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## HOW INTERACTIONS BETWEEN ECOLOGY AND EVOLUTION INFLUENCE CONTEMPORARY INVASION DYNAMICS

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**Abstract.** The literature on biological invasions has principally focused on understanding the ecological controls and consequences of invasions. Invading populations, however, often experience rapid evolutionary changes associated with or soon after their introduction. Ecological and evolutionary processes can, therefore, potentially interact over relatively short timescales.

A number of recent studies have begun to document these interactions and their effect on short-term invasion dynamics: (1) The degree to which founder effects, drift, and inbreeding alter the genetic composition of introduced populations is mediated by migration and dispersal patterns, the population dynamics of founding populations, and life history. The genetic changes associated with founding can themselves feed back on population dynamics and life history. (2) Patterns of human-mediated dispersal and landscape change can influence the frequency and pattern of hybridization, which in turn can alter invasion dynamics. These altered invasion dynamics can influence the frequency and pattern of subsequent hybridization and introgression. (3) Strong selection can rapidly generate ecotypic specialization. Dispersal patterns, founder effects, genetic system, and life history influence the rate of local adaptation, its persistence, and its distribution in a landscape. (4) Introduced populations are subject to selection on life history traits and can serve as selective pressure on the life history traits of native populations. Life history evolution in both natives and aliens can influence ecological interactions and population dynamics, which in turn can influence the evolution of life history.

Too few studies have investigated these interactions to definitively assess their overall generality or to determine how the relative interaction strength of ecology and evolution varies across taxa or ecosystems. However, the studies that do exist report interactions from a wide breadth of taxa and from all stages in the invasion process. This suggests that ecological–evolutionary interactions may have a more pervasive influence on contemporary invasion dynamics than previously appreciated, and that at least in some situations an explicit understanding of the contemporary co-influence of ecology and evolution can produce more effective and predictive control strategies.

*Key words:* alien species; dynamics; evolution; global change; interactions.

### INTRODUCTION

The revolution in our mechanistic understanding of biological evolution began with observations of the spectacular divergence of remote animal and plant populations (Wallace 1855, Darwin 1859). Ever since, the ecological processes involved in dispersal and colonization have been integral components of evolutionary theory and of the best empirical examples of evolu-

tionary change (e.g., Wright 1932, Mayr 1970, Hanski and Gilpin 1997).

In contrast, evolution has not been well integrated into our understanding of the ecological dynamics of colonizing populations. This is despite growing evidence that recently introduced populations often experience rapid evolutionary changes in morphology, behavior, and life history (Cox 1999, Mooney and Cleland 2001, Reznick and Ghalambor 2001). Most of invasion biology has focused instead on a set of seemingly more immediate ecological questions (see Drake et al. 1989): Which species are potentially invasive? Which communities are susceptible to invasion? What

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will be the ecological effects of an invasion? These questions implicitly treat invading organisms and the native communities they encounter as both ecologically and evolutionarily static.

However, recent reviews have emphasized the importance of process over typological schemes. A number of ecological processes such as the pattern of propagule supply, fluctuations in climate, novel or episodic physical disturbances, and changes in landscape patterns have been shown to dynamically influence the success and progression of invasions (Lonsdale 1999, Mack 2000, Mack et al. 2000).

In addition to these ecological processes, a number of evolutionary processes, such as hybridization and strong selection, have also been shown to occur in introduced populations over short time scales (Thompson 1998, Sakai et al. 2001, Hänfling and Kollman 2002, Lee 2002, Allendorf and Lundquist 2003). This suggests that at least in some cases ecological and evolutionary processes can interact contemporaneously in meaningful ways. Although still relatively few, a number of recent studies have documented these interactions in ongoing invasions. They allow an assessment of the ways in which ecological and evolutionary processes interact to govern the contemporary epidemiology of invasions.

#### FOUNDING PROCESSES

A principal assumption of classic range expansion models is that long-distance dispersal is negligible (Skellman 1951, Okubo 1980). Although these models describe the spread of a number of introduced populations well, many taxa display more extreme (leptokurtic) dispersal patterns (Kot et al. 1996, Higgins and Richardson 1999). In addition, humans often disperse populations in multiple long-distance jumps (Novak and Mack 2001, Suarez et al. 2001). As a consequence, introduced populations are often comprised of a number of spatially isolated invasion foci (Moody and Mack 1988).

