THE POPULATION BIOLOGY OF INVASIVE SPECIES

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■ **Abstract**   Contributions from the field of population biology hold promise for understanding and managing invasiveness; invasive species also offer excellent opportunities to study basic processes in population biology. Life history studies and demographic models may be valuable for examining the introduction of invasive species and identifying life history stages where management will be most effective. Evolutionary processes may be key features in determining whether invasive species establish and spread. Studies of genetic diversity and evolutionary changes should be useful for

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understanding the potential for colonization and establishment, geographic patterns of invasion and range expansion, lag times, and the potential for evolutionary responses to novel environments, including management practices. The consequences of biological invasions permit study of basic evolutionary processes, as invaders often evolve rapidly in response to novel abiotic and biotic conditions, and native species evolve in response to the invasion.

INTRODUCTION

The impact of invasive species on native species, communities, and ecosystems has been widely recognized for decades (Elton 1958; Lodge 1993a,b; Simberloff 1996), and invasive species are now viewed as a significant component of global change (Vitousek et al. 1996). The severe economic impact of these species is evident; costs of invasive species are estimated to range from millions to billions of dollars annually (U.S. Congr. Off. Technol. Assess. 1993, Pimentel et al. 2000). In addition to economic impacts, invasive species have severe negative consequences for biodiversity. Numerous studies have summarized the impacts of invasive species on native species and community structure (Williamson 1996, Wilcove et al. 1998, Parker et al. 1999, Sala et al. 2000, Stein et al. 2000), and ecosystem-level effects of invasive species are now under study (Vitousek & Walker 1989, Mooney & Hobbs 2000). The impacts of invasive species are eventually expected to be severe throughout all ecosystems, as increasing numbers of nonindigenous (exotic, alien) species become established in new locations (U.S. Congr. Off. Technol. Assess. 1993). In response to the problem, Executive Order #13112 of February 1999 directed several federal agencies "to prevent the introduction of invasive species and provide for their control and to minimize the economic, ecological, and human health impacts that invasive species cause" (Fed. Regist. 64(25):6183–86).

Invasive species have been a target of research in both natural and managed ecosystems as weed scientists, resource managers, conservation biologists, and restoration biologists test various approaches for managing the impacts of these taxa. Although many of these studies are a synthesis of both basic and applied research, there is increasing recognition of the unrealized potential contributions of basic research to the study of invasive species. The purpose of this review is to elucidate the particular role that population biologists can play in studies of invasive species, through life history studies, demographic models, and knowledge of the ecology and evolution of both invasive and native species in a community context (Figure 1). Not only do questions and methods of population biology hold promise for understanding and managing invasiveness, but invasive species offer significant opportunities to study basic processes in population biology. Invasions are like natural experiments, but it may be that the processes are far more rapid than those in purely native systems.

Although the discipline of population biology has already contributed to studies of invasive species biology, untapped potential contributions are even greater,
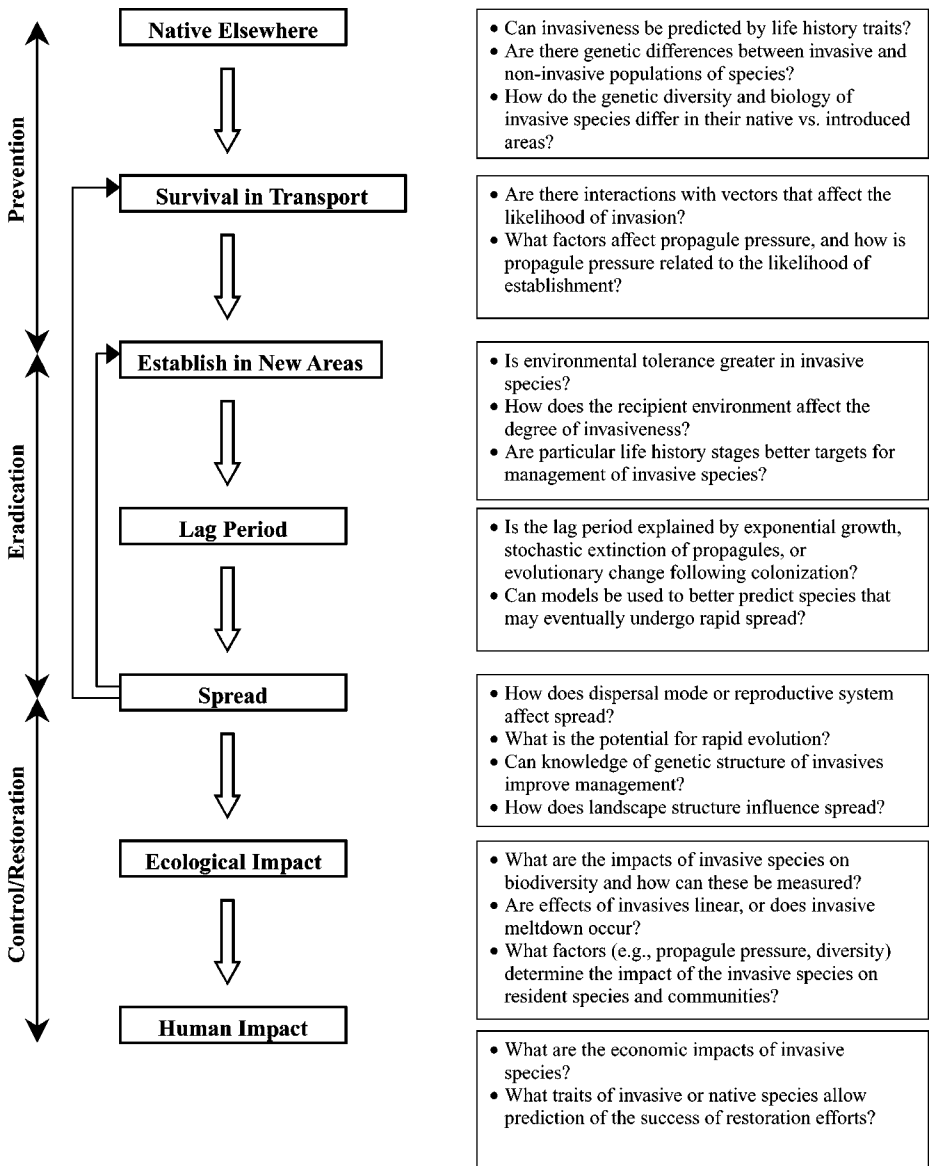
Prevention

Eradication

Control/Restoration

Native Elsewhere

- Can invasiveness be predicted by life history traits?
- Are there genetic differences between invasive and non-invasive populations of species?
- How do the genetic diversity and biology of invasive species differ in their native vs. introduced areas?

