15

The Next Communities: Evolution and Integration of Invasive Species

SCOTT P. CARROLL

CHARLES W. FOX

On a global basis . . . the two great destroyers of biodiversity are, first, habitat destruction and, second, invasion by exotic species.

E. O. Wilson (1997) in *Strangers in Paradise*

Among the global perspectives gained by Darwin during his 5-year circumnavigation aboard the *Beagle,* those afforded by witnessing the prevalence and impact of introduced plants and animals were probably seminal to the transformation of his worldview. Exploring the continents of the southern hemisphere and the remote outposts of midoceanic islands, he saw biota replaced, natural economies disrupted, and species deeply altered from their original states. The first volume of Sir Charles Lyell's new *Principles of Geology* series (1830), an embarkation gift from Fitzroy, the *Beagle's* captain, had convinced Darwin that the natural forces he observed linked directly back to those that shaped the world prehistorically. And now he viewed landscapes that appeared as if painted over and repopulated with the familiar characters of the European countryside. Such cataclysms of biotic replacement, following closely on the modest actions of agrarian settlers, could be likened to the first colonizations of new lands, in which the fitting of life forms to the environment, and the assembly of living communities, could be closely inferred.

Since then, human-altered environments have yielded some of evolution's key lessons. The cases of industrial melanism in moths (Kettlewell, 1956), adaptations to toxic waste (Antonovics et al., 1971) and fertilization treatment (Snaydon, 1970; reviewed in Silvertown et al., 2006) in

plants, responses to resource extinctions in birds (Smith et al., 1995), the appearance of antibiotic and pesticide resistance (Palumbi, 2001a), and introduced pathogens, pests, and hosts in numerous systems have all helped biologists comprehend the environmental, economic, and social importance of contemporary evolution—evolution occurring on *ecological* timescales of days to years rather than on timescales of centuries to millennia (Carroll et al., 2007). We now realize that contemporary evolution is commonplace (see, for example, Palumbi, 2001a) and that it can have substantial ecological consequences and conservation implications (Carroll et al., 2007).

Among the human agents altering earth's habitats, species introductions offer particularly informative accidental experiments because they mimic natural events important in structuring natural communities (Vermeij, this volume). The movements of species and the peregrinations of continents have shaped the earth's terrestrial and marine biogeography throughout the history of life. During the past few centuries in particular, human transport has augmented rates of biotic exchange among the earth's realms far beyond preindustrial norms (Elton, 1958). As we similarly alter other planet-level processes, including climate and nutrient cycling, the resulting disruption of established patterns of community dynamics may create greater

ecological opportunities for invaders (Dukes & Mooney, 1999) while simultaneous recasting the adaptive landscape for all species (see, for example, Réale et al., 2003; Ward et al., 2000). For example, disturbance events should favor stress-tolerant individuals, and Kneitel and Perrault (2006) suggested that if stress tolerance trades off with competitive ability, a prevalence of less competitive phenotypes may render communities more vulnerable to invasion during postdisturbance conditions.

Invasive species provide a tool to study the ecological and evolutionary processes that produce communities (Strauss et al., 2006b). A biotic community is an aggregation of different species living and interacting within an abiotic realm. Constituent members may be largely independent and their associations happenstance, or they may be closely interdependent over vast periods of time, their histories inextricably linked. Each species has characters that are independent of their grouping, and others that depend directly on it and that will change if different species are assembled or if abiotic conditions change. These sorts of variation mean that what we call a *community* is somewhat arbitrary, and that its meaning will differ among taxa as well as within taxa at different places and times. Many of the factors that broadly determine community assemblage, including range expansions, occur naturally and have been common throughout earth's history. However, most of the species movements responsible for generating current patterns of species and community diversity were prehistoric. Thus, the process producing current diversity can only be inferred, largely from modern patterns. To the extent that anthropogenic species introductions are accidental experiments in community ecology, they may offer insights into how communities assemble and function.

Species invasions are unique among the anthropogenic disturbances in that they are naturally dynamic without continued disturbance; organisms interact, but these interactions evolve. In terms of their ecological consequences, this makes species introductions a particularly unpredictable form of environmental perturbation (Pimentel et al., 2000). What will biotic communities look like in 1,000 years or in 10,000 years, and how will they function? What is the role of genetic change in the transition from the colonization of a new habitat to the biotic integration of a population into a new community, and do the effects of an invader change over time? In the face of ongoing evolution, what would creating *sustainable* conservation management involve? These questions address temporal change on scales from seconds to millennia. Although it is common to think of biotic invasions mainly in ecological or management terms, only with an evolutionary perspective do we have the potential of ultimately linking such questions into an integrated framework.

The Consequences of Species Invasions

According to the principles so well laid down by Mr. Lyell, few countries have undergone more remarkable changes, since the year 1535, when the first colonist of La Plata landed with seventy-two horses. . . . The countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer, and ostrich [rhea]. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the pecarri; packs of wild dogs may be heard howling on the wooded banks of the less frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills.

Charles Darwin (1860, p. 120) reflecting on, the landscapes of southern South America that he encountered in 1832, three centuries after Spanish settlement

Not all introduced, alien, species become invasive when introduced to new environments. Indeed, most alien species fair poorly, or at best maintain small population sizes in their new communities, and some would quickly go locally extinct without continued human intervention. Although these species may be ecologically significant in certain contexts, it is the invasive species—those with populations that grow rapidly, spread geographically, and integrate into and frequently dominate native communities—that are of major conservation significance and are thus the focus of this chapter.