The frequency at which new invasion foci are formed, their spatial pattern, and the source of their recruits is most proximately determined by the life history of the introduced taxa, landscape patterns, and human influence. However, evolutionary changes can also alter introduction and dispersal patterns over relatively short timescales. Many species of agricultural weeds have evolved to mimic crop morphology and life history, which greatly increases the probability that they will be transported as agricultural contaminants (Harlan 1965). Similarly, driven by drastic human land use changes, the principal mosquito vector of dengue fever (*Aedes aegypti*) evolved from forest relatives to be almost wholly commensal with humans. This shift greatly increased the frequency of long-distance dispersal of both *A. aegypti* and dengue fever around the globe (Monath 1994). In one case, a specific dispersal-related trait has been shown to rapidly evolve following

introduction. Populations of weedy Asteraceae on isolated islands off the British Columbia coast have evolved reduced dispersal by decreasing pappus size, only a few generations following their long distance colonization from the mainland (Cody and Overton 1996).

Founding foci are subject to genetic bottlenecks, random genetic drift, and increased levels of inbreeding (Nei et al. 1975, Barrett and Husband 1990). These can reduce allelic diversity and heterozygosity, lead to rapid genetic differentiation among invasion foci, and promote the fixation of deleterious alleles (Ellstrand and Elam 1993, Young et al. 1996). However, the degree to which these genetic changes occur as well as their influence on fitness depend on several ecological factors. These include the initial size and diversity of founding foci, how quickly foci increase in size, the levels of dispersal between foci and source populations, and the specific life histories of the taxa involved (Nei et al. 1975, Hewitt 1999). It has only been recently that empirical studies have investigated these interactions in introduced populations.

Plants with tristylous breeding systems offer a model system. Within a population, style morph (mating type) frequencies are in an equilibrium established by disassortative mating. When new population foci are established founder effects and drift can disrupt these frequencies. The pattern of this disruption, however, depends on an interaction with the ecological features of the tristylous population. Eckert and Barrett (1992) modeled this process for two tristylous species in North America: the nonnative *Lythrum salicaria* and the native *Decodon verticillatus*. Their model predicted that the frequency of morph loss should be higher in small populations and in populations that depart from disassortative mating, are clonal, or have high rates of self-fertilization because these tend to reduce the strength of the frequency-dependent selection maintaining morph frequencies within populations. Empirical data for the two species supported these predictions. In both *L. salicaria* and *D. verticillatus*, small populations have higher rates of morph loss than large populations. In addition, morph loss was lower in self-incompatible *L. salicaria* compared with self-compatible and clonal *D. verticillatus*. Landscape patterns and the spatial distribution of population foci can also influence the pattern of morph loss. There is a greater incidence of morph loss in introduced populations of *L. salicaria* compared with populations in its native European range. This is despite the fact that European populations are smaller on average and experience frequent episodes of dispersal and colonization. Eckert et al. (1996) suggest that the difference might reflect higher rates of gene flow between European populations that restores morphs lost during founding. European populations are closer together than North American populations and are often loosely linked by scattered individuals.

Repeated introductions, particularly if they come from disparate portions of a large native range, can ameliorate reductions in genetic diversity associated with founding. The epidemiological history of *Phytophthora infestans*, the cause of potato late blight disease, provides an example. Prior to the 1980s, human dispersal of *P. infestans* outside of its native neotropical range essentially involved a single strain and only one of the two mating types required for sexual reproduction (Goodwin et al. 1994). The resulting genetic impoverishment of world *P. infestans* populations greatly aided the development of effective control strategies, which significantly limited local densities and rates of spread. The effectiveness of population regulation decreased dramatically in the 1980s, however, when new strains, including the second mating type, spread from Central and South America as a result of changing trade practices (Fry and Goodwin 1997). In this case, the restoration of alleles lost during founding also changed the mating system of introduced populations leading to additional increases in genetic variation.

