The role of evolution in the invasion process

Stephen J. Novak*†
Department of Biology, Boise State University, 1910 University Drive, Boise, ID 83725-1515

Biological invasions occur when organisms are transported and become established in a new range in which they persist, proliferate, and spread (1). The negative consequences of invasions include loss of native biodiversity and community structure (and in extreme cases, the extinction of native species) (2); modification of ecosystem processes such as nutrient cycling and productivity patterns; alteration of disturbance regimes, especially the frequency of wildfires (3); reduced agricultural productivity; human health concerns; and enormous economic costs (1, 4). Consequently, invasive species are now considered to be one of the leading contributors to global change (5) and thus have been the focus of an extensive amount of ecological and ecosystem-level research. Much of this research has focused on answering a series of questions associated with predicting invasions: Which species will become invasive? Which life-history traits contribute to invasiveness? Which communities are susceptible to invasion? What will be the ecological and ecosystem-level consequences of invasion? Unfortunately, answers to these questions remain elusive (1). It is surprising to note, however, that little research has focused on the evolutionary aspects of biological invasions and addressed how evolutionary mechanisms may contribute to the success of an invasion (2, 6, 7). In contrast, the research of Laverne and Molofsky (8) reported in this issue of PNAS examines the factors that contribute to range expansion and the invasiveness of Phalaris arundinacea L. (reed canarygrass) in North America and provides powerful insights into the role of evolution in the invasion process.

Background

The invasion process can be viewed as a series of steps that are initiated when propagules of a species (seeds, eggs, larvae, vegetative material, mature individuals, etc.) are sampled in their native range and transported to a new area (1, 4). These immigrants probably experience high mortality rates while in transit, and soon after colonizing their new territory, because of myriad biotic and abiotic forces. Thus, only a small fraction of the species that are sampled and brought to a new range become established and persist (1). Such species are said to be naturalized, and most remain permanently within this category. After an indefinite lag period, a few naturalized species become fecund, vigorous, and wide-ranging that they can cause enormous ecological and economic damage in the new range and are termed invasive (1, 4). The great irony of biological invasions is that, despite their substantial adverse consequences, very few species that are sampled in a native range and transported elsewhere will ever become invasive (9).

Small population sizes often occur with the establishment of nonindigenous species in their new range, and small populations are prone to alterations or reductions of genetic diversity through founder effects and genetic bottlenecks (10). Reduced genetic diversity will limit the evolutionary potential of nonindigenous populations in their new range (i.e., limit their capacity to evolve). Propagule pressure (the number of propagules arriving in the new range) is now recognized as one of the key factors influencing the establishment of nonindigenous species and ultimately whether an invasion occurs (11, 12). With increasing propagule pressure, the size of founder populations and/or the number of founder events will be greater. Propagule pressure influences the genetics of nonindigenous populations in two ways: (i) larger founder populations would retain a larger proportion of the genetic diversity of the species’ native range and genetic bottlenecks would not occur or be severe, and (ii) multiple founder events (i.e., multiple introductions) may originate from genetically divergent native populations and lead to the formation of populations in the new range that are genetic admixtures (they combine the genetic diversity of several sources) (2, 10). Multiple introductions can result in nonindigenous populations with similar or even greater genetic diversity (and evolutionary potential) than native populations. Thus, investigations of evolutionary aspects of biological invasions must take into account the introduction dynamics of an invasive species, which directly influences the amount and distribution of genetic diversity of a species in its new range (10). Second, this research should assess whether an invasion results from the introduction of preadapted genotypes or occurs as a consequence of postimmigration evolution through hybridization, selection (13, 14), or both.

Experimental Evidence for Evolution in P. arundinacea

This is just the approach taken by Laverne and Molofsky (8) in their research on the invasion of the perennial grass P. arundinacea in North American wetlands. Moreover, the information that they have assembled and their experimental design are well suited for critically assessing evolutionary aspects of this invasion (10, 15): they use information on the geographic distribution of P. arundinacea in both its native and introduced ranges, provide some historical context for the species’ introduction and spread in North America, analyze both native and introduced populations within their study, use genetic markers to assess introduction dynamics of the species into North America, determine both the amount and distribution of genetic diversity in native and introduced populations, assess whether the species experienced a genetic bottleneck with its introduction, and perform greenhouse studies to determine the heritability of phenotypic variation and field experiments to determine phenotypic plasticity in native and introduced populations of the grass.

P. arundinacea is native to circumboreal regions of Eurasia, and historical evidence suggests that it was repeatedly and deliberately introduced into North America for agronomic purposes, soil management, and wastewater treatment. European populations of the grass were sampled from the central portion of its native range (the Czech Republic) and the southern margin of its native range (France). The same methodology was used in sampling populations from North America: populations

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See companion article on page 3883.