Survival in Transport

- Are there interactions with vectors that affect the likelihood of invasion?
- What factors affect propagule pressure, and how is propagule pressure related to the likelihood of establishment?

Establish in New Areas

- Is environmental tolerance greater in invasive species?
- How does the recipient environment affect the degree of invasiveness?
- Are particular life history stages better targets for management of invasive species?

Lag Period

- Is the lag period explained by exponential growth, stochastic extinction of propagules, or evolutionary change following colonization?
- Can models be used to better predict species that may eventually undergo rapid spread?

Spread

- How does dispersal mode or reproductive system affect spread?
- What is the potential for rapid evolution?
- Can knowledge of genetic structure of invasives improve management?
- How does landscape structure influence spread?

Ecological Impact

- What are the impacts of invasive species on biodiversity and how can these be measured?
- Are effects of invasives linear, or does invasive meltdown occur?
- What factors (e.g., propagule pressure, diversity) determine the impact of the invasive species on resident species and communities?

Human Impact

- What are the economic impacts of invasive species?
- What traits of invasive or native species allow prediction of the success of restoration efforts?

Figure 1 Generalized steps in the invasion process and their relationship to management of invasive species (modified from Lodge 1993b and Kolar & Lodge 2001). The transport, establishment, and spread of many invasive species as well as their effects can be characterized by a series of steps, each with questions that may be relevant to and enhanced by studies in population biology, including studies of life history traits as well as consideration of genetic and evolutionary changes. A few of the questions at each of these stages are highlighted below. Some stages are more relevant to prevention; others are more relevant for issues of control and restoration. Feedback may occur between many of these steps.

and studies from population biology may allow a proactive approach to invasive species. Studies of the phylogeographic structure (Stone & Sunnucks 1993, Bastrop et al. 1998, Pellmyr et al. 1998, Slade & Moritz 1998, Wilson et al. 1999), genetic diversity, and the potential for the rapid evolution of these species may provide novel insights into the colonization dynamics and spread of invasive taxa. The continuing development of new approaches in life-history theory may also lead to predictions of species likely to become serious pests or may identify critical life history stages during which management will be most successful. Current developments in the theory of population dynamics and population genetics may help identify the point at which control rather than eradication efforts would be more effective (Figure 1). Demographic models, including factors influencing dispersal, as well as spatial modeling of populations can be used to examine the spread and management of invasive species. More information about the genetics, evolution, and interactions of invasive species and native species in invaded communities may lead to predictions of the relative susceptibility of ecosystems to invasion, better methods for removal of key alien species, and predictions of the subsequent effects of removal.

Below we focus on the ecological and genetic features of species as well as community properties that may promote invasion, and the ecological and evolutionary effects of invasive species on communities. For each area discussed, we concentrate on how evolution could affect invasiveness, from the perspective of both the invading species and the species residing in the invaded community.

THE ECOLOGICAL BASIS OF INVASIVENESS: LIFE HISTORY CHARACTERISTICS OF INVASIVE SPECIES

Life history traits that make species more invasive have been of continuing interest because of their potential predictive power. Some studies have focused on life history traits that may predispose species to rapid population expansion, whereas others have investigated how the genetic structure of life history traits may provide species with either great phenotypic plasticity or the potential for rapid evolutionary change. In this section we give a historical approach to life history analysis illustrated by several classic botanical and agricultural studies, examine some cross-taxa comparisons, and propose a general approach to the study of life history characteristics of invasive species.

Baker (1965, 1974) discussed several traits associated with weedy plant species and proposed that species with many of these characteristics were more likely to be highly weedy than species with only a few of these traits. Traits promoting weediness included the ability to reproduce sexually and asexually, rapid growth from seedling to sexual maturity, and particularly, adaptation to environmental stress (phenotypic plasticity) and high tolerance to environmental heterogeneity. Although this concept of an "ideal weed" is cited throughout the weed literature and in the literature on exotic species (Baker 1974, Newsome & Noble 1986, Roy

1990, Schiffman 1997), few empirical data exist to support or refute Baker's list of characters (Kolar & Lodge 2001). Species with traits of Baker's ideal weed differ in their invasiveness (Thebaud et al. 1996), and many invasive species have only a subset of the traits described by Baker and others (Williamson & Brown 1986, Roy 1990).

More recently, broad-scale analyses of floras suggest that some plant growth-form and habitat characteristics can be used to predict invasion success. Analysis of exotic species introduced into the Czech Republic since 1492 showed that a species' invasion success was related to plant height, life form, and competitive-ness, and that the sunflower family (Asteraceae) was over-represented in the exotic flora compared with the native flora (Pyšek et al. 1995b). No simple biological predictor of invasion success was found, but some traits were more common in the alien flora than in the native flora and more prevalent for aliens in particular habitats. Rejmanek (1995) found that invasiveness of herbaceous species was best predicted by primary native latitudinal range. Reichard & Hamilton (1997) con-ducted a retrospective analysis of traits of introduced woody plants to distinguish invaders and noninvaders. Discriminant analysis models correctly classified 86% of invaders; high risk of invasiveness was related to vegetative reproduction (see also Daehler 1998), lack of pregermination seed treatment requirements, perfect (hermaphroditic) flowers, and a long period of time in which the fruit was on the plant. In an analysis of global data sets, agricultural weeds tended to be herbaceous, rapidly reproducing, abiotically dispersed species, similar to Baker's ideal weed, whereas plants most likely to become natural area invaders were primarily aquatic or semi-aquatic, grasses, nitrogen-fixers, climbers, and clonal trees (Daehler 1998).