By definition, invasive species are new actors within biotic communities, and necessarily play many roles in ecological webs—as predators, pathogens, parasites, competitors, mutualists, or hosts (Mitchell et al., 2006). They have important

effects on native biodiversity, and annually cause hundreds of billions of dollars in economic losses, many of which are incurred from our efforts to avert the impacts of invasive species in agricultural and natural environments (Mack et al., 2000; Mooney et al., 2005). Despite this focus on control, we are just beginning to appreciate the diversity of ways in which invasive species may alter interactions within their new, anthropogenically modified communities, and how quickly they may do so. Changes in the biology of invasive and native species are often difficult to predict, leading to unexpected outcomes that make invasive (or native) species difficult to control (Carroll, 2007a). Most directly, invasive species may affect population growth of native species. Frequently, invasive species compete with native species for resources, which leads to declines in population sizes of native species. However, because of trophic links within invaded communities, strong indirect effects may lead to the opposite affect on some taxa, with economic or even public health consequences. For example, insects introduced to control invasive spotted knapweed (*Centaurea maculosa*) in North America have fueled population growth in insectivorous native mice, resulting in an increase in their infection rate with hantavirus, the cause of an illness often lethal in humans (Pearson & Callaway, 2006).

Species involved in invasions—both the invaders and those affected by the invaders—may change phenotypically after invasion. This may be the result of phenotypic plasticity, evolved genetic change, or both. A phenotype (morphology, behavior, life history, or any other trait) is plastic when it varies depending on the environment in which individuals express that trait. Because alien species are (by definition) in new environments, it is not surprising that they commonly exhibit different phenotypes in these new environments than in their ancestral ranges. For example, the behavior of the invasive species may change in its new community, often in unpredictable ways and sometimes with devastating results for the native flora or fauna. The nocturnal, ornithophilic brown tree snake (*Boiga regularis*) has altered its habits substantially since it was introduced to Guam around 1960 and eliminated several endemic bird species. The Guam population has become more diurnal and more terrestrial, now feeding primarily on day-active skinks that sleep in relatively sheltered locations at night (Fritts & Rodda, 1998). It is unclear whether this change in behavior reflects adaptive behavioral plasticity,

evolved adaptive genetic change, or both. It is likely that the initial change is a plastic response to prey availability, but that the substantial change in prey diversity on Guam will eventually lead to evolutionary (in other words, genetically based) change in snake behavior.

Likewise, because invasive species interact with native species, and thus change the environment of the native species, it is not surprising native species may be different in the presence of invasive species. For example, predatory bullfrogs (*Rana catesbiana*), introduced from eastern into western North America, have recently led to the evolution of avoidance behavior in native western red-legged frog (*R. aurora*) populations. The behavior is plastic; red-legged frog tadpoles increase refuge use and decrease activity when exposed to bullfrog allelochemicals. However, the response is absent in red-legged frog populations still free from the invasive bullfrogs. We can thus infer that the ability to respond behaviorally to bullfrogs has evolved (and is genetically based), probably in response to bullfrog predation (Kiesecker & Blaustien, 1997).

Many reactions of natives to invasives, and vice versa, are preadapted plastic responses (Carroll & Watters, this volume). For example, native plants have evolutionary histories with their local competitors and should be preadapted to respond adaptively to alien competitors that are similar (for example, congeneric) to native competitors. Similarly, induced defensive responses mounted by plants against native herbivores may be effective against some, but not other, invasive herbivores. Thus, plastic responses that have evolved in response to native competitors or predators may mediate interactions between native and alien species, affecting which species can invade (discussed later) and the response of natives to the invaders (and vice versa). However, selection for further genetically based adaptations is probably inevitable when invasive species reach ecologically significant population sizes. Understanding these evolutionary responses is paramount for understanding and predicting long-term ecological dynamics in the invaded communities. A particularly interesting example of ecoevolutionary complexity has arisen from the interaction of the alien species involved in the effort to control invasive rabbits by introducing the *Mxyoma* virus into Australia. Initial mortality in the rabbits was extreme. A perspicacious experimental design permitted the documentation of rapid evolution of resistance in rabbits and evolution of avirulence

in the virus (Fenner & Fantini 1999). After the continent had become populated with derived races of avirulent virus and resistant rabbits, efforts to develop a lethal replacement virus (calicivirus) ultimately led to its (apparently) inadvertent release and irruption (Kovaliski, 1998). Yet, in an instance of preadaptive plasticity, some rabbits were protected by prior exposure to a related but previously unknown native virus common in moist habitats (Cooke et al., 2002). This induced cross-resistance may have facilitated the evolution of genetically based resistance to calicivirus in rabbits. Subsequent evolution of resistance to the new virus was reported in 2007 (Anonymous 2007).

It is important to remember that invasiveness, like any performance measure, is inherently context dependent. Anthropogenic reductions in habitat complexity may reduce the diversity of environments in which introduced species must act. When habitat simplification occurs through the elimination of other species, the challenges faced by introduced species may be substantially diminished. Impacts of prior invaders may reduce the biotic resistance to subsequent invaders, leading to a scenario termed *invasional meltdown* (Simberloff, 2006). In her review of the ecological genetics of invasive species, Lee (2002) concluded that the success of invaders depends more on evolvability than on phenotypic tolerance or plasticity. In biotically homogenized realms, it is possible that the comparative virtues of plasticity may be further diminished, and competition will favor a diminishing subset of species with subpopulations that are evolved *invasion specialists*. On the other hand, as illustrated in the next section, when introduced species enhance resource diversity for some natives, plasticity may continue to play a powerful adaptive role.