Using a time series of detailed censuses, Grant et al. (2001) documented how the founding of a population of Darwin's finches on the Galapagos island of Daphne led to the loss of alleles and to inbreeding in the founding population. However, in subsequent generations inbreeding and drift did not cause a decline in heterozygosity and the founding population did not diverge from populations on other islands as expected. This was because repeated immigration from these islands introduced lost alleles and increased the size of the founding population. Repeated introductions have also ameliorated genetic bottlenecks in introduced populations of limpets (*Crepidula fornicata*) along the European coast to the point that they display similar or even higher levels of genetic variation compared with native North American populations (Dupont et al. 2003).

The speed at which population size increases can also significantly influence the strength and duration of founder effects. Although European rabbit (*Oryctolagus cuniculus*) populations in Australia are descended from an initial founding population of only 13 individuals, they display no evidence of a genetic bottleneck. This is probably because the initial founding population was an intentionally diverse representation of the native genetic diversity and because post-colonization population growth was extremely rapid (Zenger et al. 2003). Similarly, marsh frogs (*Rana ridibunda*) have rapidly expanded across Great Britain from an initial introduction of 12 individuals, and Zeisset and Beebe (2003) could detect no loss in genetic variation relative to native European populations.

The idiosyncratic loss during founding or later addition of specific genetic combinations can have disproportionate effects on introduced populations. In the case of Darwin's finches on Daphne, eight years after

the population was founded a single new immigrant contributed 11 new microsatellite alleles and a new song type to the population (Grant et al. 2001). Similarly, although common reed (*Phragmites australis*) has a long history throughout much of North America, the introduction of a single novel European strain during the early 1800s is associated with a dramatic increase in its range and abundance over the last 150 years (Saltonstall 2002). Over the same time period, however, humans have increasingly disturbed marshes through nutrient enrichment and the removal of competitors, both of which cause increases in *Phragmites* abundance and spread within a marsh (Minchinton and Bertness 2003). This suggests that recent *Phragmites* population dynamics might reflect an interaction between landscape changes and the specific phenotypic characteristics of new genetic introductions.

The loss of additive genetic variance caused by founder effects has been proposed as one mechanism for the lag in spread sometimes observed in introduced populations (Ellstrand and Schierenbeck 2000). However, genetic variation influences the ecological and evolutionary characteristics of populations through an interaction with life history and genetic system. For instance, founding populations of Argentine ants in California have half the alleles of Argentinean populations. This loss of genetic diversity resulted in a loss of intraspecific aggression in California and led to the formation of vast supercolonies (Holway et al. 1998, Tsutsui et al. 2000). Similar processes influence the establishment success of other eusocial insects (Holway et al. 2002).

Life history traits can also interact with patterns of human-mediated dispersal to influence the genetic structure of founding foci in the new range. Introduced populations of the aquatic plant *Butomus umbellatus* in North America consist of sexual diploid and asexual triploid clones. Diploid clones produce copious amounts of outcrossed seed as well as highly dispersible asexual bulbils, while triploids reproduce solely through rhizome fragmentation. Eckert et al. (2003) predicted that these differences would result in greater spread and higher levels of genotypic diversity among diploids, but they found that both types were equally widespread and asexual clones actually had slightly higher levels of genotypic diversity. This is apparently because triploid clones are favored in the horticulture industry, and repeated horticultural introductions have fostered genotypic diversity and spread.

#### HYBRIDIZATION

There is strong evidence that introduced plant and, to a lesser extent, animal taxa frequently hybridize with native relatives and with other introduced taxa (Abbot 1992, Rhymer and Simberloff 1996, Ellstrand and Schierenbeck 2000, Vilà et al. 2000). Hybridization can interact with ecological processes in two ways. First, patterns of introduction and dispersal along with land-

scape structure can influence the frequency that hybrids form as well as their subsequent spread. Secondly, hybridization can significantly change the population dynamics of introduced taxa, altering the pattern of future hybridization.