*Present address: Commonwealth Scientific and Industrial Research Organization European Laboratory, Campus International de Baillarguet, 34980 Montferrier-sur-Lez, France.
†E-mail: snovak@boisestate.edu.

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from Vermont are located at the center of its invasive range, and populations from North Carolina are at the southern migration front. This sampling design not only allows Lavergne and Molofsky (8) to assess whether the North American population of _P. arundinacea_ has experienced a reduction in genetic diversity, it also allows them to compare the genetic diversity of populations near where the plant was originally introduced (Vermont) with populations from a region where it has just recently spread (North Carolina). Interestingly, this design also allows Lavergne and Molofsky to compare the genetic diversity of populations located on the margins of both the native and introduced ranges, France and North Carolina, respectively.

The amount and distribution of genetic diversity in native and introduced populations of _P. arundinacea_ was determined by using starch-gel enzyme electrophoresis. This technique revealed high amounts of genetic diversity in both native and introduced regions and populations of this species, and it is very important to note that the values for all genetic diversity parameters (figure 1 in ref. 8) are greater in the introduced range (even North Carolina) than the native range, although these differences are not always statistically significant. In addition, the geographic distribution of unique alleles from both the Czech Republic and France indicates multiple introductions from different regions in Europe (figure 2 in ref. 8). In fact, several alleles were detected in introduced populations, and their counterparts were not observed in any of the native populations included in this study, suggesting that populations from elsewhere in Europe probably supplied emigrants to North America. These results for _P. arundinacea_ join a growing body of evidence indicating that multiple introductions of invasive species may be the rule rather than the exception (10). Also, multiple introductions appear to reduce the occurrence and/or severity of genetic bottlenecks anticipated in recently founded populations. These results appear to be common among deliberately introduced species (10), such as _P. arundinacea_.

One of the most exciting findings of this work emerges from the analysis of multilocus genotypes in native and introduced populations of _P. arundinacea_. Only 1.5% of North American multilocus genotypes were detected in European populations, despite the fact that the two regions shared 85% of their alleles. These data indicate that many (98.5%) North American multilocus genotypes of _P. arundinacea_ are novel allelic combinations that have arisen as introduced European genotypes were reshuffled and recombined during sexual reproduction. Thus, the multilocus genotypes currently found in North America may never have occurred previously in the evolutionary history of this species. A similar pattern has been reported in several other invasive species (16, 17), but it is by no means common. Plants with the North American and European multilocus genotypes were found to be phenotypically divergent when grown in a common garden (greenhouse) experiment. North American genotypes emerged faster and exhibited higher emergence probability, tillering rate, leaf production, total biomass production, and above-ground biomass production (figure 4 in ref. 8). Thus, the newly created multilocus genotypes possessed a higher potential for vegetative establishment, biomass production, and clonal spread, and these differences were consistently expressed, even under field conditions.

These traits are associated with increased invasiveness in North American populations of _P. arundinacea_ and appear to have originated through rapid phenotypic evolution. North American populations also exhibited greater broad-sense heritability for phenotypic traits such as emergence time, tillering rate, and root biomass than European populations (figure 5A in ref. 8). Heritability is the measure of the genetic contribution to the overall phenotypic variability of a trait, and higher heritability values for these traits suggest that North American populations possess the genetic raw material to respond to changing selection regimes (i.e., they have higher evolutionary potential). In fact, significant phenotypic differences were observed within each region in North America, suggesting that these traits are responding to divergent selection pressures. And when clones were transplanted along a moisture gradient under field conditions, North American populations also exhibited higher phenotypic plasticity than European populations for several traits (figure 5B in ref. 8). Thus, introduced populations not only possess greater heritability (genetic variance) for traits conferring invasiveness but also display greater phenotypic plasticity (the ability to alter phenotypic expression in response to changes in environment).

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**Concluding Remarks**

The work by Lavergne and Molofsky (8) clearly demonstrates that the invasion of _P. arundinacea_ in North American wetlands stems from multiple introductions that sparked postimmigration evolution and was not caused by the introduction of preadapted genotypes. Few studies with invasive plant species have been this comprehensive and therefore convincing (but see ref. 18). In addition, these results form a cautionary tale: multiple introductions, even of species that are already present in a new range, should be avoided because the new immigrants might contribute to invasiveness. Finally, this study also demonstrates that invasive species are excellent model systems for addressing basic questions in evolution, ecology, and biogeography (19).

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