An Evolutionary Approach to Invasion Biology

Evolutionary investigations of species invasions, then, have at least a twofold value: What they reveal about the role of ongoing evolution in determining ecological dynamics may in turn be used to predict and manage the impacts of such change in threatened communities (Carroll 2007a; Strauss et al., 2006a; Vermeij, this volume). Adaptive change in both native and alien taxa may determine how communities reconfigure after invasion (Gilchrist & Lee, 2007; Lambrinos, 2004; Strauss et al., 2006a). This chapter focuses on three aspects of an evolutionary

approach to biological invasions. First, to the extent that closely related species have similar needs and abilities, how does phylogeny inform us about which species are likely to invade? Second, beyond homologous preadaptation, to what extent does invasion success rely on additional, contemporary, adaptive evolution? Third, how commonly will the biotic changes brought about by invasive species be great enough to select for evolutionary responses in native taxa, and what are the implications for biotic interactions and community structure? After addressing these topics, we then conclude by considering how such changes may alter the dynamics, predictability, and management requirements of biotic invasions. We emphasize the importance of assessing invasions on carefully described time lines beginning at or near colonization.

CONCEPTS

Who Invades?

> As the species of the same genus usually have . . . much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them.
> Darwin (1859, p. 60)

Only a small proportion of introduced species become invasive (Williamson & Fitter, 1996). However, because of the environmental and economic impacts, and forecasts of increasing rates of species introductions (Levine & D'Antonio, 2003), biologists have expended considerable effort to identify the attributes of species or habitats that predict invasiveness, in the hope of anticipating and thereby perhaps preventing invasions. Generalization has proved difficult, however (Levine et al., 2003); some invaders do have traits in common, but such lists are generally applicable to only a small group of species, and there are many exceptions (Rejmanek & Richardson, 1996). It is clear that both the properties of the species and the community to which it is introduced must be considered simultaneously—in other words, the key to understanding invasiveness emerges from the match between the invader and its new community (Facon et al., 2006; Ricciardi & Atkinson, 2004).

Information about phylogeny may aid in predicting the opportunities and risks faced by colonists. Much of the discussion has focused on plant

invasions. In an early expression of the integrated perspective, Darwin (1859) proposed that species introduced to a region for which they are suited to abiotic conditions would more likely naturalize if the extant community lacked their close relatives. If congeners were present, he reasoned, they would likely use the same resources, leaving little niche opportunity for the new arrival (called *phylogenetic repulsion* by Strauss and colleagues [2006b]).

A complementary conjecture to Darwin's *naturalization hypothesis* is the *enemy-release hypothesis* (reviewed by Colautti et al., 2004), which similarly uses phylogenetic inference in predicting that colonists will more likely succeed if they are not attractive or susceptible to the specialized pests of the native inhabitants. Both hypotheses propose that a colonist will experience reduced *biotic resistance* if it is not too closely related to members of the native community. Contrasting with these hypotheses, Duncan and Williams (2002) suggested that closely related species might naturalize more readily because of conserved traits that render the alien preadapted to the new environment (*phylogenetic attraction* [Strauss et al., 2006b]). This preadaptation could be to abiotic conditions or to any aspects of biotic interactions that may be common to the types of communities they inhabit.

Application of Evolutionary Hypotheses

Attempts to assess the respective merits of these hypotheses have reached mixed conclusions (see, for example, Colautti, 2004; Strauss et al., 2006b), perhaps in part because of the complexities involved in making community-level predictions (see, for example, Urban, 2006). Nonetheless, these and several other recent studies have shed light on basic aspects of the puzzle. For example, Strauss and colleagues (2006b) found that highly invasive grasses in California are, on average, less closely related to native grasses than are established but noninvasive alien grasses. Similarly, Ricciardi and Atkinson (2004) reported that phylogenetic "distinctiveness" augments the impact of invaders in aquatic systems: The highest impact invaders are most often those that belong to genera not already present in the community. Thus, the structure of niche opportunity may be especially important in facilitating the transition from established colonist to competitively superior invader. Parker and associates

(2006b) emphasized that such results demonstrate the power of using an evolutionary approach in invasion biology, but also illustrate the need for a better understanding of the mechanisms by which phylogeny influences interactions between invaders and the native species they encounter.

A few studies have examined the mechanisms by which phylogenetic relatedness affects fitness of invasive species in their new habitats. For example, in a phylogenetically controlled experiment, Agrawal and Kotanen (2003) compared the impact of native herbivores on native versus introduced congeneric herbaceous plants in northeastern North America. They found that the alien species suffered significantly greater herbivory than did natives, contrary to the predictions of the enemy-release hypothesis. However, the authors noted that the introduced plants have been in the region for at least 200 years, such that the relationships observed currently may not reflect those that attended the original invasion (for example, substantial evolution may have taken place since introduction; discussed in Carroll and coworkers [2005]). Furthermore, it is not known whether the same herbivores were attacking native versus invasive congeners, or even whether the herbivores were largely native or introduced insects.

With a meta-analysis of published herbivory and plant survival data, Parker and colleagues (2006a) assessed relative risk with respect to the origins of both the plants and the herbivores. They found that native herbivores tended to suppress introduced plants, whereas introduced herbivores attacked primarily native plants and thus promoted abundance and diversity of invasive plants. They concluded that colonizing plants in general are at risk from novel *generalist* herbivores to which they lack specific adaptation. Thus, although native herbivores may provide biotic resistance to plant invasions, the ongoing accumulation of alien herbivores substantially compromises indigenous biological control, probably through a variety of direct and indirect effects on native herbivore and plant populations.

Ricciardi and Ward (2006) further analyzed the data compiled by Parker and colleagues (2006a) and showed that the suppression of alien plants by native herbivores was greatly reduced in aliens with close relatives in the native plant community. The implication is that they share resistance traits with their relatives. This is not inconsistent with the conclusions of Parker and colleagues (2006a), but suggests that in contemporary communities the

interactions within new mixes of producers and consumers simultaneously generate several types of strong and significant effects. Moreover, both analyses suggest that the enemy-release hypothesis may be inadequate because it emphasizes the importance of escape from coadapted herbivores, whereas generalist herbivores may be more important sources of herbivory and mortality.