Characteristics common to successful colonists across taxa include *r*-selected life histories (use of pioneer habit, short generation time, high fecundity, and high growth rates) and the ability to shift between *r*- and *K*-selected strategies, but like Baker's characteristics of the ideal weed, many of these ideas have not been tested quantitatively (Kolar & Lodge 2001). Range expansion in birds is related to dis-persal ability, high rate of population increase resulting from large clutch size and production of several clutches per season, ability to compete for resources and habi-tat with native species, repeated introductions (O'Connor 1986), and association with humans (Newsome & Noble 1986). Considering both bird and plant invaders, Newsome & Noble (1986) proposed that successful invaders can be characterized as "gap grabbers" (early germinators with fast initial growth), competitors (for re-sources and nesting sites), survivors (long-lived individuals resistant to mortality), and swampers (mass germinators). Traits that characterize freshwater fish invaders include tolerance to a broad range of environmental conditions, rapid dispersal and colonization, aggressive behavior and competitiveness, and desirability to humans (edibility, sporting qualities, aesthetic characteristics, etc.) (Moyle 1986). Most vertebrate invaders have a close association with humans, as well as high abun-dance in their native range, large size, broad diet, short generation times, ability of females to colonize alone, and ability to function in a wide range of physical conditions (Ehrlich 1989).

Where generalizations fall short, it appears that features specific to the taxonomic group and to the habitat being invaded may be important in determining invasion success. Lack of preadaptation to the new climate, disturbance, competition or predation from native species, and diseases are often cited as reasons for failure of invasions (Lodge 1993b, Moyle 1986, Newsome & Noble 1986). Roy (1990) proposed that the best approach for investigating traits of invaders might be one in which species are classified into functional groups with anticipated similar traits and where the focus is narrowed to particular habitat types.

Studies of the population biology of invasive species may allow a more precise focus on specific characteristics involved in invasiveness (Crawley 1986). Stages that are necessary for successful introduction and subsequent invasion include (*a*) introduction of a species into a new habitat, (*b*) initial colonization and successful establishment of a species, and (*c*) subsequent dispersal and secondary spread into new habitats. During all stages there is great potential for genetic changes to occur through drift or selection. In the following sections we discuss factors related to these stages and identify areas for further exploration.

Introduction of Exotic Species

Most long-distance introductions of nonnative species to new areas are the direct or indirect result of human activities, and social and economic factors are often as critical as biological factors in the introduction of exotic species. Exotic plants have been introduced deliberately as forage, fiber, medicines, or ornamentals; for erosion controls; and for timber plantations (Baker 1974, 1986). Sources of accidental introductions include ballast in ships (Ruiz et al. 2000), impure crop seeds, adhesion to domesticated animals, and soil surrounding roots of nursery stock (Baker 1986). Exotic animals are often introduced deliberately in the pet trade. Activities such as agriculture, logging, and grazing further enhance establishment of exotics by creating disturbed sites for colonization. Agriculture also facilitates invasion when pests in agro-ecosystems are exposed to agricultural practices for many generations, resulting in selection for characteristics that make them persistent and noxious.

Initial Colonization Characteristics and Successful Establishment of Invasive Species

Colonization of new habitats requires that the first arrivals initiate new populations. Many of the traits historically associated with invasive species (e.g., weeds) may be related to initial colonization. For example, species in which isolated individuals can self-fertilize are generally good colonists (Baker 1965). Self-fertility is especially common in plants, but some female insects and vertebrates can store sperm and also colonize from a single introduction (Simberloff 1989, Whittier & Limpus 1996). Species with multiple reproductive strategies (e.g., both vegetative reproduction and seeds) (Huenneke & Vitousek 1990) or plants with multi-seeded

fruits may also be good colonists. Phenotypic plasticity has often been cited as a life-history trait needed for colonization of new areas because colonists must be able to cope with a range of environmental conditions (Baker 1965, 1974, Gray 1986). Comparative and experimental studies of invasive species and noninvasive congeners might elucidate the importance of phenotypic plasticity and genetic variation in the colonization by invasive species.

After initial successful colonization, the next stage of invasion is characterized by establishment of a viable, self-sustaining population. There may be little correlation between traits required for initial colonization and traits needed for establishment. Establishment in a natural community may require different traits than those required upon entering a human-disturbed habitat (Horvitz et al. 1998), and features essential for establishment may not be consistent across taxa. For example, in a study of introduced insects used as biological control agents, Crawley (1986) found that the species with the highest intrinsic growth rates were more likely to establish successfully. These insects typically had other traits characteristic of r-selected species, including smaller body size and faster time to maturity, resulting in several generations per season (Crawley 1986). In a comparison of insect orders, Lawton & Brown (1986) found that the probability of establishment was positively correlated with smaller body size, and thus possibly correlated with higher rates of population growth and higher carrying capacity. In contrast, when they examined the combined pattern of vertebrates and invertebrates, they found a positive correlation between mean body size and probability of establishment.

Rejmanek & Richardson (1996) found that invasive pine species had smaller seed mass, a shorter juvenile period, and shorter intervals between seed crops. Data on invasive pines were consistent with life-history patterns for invasive insects and birds. In general, smaller seed size was correlated with higher seed production, faster individual growth rate, and the absence of special requirements for germination (Baker 1965). In contrast, Forcella (1985) found that species of agricultural weeds with heavier seeds experienced faster germination rates and were better invaders than species with smaller seeds.

Competitive ability is another trait that may confer an advantage for invasive species during establishment. Many studies have documented invaders that show a superior ability to exploit local resources when compared with native residents (Melgoza et al. 1990, Petren & Case 1996, Kupferberg 1997, Holway 1999, Byers 2000) or when compared with noninvading introduced species (Thebaud et al. 1996). Interactions between the invader and the invaded community may be particularly important. Differences between the competing species in the home range and those in the new range may influence an invader's success and ability to dominate a community. For example, *Centaurea diffusa*, a noxious invasive weed in North America, has stronger negative effects on biomass production for North American grasses than for grasses from its native Eurasian communities (Callaway & Aschenhoug 2000). The difference appears to be mediated by allelopathy: Plants from the home range are better than those in the introduced range at competing with *Centaurea* in the presence of root exudates. The introduced

Argentine ant (*Linepithema humile*) is competitively superior to the native ant species in both interference and exploitative competition in riparian woodlands of northern California (Holway 1999). Particular life history stages of native species may be especially susceptible to invasive species. In an example of exploitative competition, invasive larval bullfrogs (*Rana catesbeiana*) were able to reduce the survival and growth rates of native larval frogs by depleting benthic algae in a river in northern California (Kupferberg 1997).