On the Baltic island of Ölan, isolated populations of the endemic *Silene uniflora* are found scattered throughout limestone heath, while the introduced *S. vulgaris* occupies disturbed habitats. Hybridization between the two species occurs when disturbed patches are created in the heath. Because these patches are ephemeral and because most hybrids require intermediate habitats that are also ephemeral, the degree of introgression between the two species is limited (Runyeon-Lager and Prentice 2000). Changes to the disturbance regime, however, would undoubtedly change the degree of introgression. Baker (1948) described a similar case of introgression in Britain between the native *Silene dioica* and the introduced *Silene latifolia*. Baker reported high rates of introgression and predicted that a hybrid swarm would soon dissolve the specific identity of the two species. Yet, today hybrids are rare. This is probably because the frequency and extent of landscape disturbance across Britain has declined significantly since World War II (Runyeon-Lager and Prentice 2000).

Introduction patterns can also influence hybrid formation. The invasion of Australia by a number of hybrid thistles in the genus *Onopordum* has involved a complex introduction history. Some hybrids probably formed prior to their introduction in Australia. Hybrids occur naturally in the native European range of the thistles, but most introduced hybrids were probably created by the horticulture industry. In addition, multiple introductions of thistle species and races that are typically spatially isolated in the native range also fostered the formation of hybrids within Australia (O'Hanlon et al. 1999). Similarly, multiple introductions into North America of different *Tamarix* species and ecotypes from across the vast range of the genus in Eurasia have resulted in a number of novel hybrid combinations in the introduced range. In addition, several hybrids were created in the horticulture trade and arrived via Europe (Gaskin and Schaal 2002).

Such cosmopolitan genetic mixing can create taxa with extraordinary levels of genotypic and phenotypic diversity. In addition, hybridization can unload deleterious alleles or fix heterotic genotypes with high vigor and phenotypic plasticity, or create taxa with transgressive phenotypes unlike either parent (Rieseberg et al. 1999, Ellstrand and Schierenbeck 2000). These genetic changes can affect the ecological interactions of introduced populations in ways that lead to increases in invasiveness (Ellstrand and Schierenbeck 2000). However, empirical studies have yet to document the mechanistic feedbacks between hybridization and population dynamics.

There is empirical evidence that changes in population dynamics caused by hybridization can influence the frequency and spatial pattern of subsequent hybrid formation. In San Francisco Bay, hybrids have formed between introduced smooth cordgrass (*Spartina alterniflora*) and the native Pacific cordgrass (*S. foliosa*) (Daehler and Strong 1997a, Ayres et al. 1999). These hybrids have expanded dramatically since their formation in the 1970s or 1980s, and, at their current rate of expansion, will cover the estimated 28 098 ha of marsh habitat in the bay in about 200 years (Ayres et al. 2004). This is despite the fact that primary hybridization between the two parental species is rare, even under direct cross-pollination in the laboratory (Ayers et al. 2003). Hybrids possess transgressive phenotypes with traits such as pollen production, reproductive output, seed viability, and environmental tolerance that are in excess of both parental lines (Ayres et al. 2003). In addition, hybrids readily backcross with each other and with both parents (Antilla et al. 2000). This positive feedback between the increased fitness of hybrids and their greater propensity for hybridization threatens the common and widespread *S. foliosa* with genetic rarity even though *S. alterniflora* remains rare and spatially restricted (Ayres et al. 2003, 2004).

#### EXPANSION AND LOCAL ADAPTATION

There is clear evidence from a range of taxa that introduced populations often quickly adapt to local conditions (Reznick and Ghalambor 2001, Grosholz 2002, Lee 2002). Most studies have only provided a static snapshot of current adaptation. Yet, how quickly local adaptation forms, its persistence, and its spread through landscapes depend on interactions between dispersal, founder effects, life history, and genetic system.

