverse communities tend to be more vulnerable to invaders (10–12).

This article is timely, as the mounting ecological and economic impacts of nonnative species are becoming increasingly apparent. The economic costs of invasive species in the United States alone have been estimated at $137 billion annually (13), and invasive species are among the leading threats to freshwater ecosystems and biodiversity (14, 15). Once invaders establish, there is often no going back because of the difficulty of eradication. Tools are urgently needed to forecast future invader spread (16) and to assess the worthiness of prevention efforts (17). Managers need a way to prioritize and direct prevention efforts for known invaders (18); for example, of the thousands of lakes in the Great Lakes region of North America, only a subset may be vulnerable to invaders on the basis of the degree of isolation and the characteristics of the ecosystem (19). Advances are also being made in identifying the troublesome invaders of the future; for example, several recent studies use a risk assessment framework to identify potential invaders (20, 21).

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The broader implications of this study (1) for public policy are clear. Simply put, an animal species that manages to make its way across the Atlantic has a much stronger chance of becoming a problematic invader than previously assumed. This article also demonstrates a close coupling between invasive introductions and human migrations between Europe and North America. Contrary to popular ideas involving ecological imperialism and biotic resistance, the direction of the invasion matters not: both continents are equally vulnerable. This finding underscores the vital importance of preventing species transport in the first place as the key to minimizing adverse impacts of invasive species. As with the popular health adage, "an ounce of prevention is worth a pound of cure," the same holds when considering species invasions (17).


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