Life-history theory predicts a trade-off between fast reproductive rates and competitive ability (MacArthur & Wilson 1967, Pianka 1970, MacArthur 1972, Grime 1979), but this trade-off may not exist for all invasive species. For example, Keddy et al. (1994) found that the invasive wetland species purple loosestrife (*Lythrum salicaria*) has very high fecundity but is also capable of suppressing the biomass of three indicator wetland species when grown in competition. Blossey & Notzold (1995) suggested that invasive species have been released from the pressure of pests in their native habitat and have reallocated biomass used for defense into both reproduction and growth. For example, in *L. salicaria* biomass of plants in the nonnative habitat was greater than biomass in the native habitat (Blossey & Notzold 1995). More comparisons of species in their native and introduced ranges would be useful to test this idea. Experimental manipulations of natural enemies and other presumed selective agents (e.g., Mauricio & Rausher 1997) would provide more direct evidence for their importance in the invasiveness of taxa.

Characteristics Leading to Spread

Once initial colonization and establishment have occurred, invasive species may spread from continuing long-distance dispersal (saltation dispersal) from foreign sources (naturally or aided by humans), and from short-distance dispersal (diffusion dispersal) with lateral expansion of the established population (Smith et al. 1999, Davis & Thompson 2000). Factors influencing the number of propagules, dispersal mode, and vital rates (births, deaths) are critical factors regulating the spread of invasive species.

Continued spread of the established population often occurs because of excellent adaptations for dispersal. Although the route of exotic introductions is usually determined in hindsight, the causes of spread are notably consistent. Wind, water, and animals, particularly birds, are most often the dispersal agents of seeds; these dispersal agents not only move seeds away from parent plants but also may spread the seeds to similar sites, thus increasing the probability of seedling survival (Schiffman 1997). Good dispersal ability is also important in invasions by birds (O'Connor 1986) and fish (Moyle 1986). Despite their importance in the continued range expansion of invasive species, quantifying both the number and distribution of propagules involved in establishment and spread has been very difficult. In an experiment manipulating propagule pressure (seed number) in patches of sedges in a riparian system, Levine (2000) found that propagule pressure was critical

in determining which patches were most likely to be invaded. Knowledge of the biology, especially dispersal characteristics, of potential invaders is valuable for developing measures to prevent their spread, which is often easier than controlling large, established populations (Goodell et al. 2000).

GENETICS AND THE EVOLUTIONARY POTENTIAL OF INVASIVE SPECIES

Genetic and evolutionary processes may be key features in determining whether invasive species establish and spread. Invasive species offer an excellent opportunity to study rapid evolution, and some of the best-documented examples of this phenomenon have come from invasive species (e.g., Ellstrand & Schierenbeck 2000, Quinn et al. 2000). Many of the best examples of rapid directional selection in species interactions involve invasive species or native species interacting with invasive species (Thompson 1998). Nevertheless, the genetics and evolution of invasive species have received far less attention than their ecology. Invasive species may evolve both during their initial establishment and during subsequent range expansion, especially in response to selection pressures generated by the novel environment. Hybridization, either interspecific or between previously isolated populations of the same species, may be one important stimulus for the evolution of invasiveness (Ellstrand & Schierenbeck 2000); inbreeding may be another important stimulus (Tsutsui et al. 2000).

It is a fundamental tenet of evolutionary biology that the rate of change in response to natural selection is proportional to the amount of additive genetic variation present (Fisher 1930). If genetic changes, and thus evolution, during and after colonization are characteristic of invasive species, it will be important to understand the role of genetic diversity during this process, and evolutionary analyses may need to be a major focus of work on invasive species biology. Furthermore, studies of genetic variation may help predict the potential for populations of invasive species to evolve in response to management practices (e.g., evolution of resistance to herbicides or biological control agents (Barrett 1992, Van Driesche & Bellows 1996).

Genetic Processes During Colonization

Colonization events may involve a population bottleneck because the number of initial colonists is often small. Genetic drift during colonization may bring about reduced genetic variation in the newly established population. This effect will be especially strong when all colonists are drawn from the same source population. Thus, a newly established population is likely to be much less genetically diverse than the population from which it is derived (Barrett & Kohn 1991). For example, introduced populations of Argentine ants are less diverse genetically than native populations (Tsutsui et al. 2000).

Reduced genetic diversity can have two consequences. First, inbreeding depression may limit population growth and lower the probability that the population will persist (Ellstrand & Elam 1993, Newman & Pilson 1997, Nieminen et al. 2001). The effects of reduced genetic diversity will be especially strong if the population remains small for a number of generations. Second, reduced genetic diversity will limit the ability of the population to evolve. An invading species may be preadapted to some aspects of its new environment, but other aspects will be novel. Although some degree of preadaptation is necessarily a prerequisite for successful invasion, it could well be that adaptive evolution following the initial colonization is equally important.

Lag Times

One common feature of invasions is a lag time between initial colonization and the onset of rapid population growth and range expansion (Mack 1985, Kowarik 1995). This lag time is often interpreted as an ecological phenomenon (the lag phase in an exponential population growth curve). Lag times are also expected if evolutionary change is an important part of the colonization process. This process could include the evolution of adaptations to the new habitat, the evolution of invasive life-history characteristics, or the purging of genetic load responsible for inbreeding depression. It appears likely that in many cases there are genetic constraints on the probability of a successful invasion, and the lag times of successful invasives could be a result of the time required for adaptive evolution to overcome these genetic constraints (Ellstrand & Schierenbeck 2000, Mack et al. 2000).

Multiple introductions are often correlated with the eventual success of non-native species' establishment and invasiveness (Barrett & Husband 1990). Indeed, North America's most successful invasive birds, the European starling (*Sturnus vulgaris*) and the house sparrow (*Passer domesticus*), both became invasive only after repeated introductions (Ehrlich 1989). Migration may be critical not only as a source of continuing propagule pressure, but also as an important source of genetic variation to the colonizing population, if multiple invasions provide the genetic variation necessary for adaptive evolution. Multiple introductions can create invasive populations that are much more genetically diverse than any single source population when the invasive species is highly structured in its native range. Different colonizing populations of the same species are likely to be genetically divergent with different levels of genetic variation and therefore have different capacities to promote invasiveness; characteristics that promote invasiveness might evolve in some populations but not others. Gene flow between populations could result in the spread of invasive genotypes. Alternatively, gene flow between populations that swamps out locally beneficial alleles could prevent evolution of invasiveness (e.g., Kirkpatrick & Barton 1997).