Phylogenetic analyses of the patterns and probabilities have recently been extended further up the scales of evolutionary time and biotic organization. Mattson and coworkers (2007) suggested that difference in the geological/climatic histories in different regions of the Holarctic realm may have created a global gradient in the susceptibility of different continents to invasion by forest. Far fewer North American natives have invaded European forests than the reverse. The authors argue that this may be because more frequent cycles of natural disturbance in Europe, related mainly to climate history, have diminished biotic heterogeneity in ways that simultaneously decrease niche opportunity for colonists and increase biotic resistance. This conclusion is consistent with the theoretical prediction of Melbourne and colleagues (2007) that environmental heterogeneity and "invasibility" should be positively correlated.

The Genetics of Invasiveness

Traversing the scale of time and biotic events to the other extreme, pioneering workers are attempting to discover the genetic bases of invasiveness through quantitative and molecular genetic analyses (Weinig et al., 2007). Such a pursuit is likely to suffer from the same limitations as efforts to define invasive phenotypes, and researchers do not anticipate the discovery of "invasiveness genes" common to numerous taxa. Instead, it is likely that a wide diversity of genes underlies invasiveness, and that the effect of specific genes on invasiveness will be context specific—in other words, which genes influence invasiveness will depend on the hurdles that a species needs to overcome in its new community. Nonetheless, some advances have been made in understanding the genetics of invasiveness. For example, the major genes affecting vegetative versus sexual reproduction and dispersal, a trait that affects weediness, have been localized in sorghum (Paterson et al., 1995). Likewise, multiple studies of *Arabidopsis* have identified specific genes that affect

responses to competitors, and competitive ability (Weinig et al., 2007). However, the degree to which any of these genes affect potential for invasiveness is unclear. Also, a particular genes *has* been implicated in promoting invasiveness in fire ants (*Solenopsis invicta*) in the United States (described in the next section), and new analyses will likely identify similar genetic elements in other taxonomic groups.

Hybridization of native and introduced species may be particularly important in allowing taxa to share attributes that result in the development of *superinvaders* (Ellstrand & Schierenbeck, 2006; Rhymer, this volume). Hybridization generates novel genotypes. Although the large majority of the new genotypes produced may be poorly adapted to the environment, "a minority of them may represent better adaptations to certain environments than do any of the genotypes present in the parental species populations" (Stebbins, 1969, p. 26). Hybridization also increases heterozygosity, which can lead to heterosis (hybrid vigor). Mechanisms that fix heterotic genotypes (such as allopolyploidy, permanent translocation heterozygosity, asexual production of embryos [agamospermy], or clonal reproduction) can preserve heterotic genotypes in a population (Ellstrand & Schierenbeck, 2006). In their survey of the relationship between hybridization and invasiveness, Ellstrand and Schierenbeck (2006) found that the majority of invasive species known to be derived from hybridization were capable of fixing heterotic genotypes.

Understanding the genetics underlying invasiveness—both the role of specific genes and the creation of new genetic variation via hybridization—in the context of specific evolutionary hypotheses may assist in the long-term management and control of deleterious traits in evolving populations.

Time Lags on the Path to Invasion

Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount. . . . striking is the evidence from our domestic animals of many kinds which have run wild in several parts of the world. . . . The obvious explanation is that the conditions of life have been very favourable, and that there has consequently been less destruction of the old and young, and that nearly all the young have been enabled to breed. In such cases the geometrical ratio of increase, the result of which never fails to be surprising, simply

explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes.

Darwin (1859, p. 64–66)

The progression from immigrant to invader often involves an initial lag, eventually followed by a period of rapid increase until the species ultimately reaches the bounds of its new range. For example, the Brazilian pepper tree *(Schinus terebinthifolius)* was introduced to Florida about 100 years ago, but it did not become widely apparent in the flora until the 1960s. It now inhabits almost 300,000 ha in South Florida, often in stands so dense as to exclude all other vegetation (Williams et al., 2007). Kowarik (1995) reviewed lag times for invasive plants in Europe and found the average "sleeper" period to be more than 150 years! Although there are many examples of such lags preceding invasions (see, for example, Mack et al., 2000), few studies have shown what factors underlie the transition.

Delays between introduction and invasion may have multiple causes, the simplest being the stochastic vagaries of multiplication for small initial populations of colonists. Such stochastic suppression will only be worsened if strong selection winnows all but the most adapted individuals from the breeding population. When colonization is by a small or closely interrelated founding population, genetic variance may be greatly reduced from that of the parental population (see, for example, Gilchrist & Lee, 2007), limiting prospects for evolution by natural selection. Even though population bottlenecks may also result in genetic reorganization that expresses new genetic variation, much of that variation may not be adaptive (Carroll & Watters, this volume). Even when some of the variation facilitates persistence, refining a new course of adaptation may require generations of further genetic compensation (sensu Grether, 2005) before selection among colonizing genotypes produces traits that vault a population out of its suppressed state by, for example, resolving a particular source of mortality at a critical phase in the life cycle.

The frequent failure of even intentional species introductions suggests a cost of maladaptation—most alien species are unsuited to their new environments or communities and either go extinct or remain at low population sizes. It is therefore likely that among successful introductions are populations that persist only through their abilities to respond adaptively to their new circumstances. Both phenotypic plasticity and genetically based evolution may be important in responses to sudden environmental changes. In particular, phenotypic plasticity may permit populations to persist long enough for novel genetic variation to arise (for example, via mutation or recombination) or until selection can sort among the variation already present in the population. Phenotypic plasticity may also allow production of a broad enough range of phenotypes that populations can bridge *adaptive valleys* (evolutionary intermediates of low fitness) that would, in the absence of plasticity, prevent local adaptation of alien species and thus prevent invasion (see for example, Carroll, 2008; Carroll & Watters, this volume; Ghalambor et al., 2007; Price et al., 2003).