In plants, high colonization ability is often associated with fixed "general purpose" genotypes characterized by high phenotypic plasticity (Baker 1974). Multiple introductions from genetically distinct native populations could lead to introgression that disrupts these genotypes, but there is little evidence for this. Instead, the few studies that have been conducted show that phenotypic plasticity and the genetic variation resulting from serial introductions have a complementary influence on spread. Introduced populations of saltcedar (*Tamarix ramosissima*) span a wide latitudinal range in western North America. Populations from the latitudinal extremes of this range (Arizona and Montana) respond to changes in temperature with highly plastic changes in traits associated with gas exchange and biomass allocation (Sexton et al. 2002). Some (but not all) of these traits also display considerable levels of genetic variation within regions for both trait means and reaction norms. There is indication that for at least one of these traits regional ecotypes have evolved, with Montana populations investing more in root mass under cold temperatures than Arizona populations. Much of the genetic variation fueling this local adaptation has

come from multiple introductions from disparate populations across a wide native range (Sexton et al. 2002). Many introduced populations of short-lived weeds display a similar combination of broad phenotypic plasticity and local ecotypic specialization (Warick 1990, Rice and Mack 1991, Allard et al. 1993, Thébaud and Abbott 1995, Weber and Schmid 1998, Neuffer and Hurka 1999). We still, however, have a poor understanding of how plasticity and local adaptation can both be maintained within populations or how they interact to influence spread.

Sexton et al. (2002) argue that phenotypic plasticity is important in the early stages of plant invasions, allowing species to rapidly expand across diverse landscapes. Later, selection favors local adaptation, and this can lead to an increase in local invasiveness. Parker et al. (2003) provide a possible example of the early stages of this process in their study of *Verbascum thapsus* along an elevation gradient in California. They found no evidence for local adaptation, and instead attributed the broad elevational success of the species to phenotypic plasticity. However, some genetic differences do exist between populations, the result of multiple introductions, founder effects, and drift. Some of the genetic differences appear to be potentially advantageous but “mismatched”: some low elevation populations exhibit traits more suited to high elevations. Gene flow between populations could promote adaptive evolution and increased invasion of high altitude habitats.

Dispersal patterns between invading populations can influence how quickly local adaptation forms. Aided by high levels of phenotypic plasticity, introduced Chinook salmon have spread to several drainage basins in the south island of New Zealand. In less than 30 generations, the different populations have also developed marked genetically based changes in life history traits that are adaptive matches to particular catchment environments (Quinn et al. 2001). The authors speculate that these adaptive changes were facilitated by a process they term “favored-founders effect” where founding colonists are a nonrandom selection of the parent population. In this case, traits associated with long distance colonization of the upper reaches of a watershed also have fitness advantages in these cold slow growth environments.

No studies have directly quantified how the evolution of local adaptation influences spread rate or the invasive impact of populations. However, Garcia-Ramos and Rodriguez (2002) have modeled how local adaptation and habitat heterogeneity might interact to influence spread rate. When the evolution of local adaptation was incorporated into models, spread rate decreased. In addition, the invasion speeds of evolution models decreased with greater spatial heterogeneity and dispersal rates. This was because strong selective differences hindered the establishment of maladaptive

genotypes and high dispersal rates tended to homogenize genetic differences.

However, at least one field study demonstrates that high rates of propagule pressure and strong habitat heterogeneity can promote the evolution of new invasive genotypes. In the grasslands of California, low fertility serpentine soils have been markedly resistant to invasion by European alien grasses, and they have served as some of the last refugia for native grassland species. Harrison et al. (2001) have shown that European grasses have evolved serpentine tolerant ecotypes on small patches and on the edges of large patches. A constant rain of propagules from the surrounding sea of alien grasses has fed a selective lottery that filtered out preadapted genotypes. As these ecotypes evolve, even large patches may become vulnerable to invasion.

#### POPULATION REGULATION AND LIFE HISTORY EVOLUTION

Implicit in the concept of invasive species is the idea that population regulation differs in critical ways between populations in the native and introduced ranges of a species (Elton 1958). However, profound differences in regulatory mechanisms such as predator–prey relationships and competitive interactions, likely impose strong selective pressure on the life history traits of introduced populations. These life history changes can occur remarkably rapidly and feedback on ecological interactions and population dynamics.