Range Expansion

From a conservation perspective, two problematic features of invasive species are dense local populations and rapid range expansion once they have become

established. Some of the genetic constraints likely to influence initial colonization will also influence the rate of spread. For example, dispersal from a point of initial colonization will mean that the invasive species may encounter novel selective regimes. The rate of range expansion, and eventually the boundary of the species, will be influenced by the ability of individuals to survive and reproduce in the new range (Antonovics 1976, Crawley 1986, Hengeveld 1990). Such concerns about the interaction of the environment and genetic changes may become increasingly important with global climate change (e.g., Geber & Dawson 1993, Barrett 2000, Carlton 2000).

The evolution of local adaptation requires genetic variation. Rapid range expansion suggests that the species is highly dispersive, and high dispersal rates are expected to bring about a large amount of gene flow (Barrett & Husband 1990). Whereas high rates of gene flow would help to bring genetic diversity to the edge of the range of a species, they may also act to constrain adaptation to local conditions. In fact, gene flow may be one limit to range expansion (Antonovics 1976, Hoffmann & Blows 1994, Holt 1996, 1997). Recent models by Kirkpatrick & Barton (1997) suggest that gene flow from the center of a species' range may prevent adaptation at the periphery, thereby preventing further range expansion. Hence, the rate and extent of invasive fronts may depend on the degree and pattern of gene flow among populations of an invasive species as the species spreads from its initial sites of colonization. Comparison of the genetic composition of recently established populations with populations in the native range of a species may provide valuable information about the process of invasion.

Protein or DNA genetic markers can be used to measure the amount of genetic diversity in the invasive population. These molecular markers can provide an indication of the amount of genetic variation lost during a colonization bottleneck or provide evidence for multiple population sources. Several studies of this type have already been conducted with invasive species (e.g., Novak et al. 1993; Novak & Mack 1993, 1995; Schierenbeck et al. 1995; Tsutsui et al. 2000; reviewed by Barrett & Husband 1990). Description of the pattern of molecular genetic variation in invasive species might also provide information about the temporal and spatial pattern of invasion (e.g., spread by a simple advancing wave front with extensive gene flow or by a series of long-distance dispersal events and establishment of outlying populations). An evaluation of molecular genetic variation of invasive populations may also allow identification of the source population or populations (e.g., Jousson et al. 2000). These phylogeographic patterns might be viewed as DNA fingerprinting at the level of populations or localities, rather than of individuals. The use of molecular genetic markers has contributed greatly to our understanding of range expansions following the ice ages, both by identifying the refugia from which range expansions have originated and the corridors of spread (Hewitt 2000). It will be interesting to see if these same techniques can be applied to recent invasive events, which presumably occur over a much shorter time frame. This approach has already proven to be valuable in identifying the geographic origins in California of the Medfly (Davies et al. 1999) as well as the origin of California wild oats (Garcia et al. 1989).

Although much information can be gained from molecular markers, characterization of the genetic variation controlling those life-history traits most directly related to establishment and spread is also critical. These traits are likely to be under polygenic control with strong interactions between the genotype and the environment and cannot be analyzed directly with molecular markers, although mapping quantitative traits affecting fitness (QTLs) (Mitchell-Olds 1995), colonizing ability (Barrett 2000), or other traits affecting invasiveness may be possible. For example, variation in the number of rhizomes producing above-ground shoots, a major factor in the spread of the noxious weed johnsongrass, is associated with three QTLs (Paterson et al. 1995). This knowledge may provide opportunities for predicting the location of corresponding genes in other species and for growth regulation of major weeds. Application of the methods of quantitative genetics could be useful for those species in which information can be obtained from a breeding design or from parent-offspring comparisons (Falconer & Mackay 1996, Mazer & LeBuhn 1999). For example, one could compare the additive genetic variance/covariance structure of a set of life history traits of different populations to evaluate the role of genetic constraints on the evolution of invasiveness. Comparisons of the heritability of a trait could be made among different, newly established populations or between invasive populations and the putative source population. Consideration of both the genetic and ecological context of these traits is critical, given the potentially strong interaction of genetic and environmental effects (Barrett 2000).

Management Implications

Consideration of population genetics, with explicit analyses of the genetic structure of invasive species, may allow more effective management of invasive species. Examples of potential applications of population genetics in studies of invasive species include predicting invasiveness to reduce the occurrence of new invasions, predicting the efficacy of alternative control efforts, and improving management of invasive species within native communities.

Successful invasion is often the result of intentional and repeated introduction of many individuals, not only because of increased propagule pressure, but also because these individuals may contain sufficient variation to circumvent the potential genetic problems associated with small population size. One implication of these results is that planned introductions (for horticulture, biological control, etc.) containing lower levels of genetic variation may be safer (but see Tsutsui et al. 2000). Managing for lower invasibility often conflicts with the needs of importers for successful use of these organisms, and more research in this area is clearly needed.

The genetic structure of populations has been shown to affect the efficacy of control of invasives. Burdon & Marshall (1981) noted that asexually reproducing weeds were more often effectively controlled by biological control than sexually reproducing weeds. They attributed the difference to the very different population

genetic structures associated with the two reproductive modes. The clonal, genetically more homogeneous, population structure of asexual species makes it easier to match a biological control agent to the host genotype and makes these weeds particularly vulnerable to biological enemies (Van Driesche & Bellows 1996). In sexually reproducing weeds, greater genetic variation apparently allows more rapid adaptive evolution and escape from the biological control agent. Finally, not all populations of an invasive species will necessarily demonstrate invasiveness; the propensity for invasiveness may be a result of genetic factors, ecological factors (e.g., presence or absence of competitors), or a combination of both. For example, there are both stable (noninvasive) and rapidly spreading (invasive) populations of purple loosestrife (*Lythrum salicaria*) in the eastern United States (P. O'Neil, personal observation). Efficient and effective management should focus first on the invasive populations. If eradication is impossible, control strategies might be employed to alter population genetic structure to reduce adaptive variation, to flood populations with maladaptive genes, or to target and destroy invasive genotypes.

THE SUSCEPTIBILITY OF COMMUNITIES TO INVASION: ECOLOGICAL AND GENETIC FACTORS

Invasibility as an Emergent Property of Communities

Few communities are impenetrable to invasion by exotic species (Usher 1988, Lodge 1993a, Gordon 1998), and communities differ in their susceptibility to invasion as well as in their ecological and evolutionary responses to these invasions. Within communities, invasibility is determined by the properties of the invasive species, the native species (e.g., relative competitive abilities, ability to resist disturbance) (Lonsdale 1999), and the community. A species may be invasive either because it shares traits with resident native species or, alternatively, because it possesses traits different from those of native species and thus can occupy "empty niches" (Mack 1996, Levine & D'Antonio 1999).