Regardless of why alien species often show time lags before becoming invasive, time delays before invasion have several important implications. First, predicting which immigrants will become invasive and which will remain rare, or will simply disappear, will be difficult to judge based on demographic measures taken over any brief period of time. Second, attempting to measure directly the factors that catalyze the transition to invasiveness in nature will require luck, patience, or a resort to indirect methods. Third, throughout the decades during which a recently resident population is comparatively quiescent, a great many ecological and evolutionary changes may take place. Because of this, the deme that ultimately invades may differ substantially in both its constitution, and the environmental challenges and opportunities it meets, from its colonizing ancestors. This possibility reduces certainty about some of the conclusions we might reach when we attempt to analyze the transition to invasiveness. Knowing the phylogenetic history, genetics, and the environmental history will all be useful.

Colonization as an Evolutionary Event

Although reduced genetic variation in founding populations may often reduce the rate at which colonists respond to selection, colonizations may in themselves be evolutionary events that promote invasiveness. In such cases, lags on the path to invasiveness may be brief, not as a result of preadaptive functionality of traits also favored in the natal environment, but as a result of accidental genetic

changes occurring during colonization. The two most environmentally and economically important invasive ants in North America, the Argentine ant (*Linepthema humile*) and the imported red fire ant, exemplify this. Like some invasive plants, these ants have reduced or eliminated many native species as they have spread since their initial introductions to the southern United States from South America about 100 years ago. Both invasions have proceeded as a result of genetically based changes in polygyny (reviewed by Tsutsui & Suarez, 2003). Ants have eusocial breeding systems, and in their case polygyny means having multiple queens per colony. Many invasive ant species form polygynous *supercolonies*. Polygyny is a derived condition in the invasive North American populations of these ants that may have facilitated their invasion, but it appears to have arisen in very different ways in the two species.

In the case of the Argentine ant, population bottlenecks and founder effects at introduction have reduced genetic diversity and increased the genetic similarity of descendant populations. A single, genetically homogenous supercolony of Argentine ants occupies virtually the entire Californian range. This supercolony has only about 50% of the alleles and one third the expected heterozygosity of populations in the native range, where populations have a genetic structure over tens to hundreds of meters, attended by substantial intercolony aggression (Tsutsui & Suarez, 2003). Inherent to their colonization of North America, then, is that genetic similarity and relatedness became decoupled. Descended from a genetically segregated condition in which relatives and nonrelatives were closely discriminated, cooperative behaviors are now displayed toward individuals who are genetically similar but distantly related. Extreme unicoloniality appears to have arisen during or shortly after introduction. Experiments suggest that the loss of intraspecific aggression in introduced populations, resulting in the "endless colony," underlies the ability of Argentine ants to displace native ants via numerical superiority (Tsutsui & Suarez, 2003).

It is important to remember that the genetic change behind the social transition that facilitated invasion was not the product of selection, but instead was the consequence of loss of variation associated with initial colonization. The phenotypic response to that change, although maladaptive under the species' former circumstances, is the adaptation that appears key to invasion

success. This adaptation is a manifestation of phenotypic plasticity, by chance beneficial, induced by the founder-effect evolution of diminished genetic variation.

The imported red fire ant (*S. invicta*) also lost genetic diversity during introduction. Although not more homozygous on average, introduced populations have only 50% of the alleles present in native populations. Both monogyne (single queen) and polygyne forms occur in the native and introduced ranges. In the United States, polygyny either arose secondarily from the monogyne or is the result of another introduction about 20 years subsequent to the first. Whatever its origin, the polygynous form is more ecologically destructive than the monogynous form, displacing both native ant species and the monogynous form (Tsutsui & Suarez, 2003). Because of its high heterozygosity, the ability to distinguish relative relatedness should not be an issue for fire ant workers. However, queens from the two forms (monogyne and polygyne) typically possess different genotypes at the general protein-9 locus. This locus (or perhaps loci in close proximity) appears to govern faculties that discriminate relatedness. The North American polygynous genotype fails to discriminate against nonrelatives in a manner analogous to that observed in North American Argentine ants (Tsutsui & Suarez, 2003). As long as the numerical superiority of large colony size is selectively advantageous, outweighing any cost of intraspecific competition, the "cooperative allele" that facilitates invasion should prevail. These conditions will probably persist as long as the population continues to expand into underexploited habitats.

The Natives are Restless: Evolution in Response to Invasion

> What havoc the introduction of any new beast of prey must cause in a country, before the instincts of the indigenous inhabitants have become adapted to the stranger's craft or power.
>
> Darwin (1860), speculating based on his observations of the remarkable tameness of Galapagos vertebrates

In the preceding sections we discussed how introduced taxa overcome novel challenges through adaptive evolution. This adaptive evolution frequently takes substantial time, likely contributing to

observed time lags between colonization and invasion of alien species. Sometimes, however, adaptive evolution occurs remarkably quickly (Lee, 2002). Whether invasive species evolve significantly before or during expansion into their new habitat, their success imposes a cost on many native species and provides benefits to others. The interactions may be direct—such as an invasive species preying on a native—or indirect, such as by altering the outcome of competition for resources. Invasive species may broadly alter ecosystem properties such as biogeochemical cycles and hydrology, changing conditions throughout ecosystems (Strayer et al., 2006). Changes in the community and ecosystem wrought by introduced taxa may be a potent source of selection on native species (Carroll 2007a, b, 2008; reviewed by Strauss, 2006a). Some of these responses will be largely demographic, but many will be evolutionary (Strauss et al., 2006a). When an alien taxon is sufficiently established to exert selective force, mutual selective shaping of existing phenotypic variation can occur among interacting taxa. Hence, it is possible that, during the next few decades, escalating habitat alteration by alien organisms will result in species that, although remaining in their native locales, evolve into organisms quite different from their current states.