In less than 100 years, introduced populations of Atlantic cordgrass (*Spartina alterniflora*) expanding across the mudflats of Willapa Bay Washington have evolved more *r*-selected life history traits, including increased selfing rates and greater reproductive effort relative to east coast populations and the first founding populations. The driving force for this evolution appears to be the strong selective difference between the dense, stable, and highly competitive environment of east coast marshes compared to the expanses of open mud in Willapa Bay (H. G. Davis, *unpublished manuscript*). Similar selection might also drive the evolution of selfing rates in the invasion of hybrid *Spartina* in San Francisco Bay. Selfing capacity varies widely among clones; viable seed set in self-pollinated clones ranges from zero to over 50% (Daehler 1998). As in Willapa Bay, high selfing capacity has clear fitness advantages in these spatially expanding populations, which suggests that the frequency of selfing should increase in the population (Daehler 1998). However, the complex hybridization dynamics occurring in San Francisco Bay probably influence this process by greatly complicating the patterns of inheritance for selfing ability.

In addition to causing ecological release, altered predator–prey relationships can also be a selective force on the life history traits of introduced populations. These evolutionary changes can potentially feed back on population dynamics and predator–prey rela-

tionships, but we currently have little empirical documentation of these feedbacks.

Blossey and Nötzold (1995) hypothesized that introduced plant populations would gradually become more invasive by accumulating competitively superior genotypes that allocated few resources to defense (the evolution of increased competitive ability, EICA, hypothesis). There is now considerable evidence that plants vary heritably in their tolerance and resistance to herbivores (Strauss and Agrawal 1999), but tests of the EICA hypothesis have so far been equivocal (Willis et al. 1999, 2000). It has been difficult to both identify evolutionary shifts in herbivore vulnerability and to demonstrate a link with changes in other life history traits such as growth rates or reproductive effort.

Even in the absence of clear adaptive tradeoffs, variation in herbivore susceptibility could still influence invasion dynamics if native herbivores or introduced biocontrol agents differentially attack vulnerable genotypes. Introduced populations of *S. alterniflora* and *S. anglica* that have been isolated from the specialist planthopper *Prokelisia marginata* are more vulnerable to planthopper attack on average than are native populations that have never been isolated (Daehler and Strong 1997b, Garcia-Rossi et al. 2003). A biocontrol program involving the release of *P. marginata* in Willapa Bay, Washington, hopes to exploit the susceptibility of the introduced populations (Grevstad et al. 2003). Interclonal variation in *Prokelisia* susceptibility is significantly greater among introduced clones than among native clones, however. Strong herbivore pressure acting on this latent variability could lead to the eventual dominance of *Prokelisia* resistant genotypes and the loss of the biocontrol agent as a population regulator (Garcia-Rossi et al. 2003).

As nonnative populations expand and increase in local abundance, they can exert an increasing selective pressure on the life history of native species. These evolutionary changes can in turn influence the population dynamics of the nonnative. Although host shifts of introduced biocontrol agents to nontarget species appear to be rare (Van Klinken and Edwards 2002), there are a number of examples of genetically based shifts of native herbivores on to introduced hosts (Cox 1999, Keane and Crawley 2002). Evidence that these host switches influence introduced population dynamics is scant, however (Keane and Crawley 2002). A possible example of such dynamics comes from host shifts on to introduced *Myriophyllum spicatum* (Eurasian watermilfoil). Introduced to North American lakes and ponds, *M. spicatum* out competes the native congener *M. sibiricum*. In less than 11 years, however, a native weevil (*Euhrychiopsis lecontei*) has formed incipient host races on *M. spicatum* (Sheldon and Jones 2001). High abundances of the weevil have been associated with large declines of *M. spicatum* within lakes, and laboratory tests have shown that the weevil can have a significant impact on the growth of *M. spi-*

*catum* although, interestingly, not *M. sibiricum* (Sheldon and Creed 1995).

#### CONCLUSIONS

These examples demonstrate that invasion dynamics can be influenced by the interaction of ecological and evolutionary processes acting over similar timescales and at any stage of the invasion process (Fig. 1). Given the overall dearth of studies, it is still not possible to definitely assess how common these interactions are or their general importance for most invasions. Still, the studies that do exist outline clear areas where interactions between ecology and evolution are likely to have an important effect on the immediate dynamics of many invasions.