High current levels of disturbance within communities may increase their invasibility (Horvitz et al. 1998), but recent studies have indicated that the spatial scale of disturbance and local species diversity are as important as the degree of disturbance in understanding invasibility (Levine 2000). Human disturbance of natural communities may have broadened the range of characteristics leading to successful colonization and thus increased the frequency of invasion into existing communities (Vitousek et al. 1996). Hypotheses on the importance of human-mediated introductions, changes in habitat quality, and broadened range of traits for successful establishment could be tested through experimental manipulations of invasive species that are actively colonizing areas.

Species composition, the functional groups present in the community, trophic structure, and the strength of interactions among trophic levels may interact in ways that buffer some communities against invasion more than others. Resistance to invasion may be enhanced in species-rich communities or in communities

with diverse functional groups (Elton 1958, Tilman 1997, Lavorel et al. 1999), although this viewpoint has been challenged by May (1972), and empirical studies are mixed in their support (reviewed in Levine & D'Antonio 1999). Empirical approaches have included spatial pattern studies correlating the abundance of invaders and community diversity, invader addition studies adding propagules to natural communities, assembly studies examining community diversity and invasion through time, and direct experimental manipulation of diversity in constructed communities. Levine & D'Antonio (1999) stressed the importance of this latter approach to understanding mechanisms underlying the interaction of species diversity and community resistance. For example, at a broad biogeographic scale, Lonsdale (1999) found a positive relationship between native plant diversity and invasibility, largely because both native and exotic richness were related to the area and habitat diversity of sites included in the analysis. Oceanic islands were more invaded than continents (Elton 1958, Lonsdale 1999), but the cause of this low resistance to invasion was unclear. Native species density was as high on islands as in continental areas, suggesting that perhaps the native island flora was less competitive, particularly when there was grazing pressure from exotic animals (Lonsdale 1999). More experimental tests of this hypothesis could address differences between island and continental areas.

Species Interactions and Invasion Resistance of Communities

Interactions among species may have an adverse effect on the demography of invasive species and prevent them from becoming established in a community. Competition may interact with resource levels to affect invasibility. Tilman (1997, 1999) suggested that the population size of individual species may be lower with lower resource levels, but lowered resource levels may prevent invasions of exotic species if the resource level falls below some threshold required by the invasive species. Reduction in interspecific interactions may also explain why exotic species often flourish in new habitats and become pests. If predators or pathogens of the invasive species are absent in the new community, rapid population growth may occur. Without these negative interactions, the invasive species may have more resources available, thus increasing its competitive abilities and ability to invade (Blossey & Notzold 1995, Van Driesche & Bellows 1996, Tilman 1999).

Native species may also decline relative to invasive species because they are more susceptible to parasites or pathogens. In South Africa the indigenous brown mussel (*Perna perna*) was more susceptible to digenetic trematodes than the invasive Mediterranean mussel (*Mytilus galloprovincialis*). The combined effects of the trematodes gave the invasive species a competitive edge over the native brown mussel (Calvo-Ugarteburu & McQuaid 1998). Occasionally, invasion resistance of the community is enhanced if native predators are able to consume exotic species and decrease their survival (Jaksic 1998). The native muricid snail (*Pteropuzpura festiva*) in San Diego Bay, California, has decimated populations of an introduced mussel (*Musculista senhousia*) because the native snail preferred

the introduced mussel over an abundant native clam (*Chione undatella*). Predation thus contributed significantly to invasion resistance in this system (Reusch 1998).

Mutualisms may facilitate invasion or contribute to invasion resistance (Richardson et al. 2000). For example, the absence of ectomycorrhizal fungi, which are spread by red-backed voles (*Clethrionomys gapperi*), limits the invasion of conifers into meadows (Terwilliger & Pastor 1999). Low visitation by pollinators to Scotch broom (*Cytisus scoparius*) slows invasive spread of this exotic shrub (Parker 1997). In contrast, invasion by exotic weeds within the California coastal prairie is facilitated by the native, nitrogen-fixing shrub (bush lupine, *Lupinus arboreus*) because of its mutualism with *Rhizobium* (Maron & Connors 1996).

Genetic Structure of Populations and the Invasibility of Communities

Species interactions contribute to the relationship between diversity, food web connectedness, and stability in communities, thus affecting susceptibility of the community to invasion. Species interactions themselves may evolve rapidly in response to introduced species (Thompson 1998, 1999). Evolutionary host shifts by native species may occur in response to the introduction of an exotic species, as in the case of the use of introduced fennel by the anise butterfly (Thompson 1993). By forging additional links among trophic levels, evolutionary modifications of species interactions after invasion may enhance community stability and resistance to further invasion. Alternatively, postinvasion evolutionary modifications of native species may further disrupt community stability, making these communities even more susceptible to invasion. In a survey of invasive plant species in Florida, Gordon (1998) found that invasive species frequently modified resource availability and competitive interactions, implying that selective pressures on native species might be altered.

Introduction of exotic predators could result in evolution of novel antipredator responses in native prey populations, which might have far-reaching community consequences. For example, brown trout (*Salmo trutta*) in the Taieri River of New Zealand have displaced native fishes, reduced the abundance of grazing invertebrates, and apparently resulted in the evolution of antipredator behaviors in these invertebrates (Townsend 1996). This evolution of antipredator behavior appears to have been responsible for an overall increase in algal biomass (Townsend 1996). Similar evolutionary changes in behavior may facilitate invasions by other species.

Communities may also be more susceptible to invasion when opportunities for hybridization between invasive species and native species are present (Levin et al. 1996). Extinction by hybridization (via either genetic assimilation or outbreeding depression) (Ellstrand & Elam 1993) may occur rapidly (Huxel 1999, Perry et al. 2001b) and lead to loss of diversity within the community. Hybridization may also introduce genes from native into invasive species and thus increase the fitness of the invasive species in the new environment (Ellstrand & Schierenbeck 2000).