Strauss and colleagues (2006a) identified more than 30 published cases of adaptive evolution in response to the ecological effects of introduced species. For example, many studies have now documented the evolution of competitive ability in native animals and plants living in communities invaded by aliens (see, for example, Calloway et al., 2005b; reviewed by Strauss et al., 2006a), although others have failed to detect evolution in natives (Lau, 2006). However, the best-studied cases are those in which native phytophagous insects have colonized alien hosts with known introduction times. These studies provide some of the most completely documented evidence of recent and ongoing evolution in response to invasion (and, similarly, agriculture). When it is possible to compare directly populations on a new host plant with those remaining on the original hosts, we can then test hypotheses about the direction, rate, and sometimes the genetic basis of adaptive evolution. During the past two centuries, and in some cases the past few decades (tens to hundreds of generations), host shifts have led to the evolution of functionally distinct ecotypes, subspecies, and even species (reviewed by Strauss et al., 2006a).

For example, to look at performance evolution in response to a new host, we have cross-reared and hybridized races of Florida soapberry bugs (*Jadera haematoloma*) that occur on the native balloon vine (*Cardiospermum corindum*) and the phylogenetically related Asian flamegold (or "goldenrain") tree (*Koelreuteria elegans*), the latter being an ornamental commonly planted beginning about 50 years ago (Carroll, 2007a; Carroll & Boyd, 1992; Carroll et al., 1997, 1998, 2001). Flamegold differs from the native in fruit size, seed nutritional quality, and seed availability. Adults of the contemporary balloon vine race closely resemble museum specimens of bugs collected prior to the introduction of *K. elegans* (Carroll & Boyd, 1992), suggesting that they retain the ancestral condition. Flamegold trees are potentially serious environmental weeds in Florida. From the bugs' standpoint, their seeds are an abundant new resource, and we predicted that the plant's differences from the native host would favor changes in a several of the insects' traits that relate to host utilization.

In rearing contemporary bugs from the native host on seeds of the introduced plant, our idea is to recreate how early colonists responded to the new host five decades ago, providing a baseline for comparing how much contemporary bugs in the derived population have changed over about 100 generations (or fewer, depending on how early most of the change has occurred). During this period, lifetime fecundity has nearly doubled, the bugs mature 25% faster, and they are 20% more likely to survive the juvenile period. The length of the mouthparts has evolved from an average of 9.3 mm to 6.9 mm in response to the smaller fruit of the invasive host, which is now preferred almost two to one in choice tests. The population frequencies of flying and flightless morphs have changed a great deal, as has the genetic control underlying the flight polymorphism. The transformation in beak length in these (and other) populations is evidenced by historical series of museum specimens (Carroll & Boyd, 1992; Carroll et al., 1997, 1998, 2003a, b, 2005). Although some of this adaptation has been facilitated by adaptive phenotypic plasticity, the majority has depended on evolved, genetic change (Carroll, 2007a). At the same time, pleiotropic loss of performance on native hosts has evolved with similar speed and often in a symmetrical manner (Carroll et al., 2001).

In a telling turnabout, New World balloon vine has become a serious invasive species in eastern

Australia during the past 80 years. A native soapberry bug on that continent has colonized it as a new host, and is in the process is evolving a longer beak (Carroll et al., 2005). We compared the efficiency with which the derived, longer beaked bugs attack the seeds of the invasive plant in comparison with the bug population still using a co-occurring native host. The derived bugs damage the seeds of the introduced host at almost twice the rate. Thus, one community-level impact of morphological evolution in response to invasion is the evolution of biological control value. Whether that control will be strong enough to select for counteradaptation in the invader is yet to be determined.

In addition to the adaptive responses of native herbivores on novel resources, the other common association is that of native aquatic species responding to novel predation risks from introduced predators. Common antipredator adaptations include morphological and behavioral changes that reduce the probability of mortality. Here, questions of how evolution interacts with prey population dynamics become especially important, because declining populations will often have reduced adaptive potential, and strong selection may lead to extinction before adaptive rescue is possible (Gomulkiewicz & Holt, 1995).

Although yet to be documented empirically, adaptations to invaders must in many cases alter the selective environments that invaders experience, resulting in reciprocal evolution. Through the (co)evolutionary responses to these interactions between invaders and natives, invasive species may gradually become "integrated" into their new biotic communities (Carroll & Watters, this volume; Vermeij, 1996), both becoming less invasive and having less impact on their new communities. The impacts of the invader, and the responses of natives and of other invaders, over both the short and long term, will determine the configuration and reconfiguration of biotic communities into the future.

FUTURE DIRECTIONS

Coevolution and the Future of Biotic Communities

. . . several hundred square miles are covered by one mass of these prickly plants, and are impenetrable by man or beast. . . . nothing else can now live. . . . I doubt whether any case is on record of an invasion on so grand a scale of one plant over the aborigines.

> Darwin (1860, p. 120), referring to the naturalization of the Mediterranean giant thistle, "cardoon" (*Cynara cardunculus*), in Uruguay

Interactions with new enemies, mutualists, and competitors comprise the new biotic environment of an introduced species, and influence its success and impact (Mitchell et al., 2006). As exotics have expanded and altered native systems around the world, conservation biologists have focused on the ecological causes and consequences of invasions (Callaway & Maron, 2006; Hufbauer & Torchin, 2007). However, invaders and natives both evolve in response to invasion, and influence the evolution of one another (Strauss et al., 2006a; Zangerl & Berenbaum, 2005). Accordingly, ecological and evolutionary processes must be considered together. Moreover, the dynamics of such interactions will likely change over time and space, and will influence additional community members both directly and indirectly.