There is clear evidence that the genetic composition and spatial genetic structure of many invading populations is strongly influenced by introduction and dispersal patterns as well as by population dynamics following introduction. Reciprocally, the genetic changes associated with founding can influence the population dynamics and ecological interactions of founding populations, but the nature of these effects is dependent on the specific life history and sexual system of the invading taxa. It has only been recently that we have gained the ability to sample population genetic structure in enough spatial and temporal detail to observe these interactions. A better understanding of these interactions has broad practical application for the control and management on introduced species. For instance, World Trade Organization agreements currently constrain the ability of nations to regulate the importation of organisms already designated as established pests, unless the nation can demonstrate that the importation of new genetic material poses a credible risk (Campbell 2001). Yet, we currently do not have a comprehensive understanding of the genetic structure of most introduced populations or a mechanistic framework to predict the ecological risk associated with specific genetic changes. More studies that track these changes and their influence on population dynamics are needed.

There is also clear evidence that the genetic composition of many introduced populations has been influenced by hybridization, either with native relatives or with other introduced taxa. The hybridization process is strongly influenced by human mediated processes such as horticultural practices, introduction patterns, and landscape modification. The population genetic consequences of hybridization can, in turn, influence invasion dynamics, although our mechanistic understanding of these feedbacks is currently weak. A better understanding of these feedbacks would significantly improve our ability to predict and manage the consequences of hybridization.

There is relatively strong evidence that selection has rapidly created local ecotypes and altered the basic life history of many introduced populations across a range