Habitat Fragmentation, Population Persistence and the Invasibility of Communities

Spread of invasive species may occur more rapidly in fragmented landscapes. For example, the brown-headed cowbird (*Moluthrus ater*), an avian brood parasite, spread rapidly in response to forest clearing following European settlement of the eastern United States some 200 years ago (Ehrlich 1989; R.D. Holt, D.E. Burhans, S.K. Robinson & S.I. Rothstein, unpublished observations). Brown-headed cowbirds may dramatically reduce the reproductive success of their avian hosts, and this species has been implicated in the decline of many neotropical bird species that breed in the temperate forests of North America. Given the severe selective pressure cowbirds exert on their hosts, the failure of these native bird species to evolve rejection of cowbird eggs may result from the source-sink dynamics of fragmented landscapes. Fragmented landscapes may support sink populations of native host species, but native species may be unable to persist (lambda <1) except for immigration from outside source populations in more contiguous landscapes (where lambda ≥1 and cowbird parasitism is less prevalent). Immigrants may therefore "swamp" genetically any adaptations that may emerge in host populations for dealing with cowbird parasitism (R.D. Holt, D.E. Burhans, S.K. Robinson & S.I. Rothstein, unpublished observations). Habitat fragmentation may therefore increase the habitat of the cowbird and at the same time prevent adaptive evolution in response to invasive species, thereby enhancing susceptibility of the community to invasion.

Population Models of Range Expansion

Several basic features of invasions, such as initial lags in population growth, rate of geographic spread, and features of geographic spread (smoothly expanding range with simple advancing wavefronts, or hopscotch jumps with long-distance dispersal), have been addressed using a variety of population modeling approaches. Predictions of the rate and direction of spread of invasive species that have already become established are critical to any management program and represent one of the central challenges in the application of theoretical models of invasive spread. A rich theoretical literature has contributed to our understanding of factors influencing broad-scale spread, such as long-distance dispersal, spatial and temporal heterogeneity, and Allee effects (Skellam 1951, Kot et al. 1996, Lewis 1997, Shigesada & Kawasaki 1997, Neubert et al. 2000). Range expansion models have been applied directly to resource management questions, such as whether barrier zones can effectively be used to slow the spread of the gypsy moth (Sharov & Liebhold 1998) and which lakes or streams are most likely to be invaded by zebra mussels (Horvath et al. 1996, Stoeckel et al. 1997, Bossenbroek et al. 2001). Nonspatial, stage-structured models can also lead to valuable insights into the population biology of invasive species (e.g., Parker 2000, Drayton & Primack 1999, Neubert & Caswell 2000) and have been used to estimate the potential effectiveness of control strategies, such as biological control agents that target specific life history stages (Shea & Kelly 1998, McEvoy & Coombs 1999).

THE ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF INVASIONS ON COMMUNITIES

Invasive species have both ecological and genetic impacts on the communities that they invade, and understanding these impacts may aid in reversing them. As shown above, ecological interactions between native and invasive species may be direct (e.g., predation, herbivory, parasitism, competition, mutualism) or indirect (e.g., habitat alteration, apparent predation, cascading trophic interactions) and result in changes in the population biology (births, death, migration) of the native species. Significant genetic and evolutionary changes in both the native and invasive species may also occur. Both genetic drift and natural selection (from biotic interactions and abiotic factors in the new environment) may cause rapid evolution in the invading species. As a consequence, rapid evolutionary changes also may occur in the native species in response to the invading species. In the extreme, hybridization and introgression between invading species and native species may result in extinction of the native species (Levin et al. 1996, Rhymer & Simberloff 1996, Perry et al. 2001b).

Most attention has been focused on a small number of exotic species with major negative impacts. A few aquatic examples offer graphic illustrations of changes in the population biology and community structure of native systems. As zebra mussels continue to spread in the Laurentian Great Lakes and inland lakes and streams of the upper-midwestern United States, native clams are smothered and extirpated and water clarity increases as phytoplankton biomass declines from filtration by zebra mussels. Vascular aquatic plants increase as a result of decreased shading from phytoplankton, and energy flow in general is shunted from the pelagic to the benthic zone (Lodge 2001). The invasive rusty crayfish (*Orconectes rusticus*) has a severe negative impact on the northern crayfish (*Orconectes propinquus*) in the upper-midwestern United States. Several direct and indirect effects of fish predators and competition for food and shelter between these two crayfish species favor the invasive species and lead to the local extirpation of the native northern crayfish in many lakes and streams (Hill & Lodge 1999, Lodge et al. 2000).

In Lake Victoria, East Africa, the predacious Nile perch remained at low population levels for many years after its introduction in the 1950s but more recently has boomed in abundance, inducing behavioral changes in native prey fishes and causing the extinction of perhaps 200 of the about 400 endemic cichlid fishes in the lake (Lodge 2001). In both these cases, invasive species changed both the behavior and ultimately the vital rates of otherwise dominant native species through the threat of predation, actual predation, changes in habitat suitability, and competition for space and food.

In an example of impacts on terrestrial systems, most of the formerly forested lowland ecosystems on the drier, leeward sides of the island of Hawaii are now dominated by invasive species such as fountain grass (*Pennisetum setaceum*). Like many other invasive grasses around the world (D'Antonio & Vitousek 1992), fountain grass has severely altered the ecological and ecosystem dynamics of

these arid regions by suppressing native vegetation and promoting fires that have proved devastating to the native flora (Cabin et al. 2000).

The same invasive species can have different impacts in different communities. For example, introductions for biological control range in effectiveness depending on the abiotic conditions, biotic interactions, and genetic structure of the target species (Van Driesche & Bellows 1996). Assessment of the potential economic and ecological damage represented by species introductions would be greatly facilitated by a clear protocol for measuring impacts of different invasive species in different communities. These protocols to compare the impacts of different species are also important if priorities for control of invasive species are motivated in part by removing the most damaging species first (Parker et al. 1999).

Evolutionary Interactions

The consequences of biological invasions represent a powerful opportunity to study basic evolutionary processes. Along with the introduction of a new species into a community comes a chance to observe how the invader evolves in response to novel abiotic and biotic conditions, as well as how resident species evolve in response to the invader (see above).

The use of molecular genetic analyses indicates that hybridization and introgression between invasive and native species may be much more common than is often recognized (Rhymer & Simberloff 1996). Hybridization and introgression can have devastating effects on native species, in some cases contributing to their demise (Levin et al. 1996, Rhymer & Simberloff 1996, Perry et al. 2001a). Invasive species may also cause the evolution of the native species (see previous sections). For example, interactions with the invasive species might lead to natural selection favoring individuals of the native species with traits that were not advantageous prior to the invasion (e.g., by altering competitive interactions, predator-prey interactions, and pollination or seed dispersal). Common garden experiments could be used to compare genetic differences in populations of native species that have been interacting with a particular invader for different lengths of time and for the analysis of genetic changes in native species with removal of invasive species.