Placing the current state of an invasion in the context of its history and time line is basic to modeling its ecological and evolutionary dynamics. To understand the keys that release an established taxon onto an invasive trajectory, Facon and colleagues (2006) framed the problem as follows: Has the invaded environment changed in a way that might favor the alien? Has the alien evolved? What is the geographic and chronological history of introductions and any subsequent spread? When did invasiveness appear in relation to any such events? The more detailed the historical information, the better the chance of constructing a realistic model of an invasion. However, collection of the pertinent data will often be only haphazard, particularly from the time before the invasion was recognized. Nonetheless, scientific records and collections sometimes preserve historical information (see, for example, Carroll et al., 2005; Phillips & Shine, 2004). In addition, inferences from comparative, experimental, and phylogenetic methods may help to fill in the gaps.

For example, biogeographic comparisons of the performance of aliens in their invaded and indigenous ranges is a fundamental experimental design for understanding the extent to which

invaders have changed plastically, genetically, or both. How do the causes of demographic variation in introduced populations compare with those in the native range (Hufbauer & Torchin, 2007)? To what extent does invasion success depend on particular qualities of an alien taxon, qualities of the invaded communities, and, especially, their interaction? As in the example of the soapberry bugs, rearing ancestral genotypes in the new environment generates the baseline phenotypes (1) to ascertain the importance of plasticity in initial adaptation and (2) to provide a basis for comparing the derived phenotypes to measure the evolutionary path they have followed. Data from the derived population in the original environment may reveal evolved loss of performance that has evolved pleiotropically as part of the response to selection in the new environment. Such data may provide insight into the phenotypic and environmental factors that promote invasiveness, and may reveal performance trade-offs and vulnerabilities that may be exploited by management practice. Lastly, hybridization of ancestral and derived populations provides information about the genetic structure of adaptive evolution, a question for which empirical information is still rare.

Analogous to the manner in which neurological damage from cerebral hemorrhages in humans has helped reveal the integrated structure and multifaceted recovery potential of the brain, ecological damage from invasions has helped illustrate the evolutionary dependence of ecological responses by providing accidental experiments that, if intentional, would be unethical. How adaptation influences the long-term effects of introduced taxa on the persistence of populations in invaded communities is just now being considered (Callaway & Maron, 2006; Hufbauer & Torchin, 2007; Kinnison & Hairston, 2007; Strayer et al., 2006). The relevant processes may be termed *eco-evolutionary* (Kinnison & Hairston, 2007). Understanding and predicting how eco-evolutionary processes will determine the structure and dynamics of invaded communities is the next big challenge for the field of invasion biology.

Biological invasions progress through phases of transport, establishment, and spread (Sakai et al., 2001). Ecological and evolutionary dynamics are likely to be relatively more or less significant at different stages of invasion, although currently we have too little understanding to generalize. Although events at any latter phase will likely be influenced by occurrences in an earlier phase, different, complementary approaches may be required to investigate each. Regarding the transport phase, for example, knowledge of the behavioral ecology of ant species—mating systems, colony size, and organizational flexibility—helped to predict emigration probability (Tsutsui & Suarez, 2003). Regarding establishment, information about the phylogeny of actual or potential invaders may yield clues about likely impacts as well as vulnerabilities that might be exploited for control. Phylogenetic proximity may reduce biotic resistance to establishment in alien plants (Ricciardi & Ward, 2006), for example, and evolution from selection during colonization may promote persistence (Carroll & Dingle, 1996; Quinn et al., 2001). Relative phylogenetic distance may promote invasiveness and spread in taxa that do establish (Strauss et al., 2006b). Unfortunately, we have a poor understanding of how to use phylogeny to predict when human intervention could prevent, or at least mediate, a pending species invasion.

The niche of an alien colonist will probably almost always differ from that of its progenitors, in part because of differences in the biotic community. If deleterious influences of natural enemies are reduced, increased performance may result in the invasive species occupying realms previously regarded as outside of the physiological tolerance of the species (see, for example, Holt et al., 2005). New evolutionary dynamics will stem from such niche shifts. For example, a leading hypothesis for the microevolutionary basis of invasion success is the evolution of increased competitive ability. This hypothesis is based on the assumption that there is an allocation trade-off between the ability to compete for resources and the ability to defend against enemies. When an alien colonizes an environment in which enemies are reduced or absent, selection should favor phenotypes that shift resources away from defense and to competitive ability (Blossey & Nötzold, 1995). This prediction has been borne out in several studies (see, for example, Siemann & Rogers, 2003; Zangerl & Berenbaum, 2005). Allocation constraints are similarly invoked in the suggestion that disturbed communities are more susceptible to subsequent invasion because they have become populated by residents with more disturbance-tolerant, but less competitive, phenotypes (Kneitel & Perrault, 2006).

Microevolutionary dynamics should be most important in the transition to invasiveness, for

which adaptive changes may be key, and also as part of the longer term integration of aliens into their new communities. As invaders outcompete natives and spread, invasives may alter the ecological conditions experienced by many native taxa. In addition, they may represent an uncontested resource that some natives may be selected to exploit. Understanding how simultaneous ecological and evolutionary processes may interact, and assessing their relative demographic importance, has received recent theoretical treatment by Hairston and colleagues (2005). They propose a quantitative means of assessing concurrent rates of evolutionary and ecological change in a population, and of measuring the direct contribution of evolution to ecological change. For a particular population attribute of interest (for example, population growth rate or equilibrium population density), time–series data may be used to assess the absolute and relative importance of ecological and evolutionary factors to that attribute through time. As an example, they modeled an evolving population of Darwin's finches. Their year-to-year analyses of population growth rate showed that microevolutionary changes had twice the impact of contemporaneous substantial ecological change—namely, the amount of rain that fell.