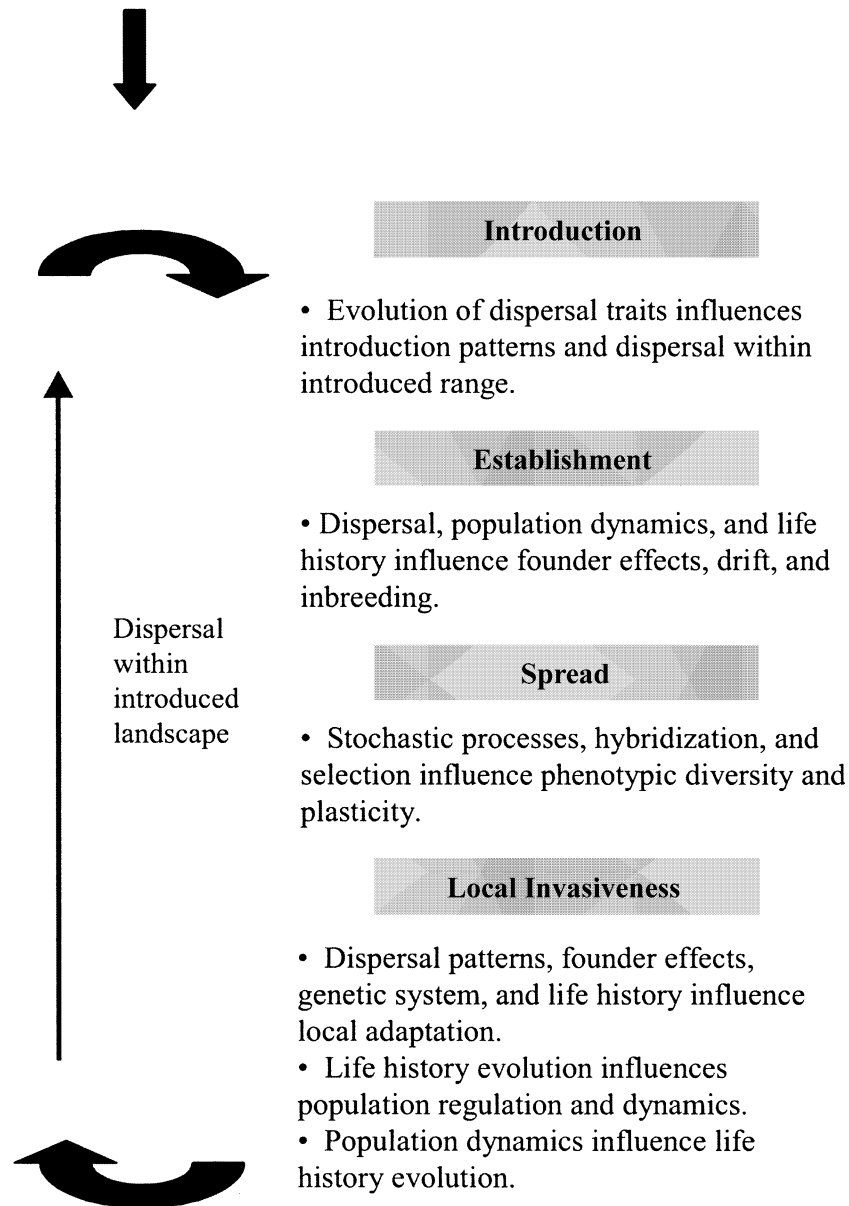


FIG. 1. The progression of invasions involves a number of ecological and evolutionary processes operating contemporaneously. Evidence exists for interactions between the two at each stage of the invasion process. Because of repeated introductions and long-distance dispersal within the introduced range, the nature of ecological and evolutionary interactions can vary across invaded landscapes. Invasion stages are modified from Kolar and Lodge (2001) and Sakai et al. (2001).

of taxa. There is also evidence that, at least among plant–insect interactions, introduced species can drive selective changes in native populations. These adaptive processes are strongly influenced by a number of ecological factors, such as dispersal rates between invasion foci, landscape patterns, and life history. Just as with stochastic processes and hybridization, selection can feed back on ecological dynamics and have a strong influence on processes such as population regulation. Our understanding of these feedbacks is currently limited. It is still unclear, for instance, to what degree

introduced plants evolve increased competitive abilities in response to reduced natural enemies, or the degree to which host shifts of native enemies can influence introduced population dynamics. The relative speed at which local ecotypic adaptation and competitive or natural enemy relationships evolve can have important implications. For instance, if local adaptation evolves quickly relative to host shifts of native natural enemies, populations of introduced taxa are likely to increase in invasiveness (measured as population density or the degree of penetration in undisturbed eco-



systems) over time. If the two rates are relatively equal, invasiveness may remain constant even if the spatial extent of an invasion continues to increase.

A more explicit understanding of the interaction between ecology and evolution will likely improve efforts to manage and predict the dynamics of introduced populations. There has been a similar recognition in the epidemiology of pathogens (Schrag and Wiener 1995, Levin et al. 1999). Processes such as host–pathogen evolution, the rapid within-host evolution of pathogens, and the evolutionary influence of meta-population dynamics within landscapes have been incorporated into epidemiological models (Levin et al. 1999, Shea et al. 2000). These have led to some predictions and strategies that an understanding of ecological dynamics alone did not provide. For instance, early attempts to develop treatment strategies for HIV infection universally failed because HIV rapidly evolved resistance to drug treatments. More successful multi-drug treatments have specifically targeted this rapid evolution by combining synchronous attacks on independent aspects of HIV life history (McGrath et al. 2001).

Efforts to control the evolution and spread of pesticide and herbicide resistance in agricultural pests also illustrate the practical importance of understanding ecological and evolutionary interactions. The evolution of pesticide resistance in crop pests is an important concern for the long-term efficacy of transgenic crops containing genes for *Bacillus thuringiensis* (Bt) toxins. Based on results from a simple two-field model, Alstad and Andow (1995) predicted that a spatial patchwork of Bt and non-Bt fields would slow the rate of resistance evolution. Peck et al. (1999) tested this prediction by modeling the factors influencing the evolution of resistance in the tobacco budworm (*Heliothis virescens*) across a large, more realistic, agricultural landscape. They showed that the size of non-Bt refuges, whether their spatial position remains the same from year to year or is rotated, the reproductive output of budworms, and their pattern of dispersal can all influence how quickly Bt resistance forms.

While the interactions influencing disease epidemiology and the spread of resistance genes in agricultural systems are likely analogous to those influencing species invasions, the interaction strength between ecology and evolution and the timescale over which the interactions occur probably varies widely across taxa and ecosystems. However, an appreciation that these interactions can potentially occur in introduced populations will likely lead to more effective and long term management practices

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