Studies of invasive species may provide opportunities to better understand aspects of community dynamics and are crucial for applications of community theory in restoration biology. For example, it is critical to understand the similarities and differences between removing invasive species and reintroducing desirable species back into invaded communities; adding a species into a community may not be the ecological and evolutionary mirror image of taking one away. More study is needed to know if the ecological theory of community assembly rules or community resilience and resistance to invasion can be applied to restoration efforts, where one goal is often to restore invaded systems to a state that more closely resembles its pre-invaded condition. Critical community studies include those that could help managers predict when an invaded community is likely to recover simply by removing invasive species or those that could predict which invasive species should be removed first and which ones may be ignored within a community. Methods of

removal may also affect the subsequent ecological and evolutionary response of the invaded community. These same issues may apply equally to the problem of determining which species to add to communities during the process of restoration. Scientists involved in the removal and restoration of invasive species can serve as partners for experiments to measure the population impacts of alternative methodologies, and to create long-term studies of population resilience after removal.

CONCLUSIONS

The synergism arising from combining ecological, genetic, and evolutionary perspectives on invasive species may be essential for developing practical solutions to the economic and environmental losses resulting from these species. As illustrated above, these approaches include an ever expanding array of tools, including molecular techniques, controlled experiments, and mathematical models. Conversely, invasive species offer unique opportunities for population biologists as natural experiments with more rapid processes than occur in most natural systems.

An analysis of the sequence of events associated with the invasion process highlights the need for ecological, genetic, and evolutionary approaches. The invasion sequence can be thought of as a series of steps, each recognizable, and each rich in questions for population biologists (Figure 1). The first question is understanding why some species become invasive and others do not. A growing body of recent literature supports the contention that statistically significant relationships exist between life history characteristics and the potential for invasiveness. This information could be put to immediate practical use in screening potential plant and animal introductions (Reichard & Hamilton 1997, Kolar & Lodge 2000).

More work on the population biology of invasive species may increase the ability to predict invasiveness in a new habitat, including the ecological role of a species in its native habitat (where it may or may not be an aggressive, colonizing species), or the presence of ecological or genetic differences between invasive populations and the populations from which they are derived. During the process of transport to a new environment, interactions between invasive species and vectors may occur, and different vectors may differentially affect birth and death rates in transit. The number of propagules is likely to be a significant element of the establishment process, and yet there are very few quantitative data relating propagule abundance to success during invasion. Despite the obvious practical significance of reducing the frequency of introduction as well as the number of individuals of invasive species involved in introductions, little theoretical or quantitative empirical work has been done to describe the relationship of these factors with the probability of establishment. Development of experimental systems, such as experimental islands to study replicated introductions, could be extremely revealing.

Another question is the extent to which anthropogenic disturbances, including invasions of other species, influence establishment. There is little information on the relative importance of phenotypic plasticity in establishment of a potentially invasive species in a new habitat, the importance of differences between the

source and recipient environments, or the extent of genetic variation in invading propagules and its relationship to successful establishment.

The lag period commonly observed during invasion processes has been variously attributed to the exponential growth process, stochastic extinction of propagules, or an evolutionary effect. Evolutionary modification of species following establishment, either through adaptive evolution after a single colonization event or by sorting of adaptive genotypes following multiple colonization events, might cause emergence from the lag period. The relative roles of density dependence and evolutionary change in generating the lag times characteristic of the population growth of many invasive species will also require more research. A greater understanding of how these potential causes of the lag phase interact should provide insights into possible management of the invasion process.

The spread of invasive species is influenced by dispersal mode, landscape structure, and the number of foci of introduction of the invasive species (Moody & Mack 1988). Mode of reproduction also influences the rate of spread of an invasive species. The reproductive system and potential for recombination may determine the rate of spread, particularly if continuous adaptation is a prerequisite for the invasion process. Information about how these factors interact will provide opportunities for management of invasive species, including prevention of introductions and control of established populations.

Many community functions are affected by the population biology of invasive species. The effects of invasive species on recipient communities are unclear; in some cases the effects may be additive, but invasive meltdown (sensu Simberloff & Von Holle 1999) with the presence of invasive species facilitating the invasion of more species is also an alternative. More studies may show when invasive species are likely to cause evolutionary changes in recipient populations that retard or increase the likelihood of further invasions. In addition, they may also help determine the rapidity of an evolutionary response in invasive species and whether this increases the likelihood of further invasion. Population biologists may use invasive species to address basic questions in population biology that at the same time provide data useful for decisions about controlling the spread and minimizing the damage from invasive species.

The stages in the invasion process shown in Figure 1 also suggest a means for evaluating threats from invasive species that directly impact plans for management of invasive species. If a species is known to have potentially severe effects on the communities it invades, then particular attention might be given to preventing the transport of the species (e.g., prevention of invasion of Hawaii by the brown tree snake). Alternatively, if the lag phase is a phenomenon resulting from evolutionary modification related to multiple introductions, there may be a need to be wary of any alien species, even those that show little indication of potential for invasiveness.

Integrating Disciplines

Advances in other academic fields may be relevant to the ideas and approaches we have outlined here. For example, the field of disease epidemiology also addresses

processes of colonization and spread and includes an extensive body of theoretical work (Heesterbeek & Zadoks 1986). The applied field of weed science has addressed many general concepts of invasion biology in the specific context of agriculturally important plant invaders, especially with respect to the life history of successful colonizing species (e.g., Forcella 1985, Forcella et al. 1986, Panetta & Mitchell 1991, Holt & Boose 2000, Woolcock & Cousens 2000). Ecotoxicology has developed approaches for measuring biological responses to pollutants, which might be analogous to invasive species (Parks et al. 1991, Bongers & Ferris 1999, Denayer et al. 1999). Links between population biology and these fields could lead to exciting and productive advances in invasion biology.

An important element in the study of invasive species is the necessary link to fields outside of the academic community. For example, federal and state agencies, conservation land trusts (such as The Nature Conservancy), and other conservation managers that detect recently arrived invasive species and monitor their spread can alert researchers so that traits associated with successful colonization can be measured. In turn, research on the ecology, genetics, and evolutionary biology of invasive species may eventually provide the practical information that will be essential for preventing the homogenization of the world's flora and fauna.

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