Accordingly, models to predict the spread of invasive species will be more effective if they are sensitive to evolution of the niche. Based on studies of the spread of the marine (cane) toad (*Chaunus marinus*) into broad areas of Australia, Urban and colleagues (2007) showed how incorporating the anuran's changing niche better describes its pattern of invasion. Cane toads have expanded into regions of Australia originally regarded as unsuitable based on the climates it inhabits in its native New World range. It is possible that some of this expansion may have been permitted by reduced stress through emancipation from biotic enemies. However, the toads are evolving longer hopping limbs at the invasion front (Phillips et al., 2006), suggesting continuing evolution of invasiveness. Moreover, the pace of the invasion into challenging climatic realms is actually accelerating, leading Urban and colleagues (2007) to infer that tolerance to abiotic physiological stress is also evolving. They speculate that the huge size to which the population has grown during the invasion has provided more opportunity for beneficial mutations to arise. Increments in the rate of spread subsequent to the appearance of each beneficial mutation would create a sequence of relative lags, each transitioning into periods of greater invasiveness for the population as a whole.

From a practical standpoint, although such eco-evolutionary factors present obvious challenges to conservation biology, they may also offer opportunities to manage and craft population and community dynamics (Carroll & Watters, this volume). At one extreme, a significant proportion of economically and environmentally deleterious bioinvasions are already regarded as lost causes, because they have escaped the phase during which direct human intervention might have offered control. Although most species may remain permanently in their new realms, as they inevitably become integrated into their new communities, certain forms of control will appear. Beyond efforts at classic biological control, in which natural enemies are imported, scientists may also exploit means of *adaptive biological control*, in which the adaptation of native species to exploit aliens is enhanced through genetic or environmental manipulation (Carroll, 2007a). Because evolutionary change may typify invasions, even in cases when aliens and natives readily coexist (Lau, 2006), it is important to consider means of managing that evolution to achieve desired demographic outcomes. This may often mean the acceptance of permanently altered communities, because some species of conservation concern have already been shown to depend on the habitats now provided by invasive taxa (see, for example, Malakoff, 1999). Although reduced local biodiversity and biotic homogenization may be the outcome in many instances of biological invasion, the longer term impacts are still poorly studied and understood (McKinney & Lockwood, 2005).

Moreover, some invasions generate the evolution of additional biotic diversity (see, for example, Carroll et al., 2007; Malausa, 2005; Schwarz et al., 2005). In addition, information gleaned from the study of invasive species has direct relevance to the restoration of threatened native species. The challenge of decimated native communities is how to bring small, vulnerable populations to self-sustaining levels. If we can maintain such populations through enough generations for adaptive processes to occur, populations may recover without continued human intervention. During such a lag phase, creative genetic and environmental management, based on tools and insights gained from the study of the very invaders that, in some cases, are

threatening the populations of natives, may be key to the restoration of endangered species (Carroll & Watters, this volume).

CONCLUSIONS

At all stages of biological invasions, from colonization of new environments, through population expansion to eventual integration of alien species into communities, evolutionary processes act simultaneously and interactively with ecological processes to mold responses of invaders and the invaded. However, our understanding of the role of evolution, and its interaction with ecological processes (eco-evolutionary dynamics), in species invasions is embryonic. For example, although the requirement for adaptive evolutionary change has been implicated in explaining time lags between colonization and invasion, we have little sense of why some species overcome this evolutionary hurdle when others do not. Likewise, although both loss of genetic variation (for example, in ants) and increase in genetic variation (through hybridization) that accompany or quickly follow colonization may influence invasions, we still know little about the genetics that underlie invasiveness.

An evolutionary approach to invasion biology offers insights both to predict biological invasions and to manage those invasions. Unfortunately, application of eco-evolutionary theory to those challenges is limited by the infancy of the field. New phylogenetic analyses have been effective in demonstrating how relatedness affects both invasiveness of species and invasibility of communities, for example, but research is still limited to a few examples and is not yet generalizable. We cannot yet predict invasions a priori. Moreover, even though adaptation of native species to invasive alien species, and vice versa, is well documented, the long-term ecological consequences of their coevolutionary interactions have barely been addressed.

The accidental experiments created by contemporary species introductions may offer the best context in which to study ongoing eco-evolutionary processes. This intersection of evolutionary and ecological research is beginning to draw the attention of a wide diversity of biologists. It nonetheless remains indefensible that, although providing data of unparalleled value, the individuals of a great many species will continue to be the hapless, unwitting victims of our own calamitous, unwitting behavior. A central hope is that we may use our nascent capacities to recognize our impacts and control our reproduction, and through the lens of science, perceive ecologically and evolutionarily sustainable means of sharing the earth, and from that process gain an understanding of our own heritage.

SUGGESTIONS FOR FURTHER READING

Mack and colleagues (2000) provide a well-organized and broadly ranging analysis of the causes and consequences of bioinvasions. Up-to-date papers that discuss many dimensions of the ecological, evolutionary, and conservation issues of invasions are provided by Sax and associates (2005) and Nentwig (2007). Strauss and coworkers (2006a) review the ecological lessons that can be learned from the study of invasive species, and responses of natives to those invasives. Thompson (2005) offers an intricate and stimulating perspective on coevolution as an ecological process.

Mack, R. N., D. Simberloff, W. M. Lonsdale, et al. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecol Appl. 10: 689–710.

Nentwig, W. (ed.). 2007. Biological invasions. Springer Verlag, Berlin.

Sax, D. F., J. J. Stachowicz, & S. D. Gaines (eds.). 2005. Species invasions: Insights into ecology, evolution and biogeography. Sinauer Associates, Sunderland, Mass.

Strauss, S. Y., J. A. Lau, & S. P. Carroll. 2006a. Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities? Ecol Lett. 9: 357–374.

Thompson, J. N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago, Ill.